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**Assessment of Upper Premolar Morphological Traits  
as Reliable Phylogenetic Indicators**

A Dissertation presented  
by  
Louise Chantale Blundell

to  
The Graduate School

For the degree of  
Master of Science  
in

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Biological Anthropology

Department of Anthropology  
University of Durham

June 2002



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Thesis

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## DECLARATION

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*house C. Russell.*

## **Abstract of the Dissertation**

### **Assessment of Upper Premolar Morphological Traits as Reliable Phylogenetic Indicators**

by

Louise Chantale Blundell

For the Degree of  
Master of Science  
in  
Biological Anthropology

Department of Anthropology  
University of Durham

June 2002

Upper premolar size and cusp heteromorphy have been used in several studies that argue for alternative phyletic placements of early and middle Miocene fossil hominoids relative to extant primate clades. The underlying interpretation is that upper premolar enlargement relative to the first and/or second molar and a reduction in upper premolar cusp heteromorphy are characteristic of extant apes. The aim of the present study is to test the strength of the phylogenetic signal contained within these characters to determine whether they diagnose the groups of living primate taxa for which they are proposed.

The hypotheses are evaluated by means of character state analysis performed on seven metric characters derived from associated upper premolar and molar data collected from seventeen extant and fifteen extinct catarrhine species. The computer programme MacClade is used to reconstruct hypothetical ancestral nodes using the phylogenetic method of character optimization.

The results indicate that there is only a very weak phylogenetic signal contained within upper premolar size and cusp heteromorphy. Both characters fail to unambiguously diagnose groups of living apes as clades. Further analyses suggest that relative upper premolar enlargement is an adaptation to hard object feeding, but the functional significance of upper premolar cusp heteromorphy remains unclear. These findings imply that phylogenetic analyses that incorporate one or both dental traits to develop a phylogenetic framework within which to place fossil taxa relative to extant anthropoids are fundamentally flawed, because neither upper premolar size nor cusp heteromorphy provide convincing evidence of common ancestry relationships.

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# CHAPTER 1

## INTRODUCTION

### OBJECTIVES

Dental characters have long been used in cladistic analyses aimed at resolving the evolutionary relations among extant primate species, and also in the phyletic placement of fossil taxa within hypothesized phylogenetic frameworks (Andrews, 1985; Chamberlain and Wood, 1987; Harrison, 1987; Hartman, 1988; Andrews, 1992; Begun, 1992; Harrison, 1993; Shoshani *et al.*, 1996; Begun *et al.*, 1997). Once a phylogenetic hypothesis of the evolutionary relations of a group of living taxa has been generated, the directionality of morphological change within these lineages can be revealed through phylogenetic analysis, and ultimately used to interpret the evolution and functional morphology of a set of taxa (Ward *et al.*, 1997). By extension, the inclusion of fossil specimens within analyses lends corroborative evidence to the branching pattern revealed, inasmuch as the fossils provide information relating to the ancestral condition at various nodes (Andrews and Martin, 1987b). Perhaps more importantly, fossil specimens provide a time scale that enables researchers to derive a phylogeny out of the set of relationships inferred by the analysis (Andrews and Martin, 1987b). It is not surprising that dental characters have played a large role in the pursuit of delineating the evolutionary relations among the Hominoidea, given the overrepresentation of dental specimens in the primate fossil record.

Most phylogenetic analyses investigating the evolutionary relationships of fossil primates tend to be dominated by craniodental characters for two very



obvious reasons. Firstly, teeth have often been considered better indicators of phylogeny because their morphology appears to be more closely constrained by genes and therefore, less likely to be influenced by environmental stresses (Ward *et al.*, 1997). As a result, teeth are considered less likely to be subject to homoplasy and for this reason, have been favoured over postcranial characters as more reliable phylogenetic indicators [but see Begun and Kordos (1997); Pilbeam and Young (2001) for a more recent interpretation of patterns of homoplasy]. Secondly, phylogenetic analyses that include fossil taxa are necessarily limited to parts of the phenotype that are most commonly preserved in the fossil record, and since teeth are more durable than bone, they frequently make up the bulk of identifiable fossil collections.

The reconstruction of meaningful evolutionary relations among fossil and extant primates, however, has proven to be an arduous task. This task has been further complicated by the inclusion of characters that are assumed to be reliable phylogenetic indicators, despite the lack of rigorous testing (Pilbeam, 1997). Since we must rely heavily on the morphological information contained within preserved dental specimens, it is essential to discover whether the characters derived from the preserved dental fossils are phylogenetically informative at low taxonomic levels. For a character to be useful for phylogenetic inference, it first must be shown to be congruent among extant primate taxa. If a character fails to diagnose groups of living taxa, then the phylogenetic signal contained within this character is comparatively weak, and the observed variation across taxa can be attributed to other factors, such as functional, diet-related adaptations. Problems occur when such characters are included in phylogenetic analyses that attempt to

place fossil taxa relative to extant species, and to one another, often resulting in misleading hypotheses of relationships.

Therefore, the need for phylogenetically informative characters is absolutely imperative in analyses that seek to derive accurate phylogenies in living groups, in order to generate meaningful inferences about the complex evolutionary history of the order Primates. This can only be achieved by testing characters *a priori* to determine their reliability as phylogenetic indicators. Perhaps Pilbeam (1997:19) expresses this most succinctly:

...we need to look carefully first for morphological characters that work well in resolving relationships in living groups, which requires that we have a well-supported phylogeny, praying that they are generally recognizable, and then - if they are - applying them to the fossil record.

The aim of the present study is to test the strength of the phylogenetic signal contained within the following two dental characters: 1) upper premolar enlargement relative to the first and/or second molar, and 2) upper premolar cusp heteromorphy. These dental characters were chosen because of their inclusion in several studies that argue for the alternative phylogenetic placement of the proconsulids<sup>1</sup> relative to recent hominoids, based on the assumption that these characters diagnose groups of living apes (Andrews, 1985, 1992; Andrews and Martin, 1987a, b; Harrison, 1987, 1993; Harrison and Rook, 1997).

Andrews (1985, 1992; Andrews and Martin, 1987a) contends that *Proconsul* shares the derived condition of a reduction in upper premolar cusp heteromorphy with the extant hominoids, but lacks the living great ape synapomorphy of enlargement of the upper premolars relative to the molars. Conversely, Harrison (1987, 1993; Harrison and Rook, 1997) argues that the genus *Proconsul* exhibits

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<sup>1</sup> A group of latest Oligocene and early to middle Miocene non-bilophodont catarrhine primates from Kenya, Uganda, and Saudi Arabia, regarded as primitive apes (Fleagle, 1999).

no convincing derived characters that link it with either the Hominoidea or the Cercopithecoidea and should therefore be recognized as a stem catarrhine, placing it in its own superfamily, the Proconsuloidea.

Thus, according to Andrews's (1985, 1992; Andrews and Martin, 1987a) phylogenetic scheme, one would expect the Hominoidea to be characterized by a reduction in cusp heteromorphy, and only the great ape and human clade to exhibit relative upper premolar enlargement. In contrast, Harrison's (1987, 1993; Harrison and Rook, 1997) phylogenetic scheme predicts that only the great apes will be characterized by both reduced cusp heteromorphy and relative enlargement of the premolars.

By testing the strength of the phylogenetic signal contained within these two dental characters, the present study will reveal whether the hypothesized synapomorphies of Andrews (1985, 1992; Andrews and Martin, 1987a) and Harrison (1987, 1993; Harrison and Rook, 1997) in fact diagnose the groups of living primate taxa for which they are proposed. These hypotheses will be evaluated by means of character state analyses performed on seven metric characters derived from associated upper premolar and molar data collected from 17 extant and 15 extinct catarrhine species. Specifically, the phylogenetic method of character optimization will be used to test the efficacy with which both dental characters can reconstruct the hypothetical hominoid or hominid<sup>2</sup> ancestor, given an established extant anthropoid phylogeny. The phylogenetic method is preferred because it allows for character optimization that consists of "*a posteriori* arguments concerning how particular characters should be polarized given a particular tree topology" (Brooks and McLennan, 1991:33). In other words, given

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<sup>2</sup> In this study, the taxonomic scheme follows that of Begun (1994:12).

a particular extant anthropoid phylogeny and the particular character states observed in the terminal taxa of the topology in question, character states requiring the fewest evolutionary steps can be reconstructed at the internal ancestral nodes of the tree, using the parsimony algorithms found at the heart of phylogenetic systematics or cladistics (Maddison and Maddison, 1987).

If, however, relative upper premolar enlargement and a reduction in upper premolar cusp heteromorphy are shown *not* to be features that diagnose groups of living apes as a clade, this indicates that these characters are not related to phylogeny and should be used with extreme caution in future analyses that attempt to develop a phylogenetic framework within which to place fossil taxa.

## **THESIS OUTLINE**

The present study is divided into the following sections: Chapter 1 gives a brief outline of the objectives of the thesis. Chapter 2 provides background information pertinent to the topics to be discussed in later sections by introducing the early and middle Miocene fossil catarrhine taxa examined in this study. This section outlines the systematics, current diagnoses, and dental morphology of the fossil taxa, and also includes a brief history of each taxon. The second section of Chapter 2 is a review of previous analyses of early and middle Miocene catarrhine upper premolar morphology, and presents the relevant hypotheses to be tested in the present study. The materials and methodology used in this study are outlined in Chapter 3, and the results of analyses involving the extant and extinct taxa are presented in two separate sections in Chapter 4. Finally, Chapter 5 summarizes the significance of the results revealed by character state analysis, and suggests possible avenues for future research.

## **ABBREVIATIONS**

BM(NH)	British Museum (Natural History), now the Natural History Museum, London. Specimens from this Museum are denoted by the single-letter prefix, M.
KNM	Kenya National Museum. Specimens from this Museum are indicated by a two-letter prefix that designates the site of origin:
CA	Chamtwarra
LC	Locherangan
LS	Lothidok
MO	Moruorot
RU	Rusinga Island
SO	Songhor
TH	Tugen Hills
WK	Kalodirr
MUZM	Makerere University Zoology Museum
UMP	Uganda Museum, Primate Collection
UCMP	University of California Museum of Paleontology
CGM	Cairo Geological Museum
DPC	Duke Primate Centre

## CHAPTER 2

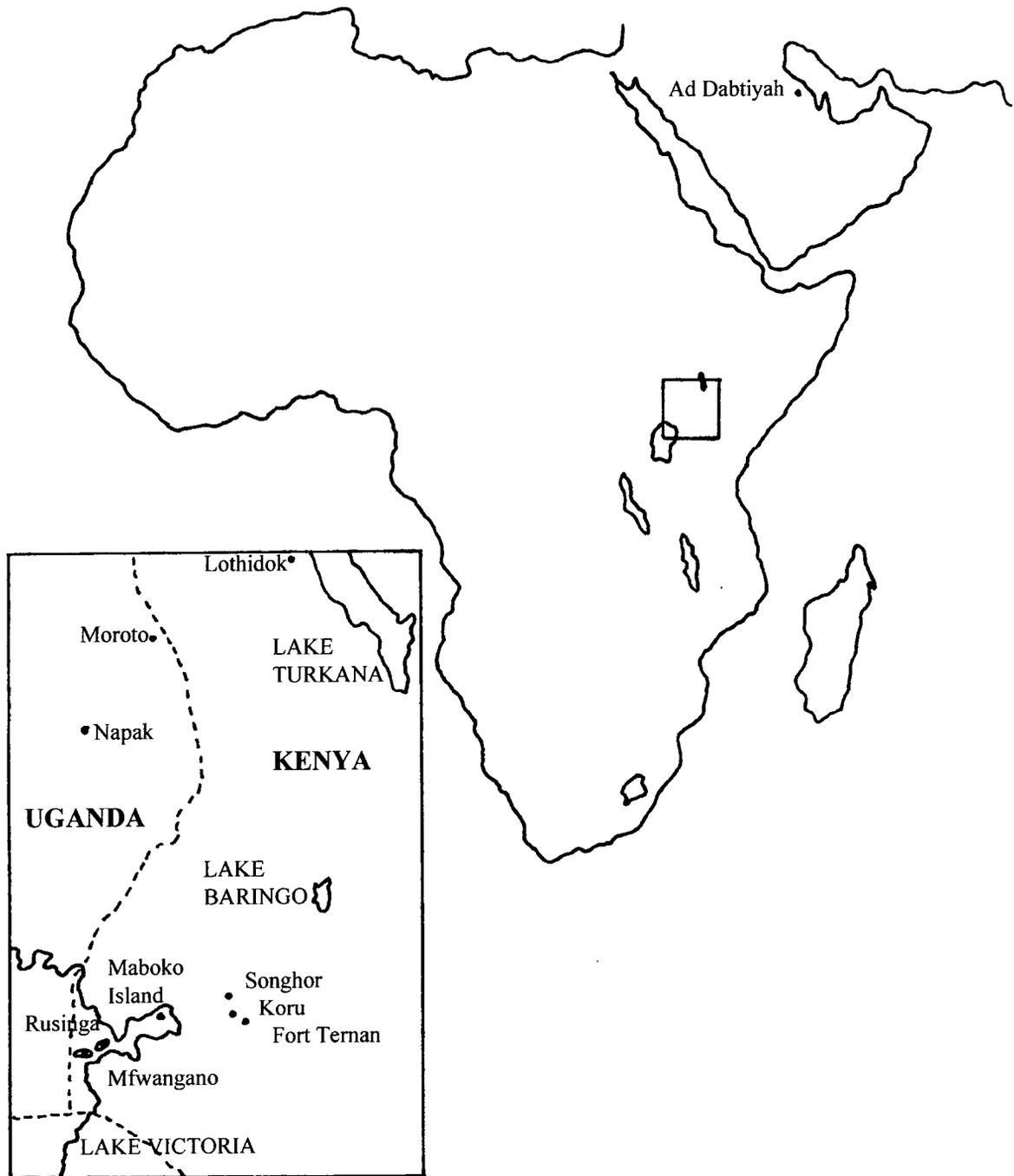
### HISTORICAL OVERVIEW

#### EARLY AND MIDDLE MIOCENE FOSSIL CATARRHINES: SYSTEMATICS, CURRENT DIAGNOSES, AND DENTAL MORPHOLOGY

##### INTRODUCTION

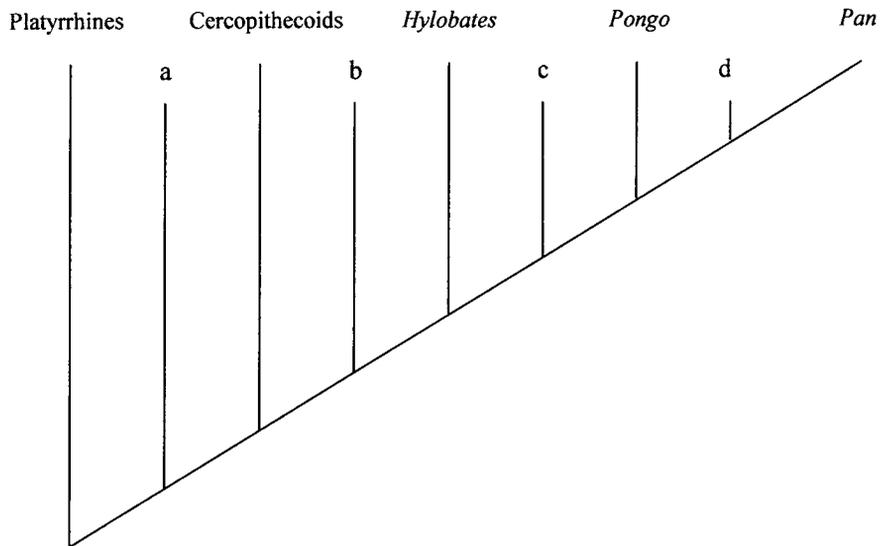
The fossil taxa included in this study derive from latest Oligocene and early to middle Miocene East African and Saudi Arabian sediments dated to approximately 26 million to 15 million years ago (Figure 2.1; Table 2.1). The majority of taxa constitute a paraphyletic group of primitive hominoids known as the proconsulids from Kenya and Uganda, of which the genus *Proconsul* is the best known. The proconsulids are considered by most researchers to be derived from early Oligocene propliopithecids such as *Aegyptopithecus* and *Propliopithecus*. Despite the fact that only a few species of proconsulids are associated with both cranial and postcranial remains, these indicate that the proconsulids not only possessed all of the anatomical features found in extant catarrhines (Fleagle, 1999), some of them have been shown to share hominoid synapomorphies (Andrews, 1985; Andrews and Martin, 1987b; Rae, 1997, 1999).

There has been considerable debate, however, concerning the phylogenetic placement of the proconsulids relative to extant primates due to the differential interpretation of some of the derived features of living apes (see Harrison, 1987). Most commonly, the proconsulids are placed below the great ape/gibbon split (Figure 2.2), as the sister taxon to later Hominoidea (Andrews, 1985, 1992; Andrews and Martin, 1987a, b; Begun *et al.*, 1997; Rae, 1999; Fleagle, 1999).



**Figure 2.1** East African and Saudi Arabian early and middle Miocene fossil localities [after Pilbeam (1969) and Rae (1993)].

Alternatively, Harrison (1982, 1987, 1988, 1993) considers them to be stem catarrhines placing them below the hominoid/cercopithecoid split, while others support the hypothesis that the proconsulids are basal great apes (Figure 2.2) (Rae, 1997; Walker and Teaford, 1989; Walker, 1997).



**Figure 2.2 Alternative phylogenetic positions of the proconsulids:** a) stem catarrhines, b) stem hominoids, c) stem great apes, and d) direct ancestors of living African great apes [after Rae (1997:62)].

*Proconsul* was the first Miocene ape to be described from East Africa (Hopwood, 1933a), and today is classified within the family Proconsulidae (Leakey, 1963). There are four species of *Proconsul* currently recognized by most workers. The medium-sized *P. africanus* is known from the localities of Koru and Songhor, which are both found in the Tinderet sequence of western Kenya (Walker, 1997). *Proconsul heseloni* (formerly included within *P. africanus*) is of similar size and derives from the Kisingiri sequence on Rusinga Island, Kenya (Walker *et al.*, 1993). The larger *P. nyanzae* is known from localities on both Rusinga and Mfwangano Islands, Kenya (Walker, 1997). Finally, the large-sized

*P. major* derives mainly from Songhor and Koru (as well as other localities of the Tinderet sequence) and Napak, Uganda (Walker, 1997).

Other early Miocene East African fossil apes currently included within the Proconsulidae<sup>3</sup> (*sensu* Fleagle, 1999) are: *Rangwapithecus gordonii*, *Dendropithecus macinnesi*, and the newly named *Kamoyapithecus hamiltoni*, although it should be noted that this latter taxon derives from latest Oligocene sediments of Northern Kenya (Leakey *et al.*, 1995).

Additional early and middle Miocene fossil taxa included in this analysis and at present classified as *incertae sedis* (Fleagle, 1999) are: *Afropithecus turkanensis*, from the early Miocene locality of Kalodirr in Northern Kenya (Leakey *et al.*, 1988a); *Heliopithecus leakeyi*, from the early middle Miocene locality Ad Dabtiyah in Saudi Arabia (Andrews and Martin, 1987a); *Morotopithecus bishopi*, from the early Miocene Karamoja District in Northeastern Uganda (Gebo *et al.*, 1997); *Turkanapithecus kalakolensis*, also recovered from the early Miocene locality of Kalodirr, Northern Kenya (Leakey *et al.*, 1988b); and *Equatorius africanus*, which includes specimens from middle Miocene localities at Maboko Island, Nachola, and the Tugen Hills, Kenya (Ward *et al.*, 1999).

The fact that these latter taxa are all classified as *incertae sedis* reflects the uncertainty surrounding their phyletic position, not only relative to extant primates, but also to one another. Unfortunately, few taxa preserve the same

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<sup>3</sup> It should be noted that this study does not include other early and middle Miocene African hominoids presently included within the Proconsulidae such as *Limnopithecus*, *Simiolus*, *Micropithecus*, and *Kalepithecus*. These fossil taxa were excluded from the present analysis since the studies under examination (Andrews, 1985, 1992; Andrews and Martin, 1987a, b; Harrison, 1987, 1993; Harrison and Rook, 1997) focus mainly on the proposed phylogenetic relationships among *Proconsul*, *Dendropithecus*, *Afropithecus*, *Heliopithecus*, and *Equatorius*.

**Table 2.1 Oligocene and Miocene Fossil Catarrhines (after Fleagle, 1999)**

<b>Species</b>	<b>Epoch</b>	<b>Location</b>
<b>Family Proconsulidae</b>		
<i>Proconsul</i>	Early Miocene	Kenya & Uganda, East Africa
<i>P. africanus</i>		
<i>P. heseloni</i>		
<i>P. nyanzae</i>		
<i>P. major</i>		
<i>Kamoyapithecus</i>	Late Oligocene	Kenya, East Africa
<i>K. hamiltoni</i>		
<i>Rangwapithecus</i>	Early Miocene	Kenya, East Africa
<i>R. gordoni</i>		
<i>Dendropithecus</i>	Early Miocene	Kenya & Uganda, East Africa
<i>D. macinnesi</i>		
<b>Family Incertae sedis</b>		
<i>Afropithecus</i>	Early Miocene	Kenya, East Africa
<i>A. turkanensis</i>		
<i>Heliopithecus</i>	Early Miocene	Saudi Arabia
<i>H. leakeyi</i>		
<i>Morotopithecus</i>	Early Miocene	Uganda, East Africa
<i>M. bishopi</i>		
<i>Turkanapithecus</i>	Early Miocene	Kenya, East Africa
<i>T. kalakolensis</i>		
<i>Equatorius</i>	Middle Miocene	Kenya, East Africa
<i>E. africanus</i>		
<b>Family Propithecidae</b>		
<i>Propithecus</i>	Early Oligocene	Egypt, NE Africa
<i>P. chirobates</i>		
<i>Aegyptopithecus</i>	Early Oligocene	Egypt, NE Africa
<i>A. zeuxis</i>		

anatomical features, which makes comparison and classification extremely difficult. This is further exacerbated by the fact that “different taxa show different mosaics of primitive and derived features of the dentition, cranium, and limb skeleton” (Fleagle 1999:467). For example, *Morotopithecus* exhibits derived hominoid features in its glenoid articular surface and lumbar vertebrae, but its proximal femoral morphology is primitive and unlike that of all extant hominoids (Gebo *et al.*, 1997). Furthermore, despite the fact that the dental morphology

preserved in *Morotopithecus* and *Afropithecus* is remarkably similar, the distinction between these two taxa is far from being resolved due to the lack of overlap in postcranial remains thus far recovered for both taxa (Fleagle, 1999).

There is, however, broad agreement among most researchers on the position of some fossil hominoid taxa, including *Proconsul*, *Afropithecus*, and *Equatorius* (Begun *et al.*, 1997). *Proconsul* is generally considered to represent a basal hominoid, exhibiting few derived features of the cranium and postcranium that would identify this taxon as part of a lineage uniquely related to living apes (Andrews, 1985, 1992; Andrews and Martin, 1987a, b; Fleagle, 1986; Begun *et al.*, 1997; Rae, 1999). Most workers also recognize *Afropithecus* as being more derived, and *Equatorius/Kenyapithecus* as being still more derived (Andrews and Martin, 1987a, b; Begun *et al.*, 1997; Leakey and Walker, 1997; McCrossin and Benefit, 1997; Ward *et al.*, 1999).

Also included in the analyses are two Oligocene taxa generally considered to represent stem catarrhines: *Propliopithecus* and *Aegyptopithecus*. Both *Propliopithecus* and *Aegyptopithecus* are most commonly regarded as “a primitive group of catarrhines that preceded the evolutionary divergence and subsequent radiations” of both living cercopithecoids and hominoids (Fleagle 1988:339). Though these taxa possess many features characteristic of anthropoids (including a fused mandibular symphysis, complete postorbital closure, and a lacrimal bone contained within the orbit), they share only few derived characters with extant catarrhines, such as loss of the maxillary and mandibular P2 (Andrews, 1985; Harrison, 1987; Fleagle, 1988). In fact, both *Propliopithecus* and *Aegyptopithecus* lack common specializations found in all living catarrhines and instead, retain certain primitive anthropoid features that firmly establish their phylogenetic

position relative to other extinct and extant catarrhines below the cercopithecoid/hominoid split; these features include the retention of an annular ectotympanic and an entepicondylar foramen (Andrews, 1985; Harrison, 1987; Fleagle, 1988). Since their relationships to the ingroup analyzed in the present study are well established, they make extremely suitable candidates for determining character polarity and were thus chosen as an outgroup to resolve relationships within the Anthroidea (Rae, 1997).

## SYSTEMATICS

Order Primates Linnaeus, 1758

Suborder Anthroidea Mivart, 1864

Infraorder Catarrhini Geoffroy, 1812

Superfamily Hominoidea Gray, 1825

Family Proconsulidae Leakey, 1963

*Proconsul africanus* Hopwood, 1933

Holotype: BM(NH) M.14084, left maxillary fragment with the crowns of C- M<sup>3</sup>

Type locality: Koru, Western Kenya

Distribution: Early Miocene of Koru and Songhor, Western Kenya

Hopwood (1933a) described the first species of the genus *Proconsul*, *Proconsul africanus*, based on a maxillary fragment [BM(NH) M.14084] obtained from Koru, Kenya. Hopwood (1933b:455-57) noted several specialized characters of the upper dentition that distinguished *P. africanus* from both extant African great apes and the fossil hominid, *Dryopithecus*: premolar cusp heteromorphy (most notable in P<sup>3</sup>), shorter antero-posterior diameter of the premolars, very pronounced cingula on the upper molars, a prominent hypocone, and a rounded, reduced third molar. Hopwood (1933b) commented on the marked overall resemblance between *Proconsul* and *Pan*, noting that the main difference between them was the more primitive appearance of the fossil anthropoid ape. In short, Hopwood (1933a, b) regarded *Proconsul* as ancestral to the chimpanzee.

MacInnes (1943) assigned additional material of a larger ape from Rusinga Island to *P. africanus* based on overall similarity to structural characters originally described by Hopwood (1933b). MacInnes (1943) attributed the variation in dental dimensions among the two samples to sexual dimorphism and interpreted the Rusinga sample as representative of males of the species, *contra* Hopwood's (1933b) interpretation of the holotype as a male. This view, however, was later revised by Le Gros Clark and Leakey (1951), who described many new specimens from Koru, Songhor, and Rusinga Island, including the '1948 skull' discovered by Mary Leakey (KNM-RU 7290). These authors concluded that the holotype of *P. africanus* was in fact a male and that the specimens described by MacInnes (1943) represented a new species, *P. nyanzae*. They considered its larger size and certain differences in morphological details sufficient to require a specific distinction, and designated the maxilla and upper dentition from Rusinga [BN(NH) M.16647] as the type of *P. nyanzae* (Le Gros Clark and Leakey, 1951).

The new Rusinga material added to the *P. africanus* hypodigm (Le Gros Clark and Leakey, 1951) then became the reference for this species, due to the fact that it was better preserved and more abundant than the Koru sample. This is especially evident in Andrews's (1978) revised diagnosis of *P. africanus*, in which his taxonomic description of the species is largely based on features preserved only in the Rusinga material (Rae, 1993). Recently, however, several workers have questioned whether the Rusinga material is conspecific with the Koru species (Kelley, 1986; Pickford, 1986; Teaford *et al.*, 1988; Walker *et al.*, 1993). In his morphological and metric analysis of canine specimens from Nyanza Valley sites, Kelley (1986) found that the Rusinga canines assigned to *P. africanus* were different than those derived from both the type locality of Koru, and from

Songhor. These findings reinforced other observed differences in the anterior dentition between *Proconsul* specimens from Koru/Songhor and Rusinga, including upper central incisor shape and the size of I<sup>1</sup> relative to the postcanine dentition (Kelley, 1986). Consequently, the author defined *P. africanus* (*sensu stricto*) as being restricted to Koru and Songhor, and the specimens from Rusinga and Mfwangano formerly placed in *P. africanus* were transferred to the *P. nyanzae* hypodigm, where Kelley (1986) considers them to represent females of the species.

Most workers involved in this debate now agree that the Rusinga material differs from the Koru sample at the species level, and that *P. africanus* is restricted to the Tinderet sites at Koru and Songhor (Kelley, 1986; Pickford, 1986; Walker and Teaford, 1989; Walker *et al.*, 1993). They are divided, however, on the issue of how many species are actually represented at Rusinga. Both Kelley (1986) and Pickford (1986) recognize only one highly dimorphic species, and refer all Rusinga material to *P. nyanzae*. In contrast, Teaford *et al.* (1988) and Walker *et al.* (1993) have argued that the levels of variation observed in the craniodental and postcranial material from Rusinga indicate that there are two species of *Proconsul* present on this island. Specifically, Walker *et al.* (1993) regard the large Rusinga species as *P. nyanzae*, and proposed a new name, *P. heseloni*, for the small Rusinga species.

*Proconsul nyanzae* Le Gros Clark and Leakey, 1950

- Holotype: BM(NH) M.16647, a nearly complete maxilla with right and left C-M<sup>3</sup>
- Type locality: Rusinga Island, Kenya
- Distribution: Early Miocene of Rusinga and Mfwangano Islands, and Karungu, Kenya

The larger *Proconsul* specimens from Rusinga Island, provisionally referred by MacInnes (1943) to *P. africanus*, were subsequently assigned to *Proconsul nyanzae* by Le Gros Clark and Leakey (1950, 1951). In addition to this material, the large Koru mandible [BM(NH) M.14086] originally described by Hopwood (1933b) was also transferred from the *P. africanus* hypodigm to *P. nyanzae* by the authors. Le Gros Clark and Leakey (1951:12) distinguished *P. nyanzae* from *P. africanus* on the basis of its larger size and certain morphological details of the dentition, including a pronounced and elaborately beaded internal cingulum on the upper molars, and only moderate reduction of M<sup>3</sup>. The authors also noted the presence of a more strongly developed posterior cingulum than anterior cingulum of the upper molars, and a smaller hypocone in relation to the protocone that is not seen to merge with the internal cingulum of M<sup>2</sup> (Le Gros Clark and Leakey, 1951:12).

In the more recent paleontological literature, the morphological homogeneity of *P. nyanzae* and *P. africanus* has been highlighted in studies that diagnose the three original species of *Proconsul* primarily on the basis of size (Andrews, 1978; Bosler, 1981). Although Andrews (1978) recognizes the similarity between the two taxa in terms of their distribution patterns and basic morphology, he considers

it unlikely that they are conspecific due to size differences, unless the combined species is shown to be exceedingly variable. Bosler (1981:158) also emphasized the similarity between *P. africanus* and *P. nyanzae* by pointing out how difficult it was to distinguish between the M<sup>1</sup> of *P. nyanzae* and the M<sup>2</sup> of *P. africanus*, in what she called “really very closely related species”.

The distinction between these two species has been a topic of debate that has largely centered on the taxonomic relationship between the samples from Rusinga and from the Tinderet sequence. While Andrews (1978) and Bosler (1981) recognize the occurrence of *P. africanus* at Rusinga Island, Kelley (1986) and Pickford (1986) argue that the size differences between the two species of Rusinga *Proconsul* are attributable to sexual dimorphism within a single species. According to their scheme, only one highly dimorphic species that also shows high levels of variation, is present at Rusinga and Mfwangano Islands (Kelley, 1986; Pickford, 1986). Those specimens from Rusinga and Mfwangano previously identified as *P. africanus* are included within the hypodigm of *P. nyanzae* as the female portion of the species, and *P. africanus (sensu stricto)* is therefore, restricted to Koru and Songhor (Kelley, 1986; Pickford, 1986).

The problem with recognizing a single, highly dimorphic species at Rusinga Island, however, is that this interpretation necessitates a degree of postcanine metric variability that exceeds the extant catarrhine maximum (Walker *et al.*, 1993). Kelley (1986:492) was well aware of this, and cautioned against “artificially restrict[ing]” fossil species by only admitting a degree of postcanine metric variability as determined from extant primate species. Kelley (1986) felt that by delimiting fossil taxa using the maximum variability observable in one extant species of a group, one was failing to fully appreciate the fact that the

biology of fossil taxa may not necessarily be duplicated in their living counterparts. As convincing as this may sound, it is hard to ignore the evidence from the postcranial remains.

Ruff *et al.* (1989) estimated body weights for both the large and small specimens from Rusinga and Mfwangano Islands based on cross-sectional properties of the femoral shaft, and the size of the femoral articular surfaces. They found two major body weight groupings among the specimens, with the larger sample averaging 37 kg, and the smaller sample averaging 9.6 kg (Ruff *et al.*, 1989). This implies that an approximately 4:1 male to female body weight ratio would have had to exist at Rusinga if only one species of *Proconsul* was present (Ruff *et al.*, 1989). This estimate of body weight dimorphism exceeds that known for all living terrestrial mammals; a fact that was instrumental in leading Walker *et al.* (1993) to reject the idea that the large and small specimens from Rusinga Island are represented by males and females of a single species.

These findings are consistent with the estimated body weights calculated for *P. nyanzae* and *P. heseloni* using distal tibial and talar articular surface dimensions (Rafferty *et al.*, 1995). The study predicted a mean body weight of 35.6 kg for *P. nyanzae* and 10.9 kg for *P. heseloni*; a result which clearly supports the presence of two species at Rusinga Island (Rafferty *et al.*, 1995).

The present study recognizes two species of *Proconsul* at Rusinga and Mfwangano Islands, the larger *P. nyanzae* and the smaller *P. heseloni*. The latter fossil taxon is considered morphologically distinct from mainland specimens of *P. africanus* and is treated separately in this study.

*Proconsul heseloni* Walker, Teaford, Martin and Andrews, 1993

- Holotype: KMN-RU 2036, partial skull with most of the upper and lower teeth, and large parts of the postcranial skeleton
- Type locality: Site R114, Kiakanga, Rusinga Island, Kenya
- Distribution: Early Miocene of Rusinga and Mfwangano Islands, Kenya

Formerly *P. africanus*, *Proconsul heseloni* was named by Walker *et al.* (1993) for the small Rusinga specimens that were different from the small species of *Proconsul* present at Koru and Songhor. *P. heseloni* is distinguished from *P. africanus* on the basis of several dental characters, including upper molars with a greater trigon breadth relative to the total breadth of the crown, and less well developed buccal cingula and occlusal ridges of the upper cheek teeth (Walker *et al.*, 1993:51). Walker *et al.* (1993:51) also list as a distinguishing character, upper premolars that are “more nearly equal in size and morphology”, combined with less extreme cusp heteromorphy on P<sup>3</sup>. The lower dentition shows differences in the moderate development of the honing facet on P<sub>3</sub>, and an M<sub>3</sub> with a massively developed hypoconulid and only moderate distal tapering (Walker *et al.*, 1993:51).

The specific distinction between *P. africanus* and *P. heseloni* has generally been accepted among most researchers, with *P. heseloni* appearing in the paleontological literature subsequent to its description (Rafferty *et al.*, 1995; Ward *et al.*, 1995; Beynon *et al.*, 1998; Fleagle, 1999; for an alternative interpretation, see Rae, 1993).

*Proconsul major* Le Gros Clark and Leakey, 1950

Holotype: BM(NH) M.16648, right mandibular body with the crowns of P<sub>4</sub>-M<sub>3</sub>

Type locality: Songhor, Western Kenya

Distribution: Early Miocene of Koru, Songhor, Chamtwara, Western Kenya and Napak, Uganda

The third and largest species of *Proconsul* named by Le Gros Clark and Leakey (1950, 1951) was *Proconsul major*, based on a massive mandibular specimen from Songhor [BM(NH) M.16648]. Le Gros Clark and Leakey (1951) distinguished this fossil taxon from *P. nyanzae* almost exclusively on the basis of the greater size and robusticity of the dentition and mandibular corpora, respectively. Allbrook and Bishop (1963) provisionally assigned ten large fossil hominoid specimens from Moroto and Napak, Uganda (comprising seven isolated teeth, two mandibular fragments, and a large palate with part of the upper dentition) to *P. major*. Pilbeam (1969) agreed with these assignments and provided detailed descriptions of this material and that of several additional isolated lower teeth recovered from Napak. As a consequence, *P. major* came to be defined largely by the Ugandan material, especially the lower face and palate from Moroto II (UMP 62-11). In the same study, Pilbeam (1969) also reassigned many of the smaller *P. nyanzae* mandibles from Songhor and Koru [including the mandible from Koru, BM(NH) M.14086, originally described by Hopwood (1933b)], which he considered to represent females of *P. major*.

The Uganda-dominated characterization of *P. major* changed, however, when Martin (1981) described newly discovered specimens of *P. major* from Koru.

Martin (1981) concluded that the Moroto material could no longer be regarded as *P. major*, even though the new Koru sample greatly increased the known range of variation of this species. Based on comparison with the expanded Kenyan sample, Martin (1981:150) highlighted the following morphological differences preserved in the Moroto palate: larger size of the anterior dentition relative to the molars; overall larger size of the upper incisors, canines, and premolars; and an absolutely larger M<sup>3</sup> in relation to the size of M<sup>1</sup> and M<sup>2</sup>. Martin (1981) refrained from naming a new species for the Moroto material, but provided a revised diagnosis of *P. major* in which he identified additional characters differentiating this fossil taxon from *P. nyanzae*.

The specimens from Moroto II previously referred to *P. major* (Allbrook and Bishop, 1963; Pilbeam, 1969; Andrews, 1978) have been subsequently reassigned to the new fossil taxon *Morotopithecus bishopi* by Gebo *et al.* (1997). The upper left canine (UMP 62-12) and left femoral fragments (MUZM 80) from Moroto II, however, have more recently been transferred from the *Morotopithecus* hypodigm and placed within *Ugandapithecus major* (Senut *et al.*, 2000), along with all specimens formerly included in *P. major*. Senut *et al.* (2000) erected a new genus, *Ugandapithecus*, for the species *P. major* since newly discovered postcranial material from Napak, Uganda revealed that the species concerned differed considerably from *Proconsul* species from the Kenyan sites of Koru, Songhor, Mfwangano, and Rusinga – at least at the generic level. Senut *et al.* (2000), therefore, recognize the occurrence of two large fossil hominoid genera at Moroto: *U. major*, which includes dental and postcranial specimens formerly included in *M. bishopi* but now considered indistinguishable from Napak *U.*

*major*; and *M. bishopi*, represented by the Moroto palate and regarded as markedly different from the former species.

The inclusion of the Napak material in the *U. major* hypodigm is consistent with Martin's (1981) interpretation that this material cannot be distinguished from *P. major*, though he did caution that the recovery of associated anterior and posterior dental specimens could change the taxonomic status of this material. Senut *et al.* (2000) excluded specimens from Meswa Bridge, Kenya (Andrews *et al.*, 1981) due to the fact that they are represented only by immature individuals, and as a result, assignments based on comparison with contemporaneous fossil species cannot be made with any degree of confidence.

The present study does not recognize *U. major* as a valid taxon and the nomen *P. major* in this study refers only to material derived from the localities of the Tinderet sequence in Kenya and to specimens from Napak, Uganda. *P. major*, therefore, is considered to be morphologically distinct only at the specific level from the other species of *Proconsul*.

*Kamoyapithecus hamiltoni* (Madden, 1980)

Holotype: KNM-LS 7, a right maxillary fragment with worn M<sup>2</sup>-M<sup>3</sup>  
and distal roots of M<sup>1</sup>

Type locality: Erageleit beds, Lothidok Hill, Northern Kenya

Distribution: Late Oligocene of the Lothidok Range, Northern Kenya

Madden (1980) was the first to describe two fossil hominoid specimens (subsequently KNM-LS 7 and KNM-LS 8) collected from Lothidok Hill in 1948 by the University of California African Expedition team, headed by H. B. S. Cooke. Although Andrews (1978) listed both specimens with material referred to *P. major*, he gave no formal description of either specimen. Madden (1980) named a new species of *Proconsul*, *P. (Xenopithecus) hamiltoni*, for one of the fossil specimens KNM-LS 7, a right maxillary fragment with heavily worn M<sup>2</sup>-M<sup>3</sup> (formerly UCMF 52112). In doing so, Madden (1980) resurrected *Xenopithecus* (Hopwood, 1933a) as a subgenus of *Proconsul*, because he felt that the species represented by the worn maxillary fragment was less derived than other species characteristic of that genus. Madden (1980:243) argued that the species included in the subgenus *Xenopithecus* differed from *Proconsul* spp. in having small, unexpanded trigons on M<sup>1</sup>-M<sup>2</sup>, and an M<sup>2</sup> with a relatively shorter crown length. They could still be accommodated within the genus *Proconsul*, however, because they shared four characters of the upper dentition with other species of the genus, including crenulated cingula and large hypocones on the first two upper molars (Madden, 1980:243).

Therefore, in Madden's (1980) taxonomic scheme two species are contained within the subgenus *Xenopithecus*: the type species, *P. (Xenopithecus) koruensis*

(Hopwood, 1933a) and *P. (Xenopithecus) hamiltoni*. Madden (1980) allocated the other fossil specimen KNM-LS 8, a worn and broken left upper canine (formerly UCMP 41979), to cf. *P. (Proconsul) major*.

In 1986, researchers from the Kenya National Museums returned to the Erageleit beds of the Lothidok Range and discovered three additional fossil hominoid specimens closely resembling the morphology preserved in the holotype of *P. (X.) hamiltoni* (Leakey *et al.*, 1995). Leakey *et al.* (1995) argued that the newly discovered material from Lothidok, along with Madden's (1980) two fossil specimens, not only belonged to the same taxon but were distinctive enough from other contemporaneous large-bodied catarrhines to warrant a new generic designation. Since the genus *Xenopithecus* was shown to be synonymous with *Proconsul* (Le Gros Clark and Leakey, 1951; Hopwood in Le Gros Clark and Leakey, 1951:106; Andrews, 1978), it was no longer available as a name for the genus of the species Madden (1980) had named. Consequently, Leakey *et al.* (1995) placed Madden's (1980) species in a new genus as *Kamoyapithecus hamiltoni*.

Leakey *et al.* (1995) distinguished *K. hamiltoni* from other East African anthropoids on the basis of several dental and mandibular characters. In particular, the authors noted that the upper fourth premolar of *K. hamiltoni* exhibits moderate to slight lingual and buccal basal flare, and that the buccolingually broad upper molars are low-crowned with uncrenulated lingual cingula and only partial buccal cingula (Leakey *et al.*, 1995:520). *K. hamiltoni* also possesses a robust upper canine with large, thick roots and a relatively short crown with a sharp distal blade (Leakey *et al.*, 1995). The second maxillary molar

is the largest in the cheek tooth series, and it possesses a hypocone set in close approximation to the trigon (Leakey *et al.*, 1995).

Leakey *et al.* (1995) listed three derived characters that might indicate a phylogenetic affinity between *Kamoyapithecus*, *Afropithecus*, *Heliopithecus*, and *Morotopithecus*: a large and robust upper canine, P<sup>4</sup> buccal and lingual flaring, and a hypocone set close to the trigon on M<sup>2</sup>. The presence of pronounced upper molar cingula, however, suggests that *Kamoyapithecus* is likely a primitive sister taxon to the latter genera (Leakey *et al.*, 1995). If this is true, *Kamoyapithecus* may represent the oldest fossil hominoid from East Africa to date.

*Dendropithecus macinnesi* Le Gros Clark and Leakey, 1950

- Holotype: BM(NH) M.16650, an almost complete mandible containing P<sub>3</sub>-P<sub>4</sub> and M<sub>2</sub>-M<sub>3</sub> on both right and left sides
- Type locality: Wakondu, Kulu Formation, Rusinga Island, Kenya
- Distribution: Early Miocene of Rusinga Island, Mfwangano Island, Karungu, Songhor and Koru, Kenya, and Napak, Uganda; possibly the Rangoye Beds at Angulo on the Uyoma Peninsula in Western Kenya

Le Gros Clark and Leakey (1950, 1951) described a new species of *Limnopithecus* from Rusinga Island, *L. macinnesi*, and distinguished it from the type species *L. legetet* in terms of its larger size, greater specialization in dental characters, and more gracile mandible. Following the description of several associated partial skeletons of *L. macinnesi* (Le Gros Clark and Thomas, 1951) and a reassessment of East African Miocene fossil catarrhines (Andrews, 1974; Delson and Andrews, 1975; Delson, 1977), Andrews and Simons (1977) proposed a new genus, *Dendropithecus*, for *L. macinnesi*. Andrews and Simons (1977) felt that a generic distinction was warranted between the two species of *Limnopithecus*, since evidence from preserved dental features indicated that *L. legetet* more closely resembled the pongid *Proconsul*, while material previously allocated to *L. macinnesi* showed greater affinities to the European pliopithecids.

Andrews and Simons (1977:164) distinguished *D. macinnesi* from all other Miocene apes based largely on characters of the anterior dentition, including high crowned and mesiodistally narrow incisors, and bilaterally compressed, strongly sexually dimorphic upper canines. With respect to the latter character, the

morphology of the upper canine of *D. macinnesi* is reminiscent of living hylobatids in that it is a blade-like, projecting tooth in both males and females (Andrews and Simons, 1977). The premolars and molars of *D. macinnesi* are characterized by “cusps set at the edge of the occlusal surface and connected by relatively well defined ridges”, resulting in large, well defined trigon and talonid basins (Andrews and Simons, 1977:165).

Postcranially, however, Andrews and Simons (1977) felt that *D. macinnesi* was markedly different from *Pliopithecus*, and exhibited a greater degree of suspensory adaptations in its forelimb, suggesting a higher level of arm swinging in its locomotor repertoire. In this regard, Andrews and Simons (1977:161) postulated that *D. macinnesi* had the “potential to be near the line of ancestry of the modern gibbon and siamang.”

Andrews (1978) later noted morphological and distributional differences between the Songhor and Rusinga samples attributed to *D. macinnesi*, and separated these two groups into distinct subspecies of *D. macinnesi*: *D. m. macinnesi* and *D. m. songhorensis*. In his taxonomic revision of small catarrhines from the Early Miocene of East Africa, Harrison (1988) excluded material previously attributed to *D. m. songhorensis* by Andrews (1978) from the hypodigm of *D. macinnesi* and described a new genus, *Kalepithecus*, for this fossil sample.

*Rangwapithecus gordonii* Andrews, 1974

Holotype: KNM-SO 700, palate with right and left C-M<sup>3</sup>

Type locality: Songhor, Western Kenya

Distribution: Early Miocene of Songhor, Rusinga and Mfwangano Islands, Kenya

Andrews (1974) named a new subgenus and species, *Dryopithecus (Rangwapithecus) gordonii*, based on a complete palate (KNM-SO 700) from the Tinderet site of Songhor. This specimen had tentatively been referred to *Proconsul* spp. (Andrews, 1970), pending further examination of the fossil sample collected from Songhor during Leakey's 1966 expedition. At the same time that *D. (R.) gordonii* was named, Andrews (1974) also described a second, smaller species of the subgenus *Rangwapithecus*, *D. (R.) vancouveringi*, based on a partial maxilla and upper dentition (KNM-RU 2058) from Rusinga Island. Despite the fact that he considered them morphologically identical, a specific distinction was made between these two taxa since the *D. (R.) vancouveringi* sample is significantly smaller than the former, and Andrews (1974) considered it unlikely that these two fossil taxa could have been sampled from the same population. Harrison (1986) has subsequently transferred the Rusinga-dominated *R. vancouveringi* material to a new genus, *Nyanzapithecus*.

Andrews (1974:189) distinguished *D. (R.) gordonii* from the similar-sized *P. africanus* on the basis of characters of the upper dentition, including high crowned and relatively narrow incisors, along with mesiodistally elongated and low cusped molars with greater secondary wrinkling on the occlusal surfaces. Other differences are listed as elongated and molariform premolars with pronounced

lingual and distal cingula, and a marked wear gradient on the molars unlike the condition seen in *Proconsul* (Andrews, 1974:189). The maxillary molars also increase in size from M<sup>1</sup>-M<sup>3</sup>, indicating no reduction of the upper third molar (Andrews, 1974).

In his taxonomic revision of East African Miocene hominoids, Andrews (1978) formally returned *Proconsul* to full generic status, recognizing three species of *P.* (*Proconsul*) and two species of *P.* (*Rangwapithecus*). Kelley (1986) later elevated *Rangwapithecus* to full generic rank, and excluded mandibular characters based on KNM-SO 1112 (left mandibular corpus with P<sub>3</sub>-P<sub>4</sub> and M<sub>2</sub>, and roots of I<sub>2</sub>-C, M<sub>1</sub> and M<sub>3</sub>) from his diagnosis, following the reassignment of this specimen to *P. africanus* by Bosler (1981). This mandibular specimen featured prominently in Andrews (1978) diagnosis of *P. (R.) gordonii*, but the P<sub>4</sub> and M<sub>2</sub> were shown by Bosler (1981) to be broader and less elongated than is typical for *Rangwapithecus*.

Order Primates Linnaeus, 1758

Suborder Anthropoidea Mivart, 1864

Infraorder Catarrhini Geoffroy, 1812

Superfamily Hominoidea Gray, 1825

Family *Incertae sedis*

*Afropithecus turkanensis* Leakey and Leakey, 1986

Holotype: KNM-WK 16999, facial and frontal region of a cranium  
with complete but heavily weathered dentition

Type locality: Kalodirr, Northern Kenya

Distribution: Early Miocene of Kalodirr, Buluk, Moruorot, and  
Locherangan, Kenya

Leakey and Leakey (1986a) named *Afropithecus turkanensis* for several specimens of a large hominoid collected from the newly discovered locality of Kalodirr, west of Lake Turkana. The fossil collection comprised several mandibles, isolated teeth, associated postcranial fragments and, most notably, a partial cranium with full dentition that was designated the type specimen (KNM-WK 16999). Approximately three years prior, Leakey and Walker (1985) had discovered one proximal phalanx and five gnathic elements of a large-bodied hominoid from the site of Buluk, northeast of Lake Turkana, that they assigned to *Sivapithecus* spp. When Leakey and Leakey (1986a) named *Afropithecus*, they noted that the new genus should also include the large hominoid material recently described from Buluk.

In addition to this material, further dental and gnathic elements attributable to *Afropithecus* have been added to the hypodigm, including two isolated teeth (KNM-LC 17590 and LC 18405) collected from Locherangan, west of Lake Turkana; these specimens are markedly smaller than those from Kalodirr and more closely approach the size of *P. nyanzae* and *Kenyapithecus* spp. (Anyonge, 1991). Anyonge (1991) speculated that this might indicate pronounced sexual dimorphism in the species. This is consistent with Leakey and Walker's (1997) interpretation that *Afropithecus* is characterized by considerable size dimorphism but lacks sexually dimorphic canines in terms of size and shape. A right juvenile mandible from Moruorot (KNM-MO 26) that has alternatively been assigned to '*Dryopithecus*' *nyanzae* by Madden (1972) and listed with material referred to *P. major* by Andrews (1978), has most recently been included in the *Afropithecus* hypodigm (Leakey and Walker, 1997).

Perhaps the most distinguishing feature of *A. turkanensis* is its distinctive long, narrow snout and anteriorly projecting premaxilla. Dentally, *A. turkanensis* exhibits several diagnostic features of the anterior dentition that suggest it was very strongly built (Leakey and Walker, 1997). These features include procumbent upper incisors with the lateral ones set back from the centrals and smaller in size, as well as elongated, anteriorly-inclined, and labiolingually compressed lower incisors (Leakey and Walker, 1997:230). In addition, the upper and lower canines are laterally splayed with long, stout roots and short, conical crowns (Leakey and Walker, 1997:230). The morphology of the cheek teeth is also distinctive in that the upper premolars and molars exhibit lingual and buccal basal flare (especially P<sup>4</sup>), and the upper molars possess a pronounced but short

mesial and lingual cingulum extending around the protocone (Leakey and Leakey, 1986a:143).

The phylogenetic affinities of *Afropithecus* have been difficult to assess, in part because the combined craniodental and postcranial fossil sample exhibits a mosaic of characters typical of both Oligocene and Miocene catarrhines. For example, the overall facial shape of *Afropithecus* has been shown to closely resemble that of the early Oligocene anthropoid *Aegyptopithecus zeuxis*, despite gross differences in body size (Leakey *et al.*, 1991). Further, *Afropithecus* exhibits highly derived characters of the dentition and mandible that suggest an adaptation to sclerocarp feeding, while its postcranial skeleton is likely very close to the primitive hominoid condition characterizing *P. nyanzae* (Leakey and Walker, 1997; Leakey *et al.*, 1988a).

Andrews (1992) grouped *Afropithecus* together with *Heliopithecus*, *Otaviopithecus* (Conroy *et al.*, 1992) from Namibia, and material from Maboko Island and Nachola (previously accommodated within *Kenyapithecus* spp.) in the tribe Afropithecini to reflect the evolutionary trend amongst these taxa towards an increase in molar enamel thickness, hyperrobusticity of the canine, and further enlargement of the upper premolars relative to the first molar. Andrews (1992) also included the Moroto palate (UMP 62-11) in this tribe on the basis of its greatly enlarged upper premolars.

In terms of dental morphology, the resemblance between the type specimen of *Afropithecus* and the Moroto palate is striking; both taxa exhibit greatly enlarged upper premolars with heteromorphic cusps and robust, low-crowned canines. As a result, Leakey *et al.* (1988a) and Andrews and Martin (1987a) speculated that both taxa might be congeneric, but specifically distinct. More recently however,

Leakey and Walker (1997) have argued that although UMP 62-11 could potentially be accommodated within *Afropithecus*, the evidence from vertebral remains likely associated with the Moroto palate (Walker and Rose, 1968) suggest that they are quite distinct from those assigned to *P. nyanzae*; the taxon most similar to *Afropithecus* in other aspects of its postcranial morphology. As a result, Ward (1993) has argued that the Moroto specimens should not be included in *Afropithecus*. Further, KNM-WK 16999 preserves a narrow, inclined incisive canal, whereas UMP 62-11 is characterized by an open canal (Leakey and Walker, 1997).

While the phylogenetic affinities of *Afropithecus* and the Moroto taxon are far from being resolved, due to the lack of overlap in associated postcranial remains, the presence of similar craniodental adaptations to sclerocarp feeding (procumbent incisors, large-rooted laterally splayed canines, together with heavy facial and mandibular buttressing) link both taxa together (Leakey and Walker, 1997). These resemblances, however, provide only weak evidence for a phylogenetic relationship, since the presence of similar feeding adaptations in both taxa are likely the result of functional convergence. In the present study, *Afropithecus* and the Moroto taxon are considered generically distinct.

*Heliopithecus leakeyi* Andrews and Martin, 1987

- Holotype: BM(NH) M.35145, left maxillary fragment with the crowns of P<sup>3</sup>-M<sup>2</sup> and the lingual alveolar margins of I<sup>2</sup> and C
- Type locality: Ad Dabtiyah, Saudi Arabia
- Distribution: Early Miocene of Ad Dabtiyah, Saudi Arabia

Andrews *et al.* (1978) were the first to describe the Ad Dabtiyah fossil hominoid sample recovered from the Dam Formation in Saudi Arabia. Though the diversity of the Arabian fauna is impressive (Hamilton *et al.* 1978), the hominoid sample is meagerly represented by a crushed left maxillary fragment [BM(NH) M.35145] and four isolated teeth [BM(NH) M.35146-9]. The taxonomic affinities of the five specimens were not determined at the time of their description and, in fact, the authors (Andrews *et al.*, 1978) initially suggested that the isolated right P<sup>4</sup> (M.35149) might belong to a separate species from the maxilla (M.35145), due to its smaller size and more mesiodistally compressed crown. When Andrews and Martin (1987a:385) later assigned all of the Ad Dabtiyah material to a new genus and species, *Heliopithecus leakeyi*, the authors noted that they no longer considered this likely “on the basis of metrical dimensions in comparison with other closely related taxa”.

More interestingly, however, the paper that named *Heliopithecus* was submitted before Leakey and Leakey (1986a) named *Afropithecus* but published afterwards; in a note added in proof, Andrews and Martin (1987a:391) questioned whether a generic distinction was justified between *Heliopithecus* and *Afropithecus*. Both taxa share greatly enlarged upper premolars with heteromorphic cusps, and upper molars that retain distinct lingual cingula. Differences

in size, however, left Andrews and Martin (1987a) little doubt that a species distinction between the Saudi Arabian and African material was warranted due to the considerably larger size of the African specimens.

The most striking feature of the type specimen of *Heliopithecus* is the great enlargement of its premolars (especially P<sup>4</sup>) relative to the first molar. Andrews and Martin (1987a) argued that the presence of relative upper premolar enlargement, together with molar enamel thickening, were two synapomorphies that linked *Heliopithecus* with the great ape and human clade; a clade that (according to the authors) also includes *Equatorius* (their 'K.' *africanus*) and *Dryopithecus*. They regarded *Heliopithecus* as a more primitive member of this clade, however, because it retains greater premolar cusp heteromorphy and cingulum development of the upper molars than that seen in *Equatorius* (Andrews and Martin, 1987a). In this respect, *Heliopithecus* resembles *Proconsul*, but is not uniquely related to it because it shares only plesiomorphic characters with this fossil taxon (Andrews and Martin, 1987a).

Andrews (1992) later commented that *Heliopithecus* and *Afropithecus* together with *Equatorius* seemed to form a natural grouping to the exclusion of *Dryopithecus*, and therefore included all three of the former genera in his newly proposed tribe, the Afropithecini. Leakey *et al.* (1988a) also recognized the affinity of *Heliopithecus* to *Afropithecus*; although the authors thought it likely that these fossil taxa were very closely related, confirmation of this is said to require additional fossil specimens that preserve the same anatomical features. At the very least, *Heliopithecus* is interesting in terms of its geographical position and age, such that it may potentially provide information on the relationships between African and Eurasian fossil primates. The deposits at Ad Dabtayah are

younger than those found at Rusinga and roughly contemporaneous with those at Maboko Island (Andrews *et al.*, 1978). Yet interestingly, the dental morphology of *Heliopithecus* appears to preserve a pattern intermediate between the geologically older genus *Proconsul* and the contemporaneous *Equatorius*.

*Morotopithecus bishopi* Gebo, MacLatchy, Kityo, Deino,  
Kingston and Pilbeam, 1997

Holotype: UMP 62-11, palatofacial specimen with complete dentition  
except for right I<sup>1</sup>, the tip of right C, and the lingual half of  
left P<sup>3</sup>

Type locality: Moroto II, Northeastern Uganda

Distribution: Early Miocene, Karamoja District, Northeastern Uganda

Craniodental and vertebral remains of a large-bodied hominoid discovered at Moroto II in the early 1960s were described and referred to *Proconsul major* by Allbrook and Bishop (1963) and Walker and Rose (1968), respectively. Despite the fact that all of the elements indicate that the fossil assemblage at Moroto II is represented by the same species (Walker and Rose, 1968) if not the same individual (Pilbeam, 1969), there has been a general reluctance “to associate the primitive teeth and face of the Moroto palate with the derived lumbar” (Gebo *et al.* 1997:401). When Gebo *et al.* returned to the fossil localities at Moroto I and II in the mid 1990s, they discovered additional postcranial remains: MUZM 80, several fragments of the right and left femora of a single individual from Moroto II; and MUZM 60, the glenoid fossa of a scapula from Moroto I. Gebo *et al.* (1997) assigned both the new and old specimens to the same species, *Morotopithecus bishopi*, since they saw no evidence to indicate that two large-bodied hominoids are represented at Moroto - one by the more primitive craniodental remains, and the other by the derived postcrania. This has not, however, gone unchallenged (Senut *et al.*, 2000).

As previously discussed in the treatment of *Afropithecus*, several researchers have recognized the striking morphological similarity between the type specimen of *Morotopithecus* and that of *Afropithecus* (Andrews and Martin, 1987a; Leakey *et al.*, 1988a; Andrews, 1992; Leakey and Walker, 1997; Fleagle, 1999). It has been hypothesized, however, that they differ markedly in the anatomy of the postcranium (Ward, 1993; Gebo *et al.*, 1997; Leakey and Walker, 1997; Fleagle, 1999). Whereas *Afropithecus* shares a more primitive postcranium with other early Miocene African hominoids such as *Proconsul*, *Morotopithecus* exhibits several derived features of the lumbar, scapular, and distal femoral regions that are more similar to those of the living apes (Gebo *et al.*, 1997; Fleagle, 1999). For example, the transverse processes of the middle lumbar vertebra associated with *Morotopithecus* (UMP 67-28) derive from the neural arch, which is an unambiguously hominoid-like trait (Sanders, 1992; Sanders and Bodenbender, 1994). The smooth, rounded craniocaudal curvature and widened superior aspect of the glenoid articular surface in MUZM 60 are also traits similar to those found in extant hominoids (Gebo *et al.*, 1997). Unfortunately, no single element of the postcranium is duplicated in both *Morotopithecus* and *Afropithecus* so that the generic distinction between the two taxa remains very much unresolved (Fleagle, 1999; Rae, pers. comm.). Based on the above distinctions, the 'Moroto palate' will nevertheless be referred to here by the generic name *Morotopithecus*.

*Turkanapithecus kalakolensis* Leakey and Leakey, 1986

- Holotype: KNM-WK 16950A and B, a partial cranium with right C-P<sup>3</sup>, M<sup>1</sup>-M<sup>3</sup>, left P<sup>3</sup>-M<sup>3</sup>, and complete mandible with left M<sub>2</sub> and right M<sub>3</sub>
- Type locality: Kalodirr, Northern Kenya
- Distribution: Early Miocene of the Lothidok Range, Northern Kenya

Leakey and Leakey (1986b) named *Turkanapithecus kalakolensis* for a relatively complete cranium and associated mandible (KNM-WK 16950A&B) of a medium-sized hominoid recovered at a locality within the Kalodirr Member of the Lothidok Formation. The Lothidok Range, situated in the Turkana Depression of Northwestern Kenya, has proven to be a rather fruitful location for yielding morphologically distinct fossil hominoids. For example, the same locality within the Kalodirr Member of the Lothidok Formation has also yielded numerous craniodental and postcranial specimens assigned to the larger-bodied fossil ape *A. turkanensis* (Leakey and Leakey, 1986a), and the Eragaleit beds within the Kalakol basalts that conformably underlie the Lothidok Formation (Boschetto *et al.*, 1992) have provided the latest Oligocene fossil hominoid, *K. hamiltoni* (Leakey *et al.*, 1995). All three taxa preserve unique dental features, and both Leakey and Leakey (1986b) and Boschetto *et al.* (1992) have suggested that the assemblage of fossil primates recovered thus far from the Lothidok Range (and possibly Buluk, as well) seems to be distinct from those in western Kenya and Napak.

*Turkanapithecus* is distinguished from all other known fossil hominoids by the distinct morphology of its upper cheek teeth (including the fourth premolar), such

that all teeth characteristically preserve a mesiobuccal cingulum that borders the paracone and terminates distally in a small cuspule (Leakey and Leakey, 1986b; Leakey *et al.*, 1988b). In addition to this, M<sup>2</sup> (and possibly M<sup>3</sup>, as well) is unique among fossil primates in possessing well-developed, beaded mesial and lingual cingula that are separated at the mesiolingual corner of the tooth by a distinct accessory cuspule (Leakey and Leakey, 1986b; Leakey *et al.*, 1988b).

Leakey *et al.* (1988b:287) listed several cranial features further distinguishing *Turkanapithecus* from the similar-sized and roughly contemporaneous species *P. africanus*, including a somewhat square maxilla that lacks postcanine fossae, the presence of distinct supraorbital tori, and the root of the zygomatic arch originating above M<sup>1</sup>, rather than M<sup>2</sup>. The dentition of *Turkanapithecus* shows further differences in its smaller size relative to the skull and mandible, and notably, in the lesser degree of buccolingual expansion of the upper premolars (Leakey *et al.*, 1988b).

In fact, there is only one specimen, the type of *Xenopithecus koruensis* [BM(NH) M.14081], with which *Turkanapithecus* shares the following affinities in upper molar morphology: “rather crowded cusps, the distinct and beaded cingulum, and the marked lingual expansion at the protocone” (Leakey *et al.* 1988b:287). It should be noted, however, that this specimen was designated the holotype of *Xenopithecus koruensis* by Hopwood (1933a), but was subsequently referred to *P. africanus*, with the approval of Hopwood [Le Gros Clark and Leakey (1951:106)].

*Equatorius africanus* (Leakey, 1962)

Holotype: BM(NH) M.16649, a partial left maxilla with P<sup>3</sup>-M<sup>1</sup>, roots of M<sup>2</sup>, and part of the alveolus of C

Type locality: Maboko Island, Western Kenya

Distribution: Middle Miocene of the Maboko Formation on Maboko Island, Ombo, Majiwa, Nyakach, and Kaloma, Kenya; the Aiteputh and Nachola Formations at Nachola, and Kipsaramon in the Muruyur Formation in the Tugen Hills, Kenya

The holotype of *Equatorius africanus* [BM(NH) M.16649] has had a rather long, complex and controversial history, appearing in the hypodigms of no fewer than four different genera since its discovery (Pickford, 1985). This specimen was originally figured and provisionally assigned to *P. africanus* by MacInnes (1943). Le Gros Clark and Leakey (1951) then designated it the holotype of *Sivapithecus africanus*, citing a very close resemblance to the Indian species *S. sivalensis* in terms of dental proportions and molar cusp pattern, but exhibiting certain distinctive features that necessitated separation at the specific level. When Simons and Pilbeam (1965) formally reduced *Sivapithecus* to sub-generic rank, they also argued that Le Gros Clark and Leakey's (1951) *S. africanus* was both generically and specifically identical to *Dryopithecus (Sivapithecus) sivalensis*, and synonymized it with the latter species. Leakey (1967) did not agree with this, however, and argued for the generic distinctiveness of the East African genus *Kenyapithecus* from Asiatic forms including *Sivapithecus*; he transferred *S. africanus* to the genus *Kenyapithecus*, since he regarded it as more closely related

to the type species, *K. wickeri*, than to any other fossil species. Finally, Andrews (1978) included BM(NH) M.16649 in the hypodigm of *P. nyanzae*, though he did not maintain this opinion for any great length of time (Andrews *et al.*, 1979).

The rather long and complicated path travelled by BM(NH) M.16649 to ultimately end up as the designated type specimen of the new combination *Equatorius africanus* (Ward *et al.*, 1999) is in part related to the confusion surrounding its exact provenience. MacInnes (1943) had listed the partial maxilla with specimens collected from Rusinga Island and later, both Le Gros Clark and Leakey (1951) and Leakey (1967) gave its exact provenience as locality R.106 on Rusinga Island. It is entirely plausible therefore, that the Rusinga provenience of M.16649 led Leakey (1967, 1968) to erroneously assign many mandibular fragments and isolated teeth of *P. nyanzae* and *P. major* to *K. africanus* (Pickford, 1985; McCrossin and Benefit, 1997); hence, Andrews's (1978) inclusion of M.16649 in the hypodigm of *P. nyanzae*. As a consequence, *Kenyapithecus* came to be associated with several features "uncharacteristic" of the genus (as known from the type species *K. wickeri*), including "a slender mandibular corpus, strong superior transverse torus, and retention of beaded molar cingula" (McCrossin and Benefit 1997:242). The Rusinga provenience of M.16649 was subsequently challenged by Andrews and Molleson (1979) however, who, upon examining the matrix attached to the specimen, concluded that it was more likely to have come from Maboko Island rather than Rusinga.

The mandibular fragments and isolated teeth attributed to *K. africanus* by Leakey (1967, 1968) were reverted back to the *P. nyanzae* hypodigm after Pilbeam (1969) provided a long list of objections to Leakey's assignments. Up until 1985, the hypodigm of *K. africanus* consisted therefore, of only three gnathic

specimens from Maboko Island and two isolated teeth from Majiwa added by Pickford (1982). In 1985, Pickford allocated 56 additional craniodental specimens from Maboko to the hypodigm of *K. africanus*, and also provisionally assigned the Maboko hominoid postcranial bones (previously accommodated within *P. nyanzae*) to *K. africanus*. In the same paper, Pickford (1985) predicted that morphological differences between *K. wickeri* and *K. africanus* might eventually necessitate their separation at the generic level.

The discovery of a partial hominoid skeleton with associated dentition (KNM-TH 28860) from Kipsaramon in the Tugen Hills, demonstrated that all material previously accommodated within *K. africanus* represented a new genus of Middle Miocene hominoid that was distinct from the younger, more derived *K. wickeri* sample (Ward *et al.*, 1999). *Contra* McCrossin and Benefit (1997), Ward *et al.* (1999:1385) argued that *K. wickeri* is morphologically derived in comparison to *Equatorius* in several features of the dentition, and that differences between the Fort Ternan and Maboko/Nachola samples are not merely “artifacts of small sample size”. This is supported, they argued, by the presence of presumed autapomorphic dental features characterizing *K. wickeri* in another Middle Miocene fossil ape from Paşalar in Turkey (Ward *et al.*, 1999). By separating the two taxa at the generic level, *Kenyapithecus* would no longer constitute a paraphyletic taxon (Ward *et al.*, 1999).

Ward *et al.* (1999:1383) distinguished *E. africanus* from *K. wickeri* based on characters of the anterior dentition that include a mesiodistally broad I<sup>1</sup> (in relation to its height) with low-relief marginal ridges, an I<sup>2</sup> with a unique and “highly asymmetric mesial-to-distal ‘spiraled’ lingual cingulum”, and a low-crowned C<sub>1</sub>. The maxillary and mandibular cheek teeth of *E. africanus* show further

differences in the weak development of premolar and molar cingulae, and the buccolingual and mesiodistal expansion of the upper premolars (relative to M<sup>1</sup>) combined with a reduction in cusp heteromorphy (Ward *et al.*, 1999). Cranially, *E. africanus* is distinguished by the low origin of the zygomatic root off the alveolar process of the maxilla and the expansion of the maxillary sinus into the premolar region of the alveolar process (Ward *et al.*, 1999).

In the present study, terms appearing in the paleontological literature referring to the 'Maboko hominoid' or 'Maboko *Kenyapithecus*' will henceforth be replaced by the generic name *Equatorius*.

## STEM CATARRHINES

Order Primates Linnaeus, 1758

Suborder Anthroidea Mivart, 1864

Infraorder Catarrhini Geoffroy, 1812

Superfamily Hominoidea Gray, 1825

Family Propliopithecidae Straus, 1961

*Propliopithecus chirobates* Simons, 1965

Holotype: CGM 26923, a nearly complete mandibular corpus with left and right C-M<sub>3</sub> and incisor alveoli

Type locality: Upper Fossil Wood zone, Jebel el Qatrani Formation, Fayum Province, Egypt, Quarry I

Distribution: Early Oligocene of Jebel el Qatrani Formation, Fayum Province, Egypt, Quarries I, M

Simons (1965) erected a new genus and species of fossil anthropoid, *Aeolopithecus chirobates*, solely based on a nearly complete mandible (CGM 26923) recovered from Quarry I of the Qatrani Formation in the Fayum Depression by the 1963-1964 Yale Paleontological Expedition. At the time, Simons (1965) distinguished this specimen from *Propliopithecus haeckeli* from the same deposits on the basis of its marked premolar heteromorphy, larger canines, and more procumbent incisors. The former two characters however, are related to the fact that CGM 26923 represents a male of the species and appropriately, *A. chirobates* was transferred to the genus *Propliopithecus* (Szalay and Delson, 1979), since it closely resembles the type species *P. haeckeli* in the

following (more taxonomically informative) characters: first and second lower molars more nearly equal in size, lower molars with more marginally placed cusps and steep-sided crowns, and well-developed cingula on the lower premolars (Kay *et al.*, 1981).

Interestingly, when Simons (1965) first described *P. chirobates*, he tentatively assigned it to the family Hylobatidae. He identified the presence of a greatly reduced M<sub>3</sub>, long canines, a high and deep genial fossa, and posterior shallowing of the mandibular corpus as characters linking *P. chirobates* to both living and fossil hylobatids (Simons 1965:136-137). Most of these are primitive characters, however, and Kay *et al.* (1981) found that new material attributed to *P. chirobates* did not substantiate the presence of the latter character listed above. In short, *Propiopythecus* is so primitive in all aspects of its morphology, it is improbable that this genus could be uniquely linked to any group of extant hominoid, or extant catarrhine, for that matter (Kay *et al.*, 1981).

*Aegyptopithecus zeuxis* Simons, 1965

- Holotype: CGM 26901, left mandible of a juvenile with P<sub>4</sub>-M<sub>2</sub>
- Type locality: Upper Fossil Wood zone, Jebel el Qatrani Formation,  
Fayum Province, Egypt, Quarry I
- Distribution: Early Oligocene of Jebel el Qatrani Formation, Fayum  
Province, Egypt, Quarries I, M

Simons (1965) named a second fossil anthropoid from the Fayum Depression, *Aegyptopithecus zeuxis*, based on three mandibular corpora, one of which was recovered from the same locality as *P. chirobates* during the 1963-1964 field expedition. Simons (1965:135-136) distinguished the absolutely larger *A. zeuxis* from the contemporaneous *Propliopithecus* on the basis of a number of dental and mandibular characters, including relatively larger canines, premolar heteromorphy, and a relatively more vertical and broader ascending ramus of the mandible.

In 1979, Szalay and Delson proposed that the generic distinction between *Aegyptopithecus* and *Propliopithecus* be discarded. This was rigorously challenged by Kay *et al.* (1981:312-313), who, after examining several additional specimens recovered from field excavations between 1977 and 1979, identified other taxonomically important dental features that clearly distinguished *A. zeuxis* from *Propliopithecus*, such as: a consistently larger and longer M<sub>2</sub> relative to M<sub>1</sub>, and more buccolingually compressed lower molar crowns with margins that slope outward, resulting in a more bulbous appearance. Further differences include the lack of a lingual cingulum on P<sub>4</sub> and high-crowned, narrow lower incisors (Kay *et al.* 1981). Like *Propliopithecus*, *A. zeuxis* exhibits strongly sexually dimorphic

lower canines in both size and shape, and very strongly developed upper premolar and molar lingual cingula.

## PREVIOUS ANALYSES OF EARLY AND MIDDLE MIOCENE CATARRHINE UPPER PREMOLAR MORPHOLOGY

### INTRODUCTION

Recently, systematic hypotheses have tended to position the proconsulids nearer to the beginning of the presumed evolutionary trajectory of catarrhines, placing them either as stem apes (Andrews, 1985, 1992; Andrews and Martin, 1987a, b; Rae, 1999) or basal catarrhines (Harrison, 1987, 1993; Harrison and Rook, 1997), rather than closer to the direct ancestry of extant apes as originally proposed by Hopwood (1933a, b). Amongst the genera of uncertain familial affinity that are also included in this study, *Afropithecus*, *Heliopithecus*, and *Morotopithecus* have alternatively been grouped together and positioned as the more distantly related sister group to the living great apes and humans in relation to *Equatorius* and *Dryopithecus* (Andrews and Martin, 1987a), or included in the Afropithecini along with *Equatorius*, in an heterogeneous association of taxa named the Dryopithecinae that are considered to represent basal hominids (Andrews, 1992). In stark contrast, Gebo *et al.* (1997) have argued that not only is *Morotopithecus* more closely related to extant hominoids than *Afropithecus* (due to its lumbar and scapular anatomy), it should more appropriately occupy a position *before* the split of the hylobatids as the sister taxon of all living hominoids rather than a position closer to the direct ancestry of living great apes.

These studies have used relative upper premolar enlargement and/or a reduction in upper premolar cusp heteromorphy to argue for the alternative phylogenetic placement of these early and middle Miocene fossil hominoids relative to extant primate clades, based on the interpretation that both dental features are characteristic of extant apes. This section reviews current hypotheses

that incorporate one or both of the dental characters to justify the phyletic position of fossil taxa relative to extant clades.

### **RELATIVE UPPER PREMOLAR ENLARGEMENT**

Previous hypotheses of upper premolar size evolution have postulated one change in crown size relative to the first and/or second molar throughout the course of hominoid evolution. The primitive hominoid condition is considered to be characterized by upper premolars that are small relative to molar size, while the derived hominid condition is regarded as being defined by upper premolar enlargement relative to the molars (Andrews and Martin, 1987a; Andrews, 1992; Harrison and Rook, 1997). Differences in the expression of these characters states across fossil taxa have been used either to distinguish between species (Gebo *et al.*, 1997) or, conversely, to group species together with the extant Hominidae, thus linking them to the great ape and human clade (Andrews and Martin, 1987a; Andrews, 1992; Harrison and Rook, 1997).

### **RELATIVE UPPER PREMOLAR ENLARGEMENT AS A HOMINID SYNAPOMORPHY**

Gebo *et al.* (1997:404) cite “larger premolars relative to M<sup>1</sup>” as a feature distinguishing *Morotopithecus* from both *Afropithecus* and *Proconsul*. In their taxonomic scheme, *Morotopithecus* is considered to represent the sister taxon of all extant apes, being more closely related to the living hominoids than *Afropithecus* (Gebo *et al.*, 1997). In contrast, Andrews and Martin (1987a) note that *Heliopithecus*, *Afropithecus*, *Morotopithecus*, and *Equatorius* all share distinctive upper premolar enlargement. For this reason, the authors link the fossil

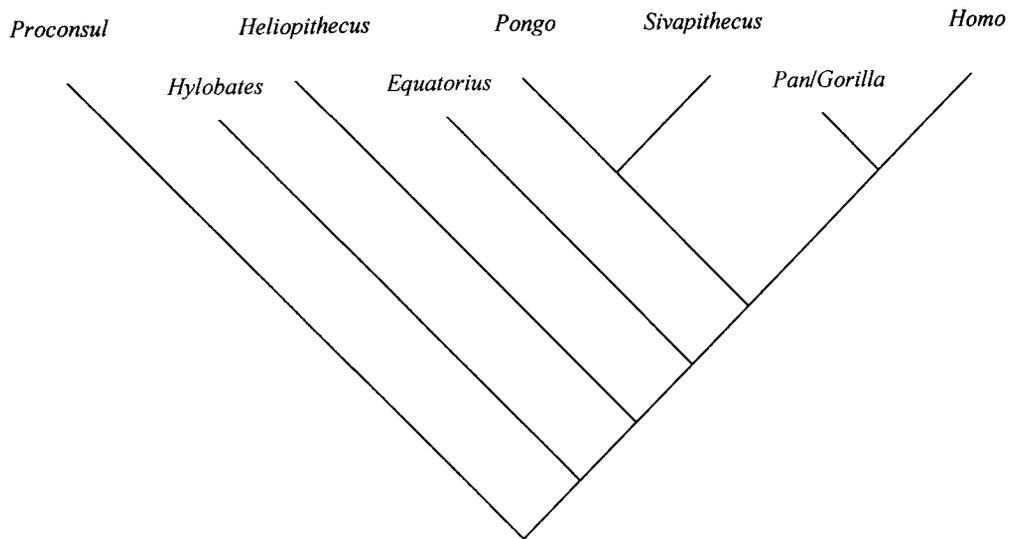
taxa with the Hominidae, since they consider enlarged premolars to be an important feature “characteristic of the great ape and human clade” (Andrews and Martin, 1987a:384). *Heliopithecus*, *Afropithecus*, and *Morotopithecus*, however, all retain what Andrews and Martin (1987a) interpret as ‘ancestral’ hominoid characters (such as premolar cusp heteromorphy and greater cingulum development on the upper molars), and therefore, they consider this group to be less closely related to great apes and humans than both *Equatorius* and *Dryopithecus*, but linked with them through premolar enlargement. Thus, in Andrews and Martin’s (1987a) phylogenetic scheme, the group including *Heliopithecus*, *Afropithecus*, and *Morotopithecus* diverges after gibbons but before *Equatorius*, so that both occur as successive sister groups to the great ape and human clade (Figure 2.3). The fossil taxon *Dryopithecus* is curiously absent from their phylogeny, since Andrews and Martin (1987a:390) consider its position relative to *Equatorius* “not certain”, even though the authors imply that *Dryopithecus* is more derived than *Equatorius* in the complete loss of upper molar cingulum development.

To highlight the significance of relative premolar enlargement in hominoid evolution, Andrews and Martin (1987a) calculated crown module ratios<sup>4</sup> for both the third and fourth upper premolars relative to M<sup>1</sup>. The authors found that *Afropithecus*, *Heliopithecus*, *Equatorius*, and *Morotopithecus* all exhibited a third upper premolar that was more similar in relative size to the extant great apes than to other Miocene hominoids (including *Proconsul*, *Dryopithecus*, and *Sivapithecus*), and a fourth upper premolar that differed from both extant and

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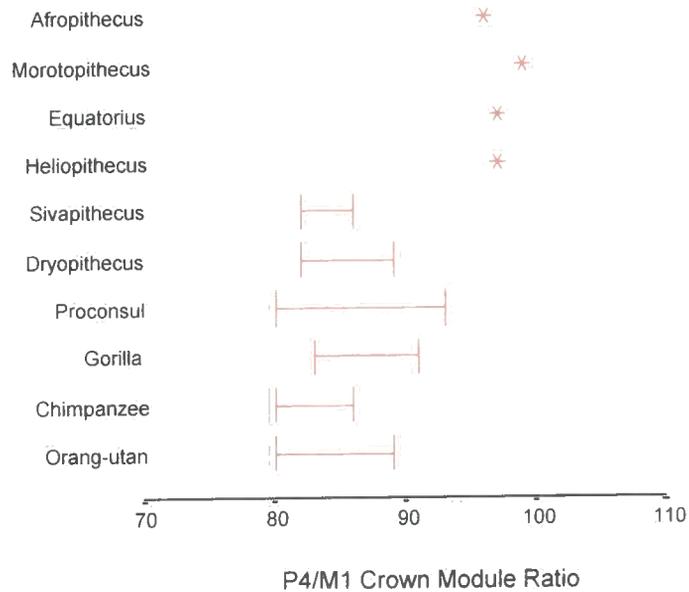
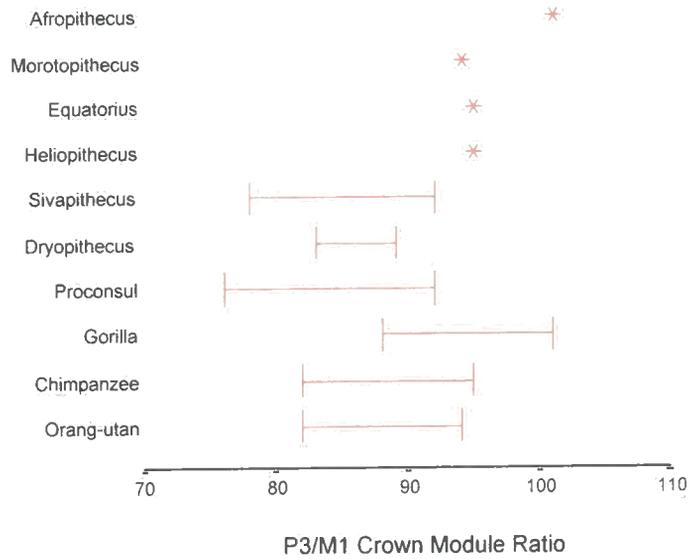
<sup>4</sup> Andrews and Martin’s (1987a:387) crown module ratio is a ratio of premolar/molar crown size calculated for the crown modules (crown length + crown breadth/2).

extinct Miocene apes in being unusually enlarged (Figure 2.4). More specifically, the authors found that the  $P^3/M^1$  crown module ratios of all four fossil taxa fell outside the ranges of both the orang-utan and the other Miocene hominoids, but within the gorilla range and at the upper limit of the chimpanzee range. Thus, their data show that *Afropithecus*, *Heliopithecus*, *Morotopithecus*, and *Equatorius* share a relatively larger  $P^3$  only with extant African great apes, to the exclusion of *Proconsul*, *Dryopithecus*, and *Sivapithecus*.



**Figure 2.3 Cladogram depicting the proposed phylogenetic relationships of *Heliopithecus leakeyi* [after Andrews and Martin (1987a:391)].**

Interestingly, however, the  $P^4/M^1$  crown module ratios for all four fossil taxa fall outside the ranges of both the extant great apes and extinct Miocene hominoids. Based on these data therefore, it appears obvious that *Afropithecus*, *Heliopithecus*, *Morotopithecus*, and *Equatorius* share upper fourth premolar enlargement that not only distinguishes them from extant great apes, but also from other Miocene hominoid genera. In fact, the data show that these four fossil taxa



**Figure 2.4 Crown module ratios calculated for the third and fourth upper premolars [after Andrews and Martin (1987a:387)].**

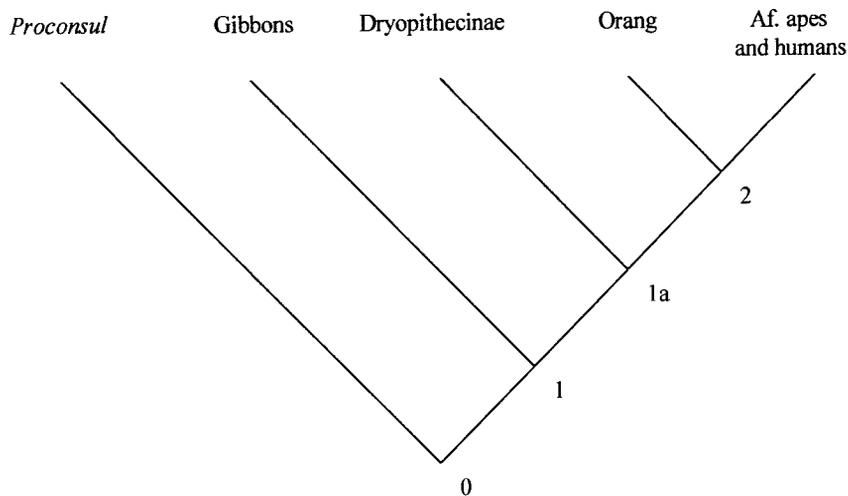
exhibit exceptionally large upper fourth premolars relative to  $M^1$ , so much so that they exceed all known extant and extinct hominoid size ranges.

Furthermore, based on the presentation of their data, it also seems reasonable to interpret relative upper anterior premolar enlargement as a synapomorphy

linking the four fossil taxa to the great ape and human clade. The interesting point to be made here, however is that, of the three Miocene hominoid genera from which *Afropithecus*, *Heliopithecus*, *Morotopithecus*, and *Equatorius* can be distinguished, both *Dryopithecus* and *Sivapithecus* are geologically younger than the former four taxa and are also considered by most researchers to be more closely related to extant hominids. Yet both *Dryopithecus* and *Sivapithecus* exhibit relatively smaller upper anterior premolars in relation to those of the extant great apes; in fact, they fit very comfortably within the *Proconsul* range.

It follows that if one were to code relative upper anterior premolar enlargement and map it onto the phylogeny given by Andrews and Martin (1987a:391) with *Dryopithecus* occupying the node above *Equatorius* (as implied by the authors), the last common ancestor shared by *Equatorius* and *Dryopithecus* (as the sister group to living great apes) would be equivocal, due to the 'plesiomorphic' expression of this character in both *Dryopithecus* and *Sivapithecus*. Three explanations are possible, of which the first and second deal with the two basic types of homoplasy: firstly, the condition of relatively smaller anterior upper premolars may have arisen independently in *Proconsul*, *Dryopithecus* and *Sivapithecus* (convergent evolution); secondly, the expression of relatively smaller upper premolars may represent a reversal to the plesiomorphic condition (represented by *Proconsul*) in both *Dryopithecus* and *Sivapithecus*; or thirdly, the observed variation across taxa can perhaps be attributed to functional, diet-related adaptations rather than phylogeny. Another plausible (and indeed testable) interpretation of their data suggests that the distinctive upper premolar enlargement observed in *Afropithecus*, *Heliopithecus*, *Morotopithecus*, and *Equatorius* represents an autapomorphic character shared by a clade including all

four fossil taxa and therefore, is phylogenetically informative only inasmuch as it represents a synapomorphy of an afropithecine clade.



**Figure 2.5 Cladogram depicting Andrews's (1992:642) proposed relationships of the fossil hominoids.** Characters defining nodes 0 and 1a include: reduction in cusp heteromorphy on the upper premolars (node 0), and relative upper premolar enlargement together with retention of varying degrees of cusp heteromorphy (node 1a).

In his review of the relationships between fossil and extant hominoids, Andrews (1992) included *Equatorius* within the tribe Afropithecini along with *Afropithecus*, *Heliopithecus*, *Morotopithecus*, and *Otaviopithecus*. Andrews (1992:642) identified upper “premolar enlargement combined with retention of varying degrees of cusp heteromorphy” as one of four features characteristic of the Dryopithecinae (node 1a in Figure 2.5), within which he further distinguished the tribe Afropithecini from both the Kenyapithecini and Dryopithecini by yet “further enlargement of the premolars” and an increase in molar enamel thickness. Presumably to avoid the pitfalls of positioning the fossil taxa included within the three tribes of the Dryopithecinae as successive sister groups to the living great

apes based on this dental character, the Dryopithecinae appears as a tricotomy (node 1a in Figure 2.5). The Proconsulidae (node 0 in Figure 2.5) retains the primitive hominoid condition of relatively small upper premolars, but is linked to the Hominoidea by a reduction in upper premolar cusp heteromorphy.

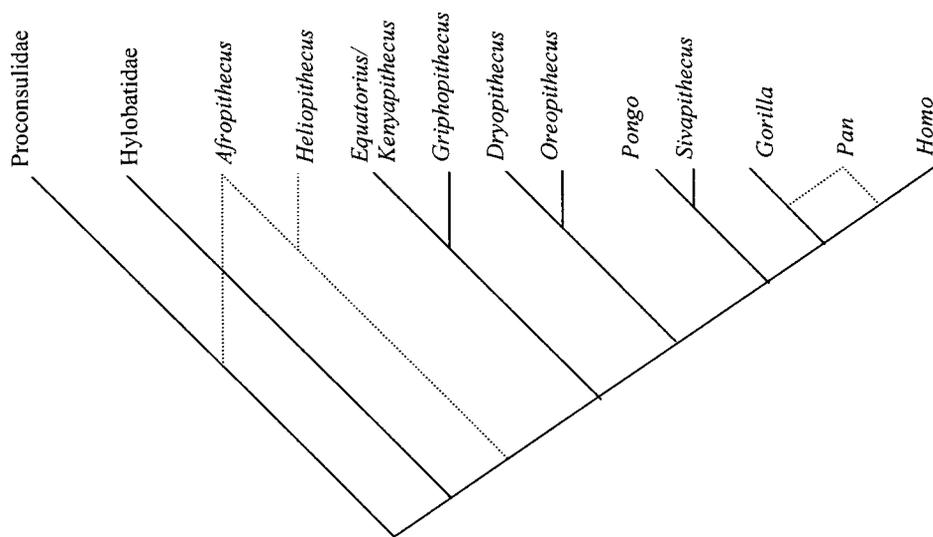
Andrews's (1992) inclusion of three tribes within the subfamily Dryopithecinae is intended not only to reflect the uncertainty surrounding the phylogenetic associations of these taxa with one another and with later hominoids, but also to convey a certain morphological distinctiveness between all three groups. According to Andrews (1992), the molar enamel thickening and enlargement of the upper premolars characteristic of the Afropithecini represent an evolutionary trend towards processing harder fruit objects.

Like Andrews (1992) and Andrews and Martin (1987a), Harrison and Rook (1997) also found relative upper premolar enlargement to be a derived feature of extant hominids. They calculated crown area of both the third and fourth upper premolars relative to the second molar<sup>5</sup> and found that "hylobatids and proconsulids can be distinguished from extant hominids by having relatively much smaller premolars" (Harrison and Rook, 1997:348). Thus, Harrison and Rook (1997) also interpret large upper premolars in relation to the molars as a hominid synapomorphy. The difference, however, is that according to their taxonomic scheme, the Proconsulidae is excluded from the Hominoidea and placed within its own superfamily the Proconsuloidea, as a group of stem catarrhines (Harrison and Rook, 1997). The Afropithecidae (includes *Afropithecus* and *Heliopithecus*) is only tentatively retained in the Hominoidea as the sister group to the Hominidae

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<sup>5</sup> Harrison and Rook's (1997:349) index for calculating the relative size of upper premolars is length x breadth of upper premolar x 100/length x breadth of M<sup>2</sup>.

since Harrison and Rook (1997) believe it might eventually prove better placed within the Proconsuloidea (Figure 2.6). Of the fossil taxa included in the present study therefore, only *Equatorius* is listed in the family Hominidae.



**Figure 2.6** Cladogram depicting Harrison and Rook's (1997:356) inferred relationships between fossil and extant catarrhines.

## UPPER PREMOLAR CUSP HETEROMORPHY

Previous hypotheses of upper premolar cusp height evolution have postulated one or more changes in the height of the paracone relative to the protocone throughout the course of catarrhine evolution. Researchers have used these hypotheses to support the phylogenetic placement of the fossil taxon *Proconsul* relative to extant catarrhines, arguing for its position as either the sister group of the extant Hominoidea (Andrews, 1985, 1992; Andrews and Martin, 1987a, b) or as the sister taxon of both living cercopithecoids and hominoids (Harrison, 1987; Harrison and Rook, 1997). The result of this differential phylogenetic

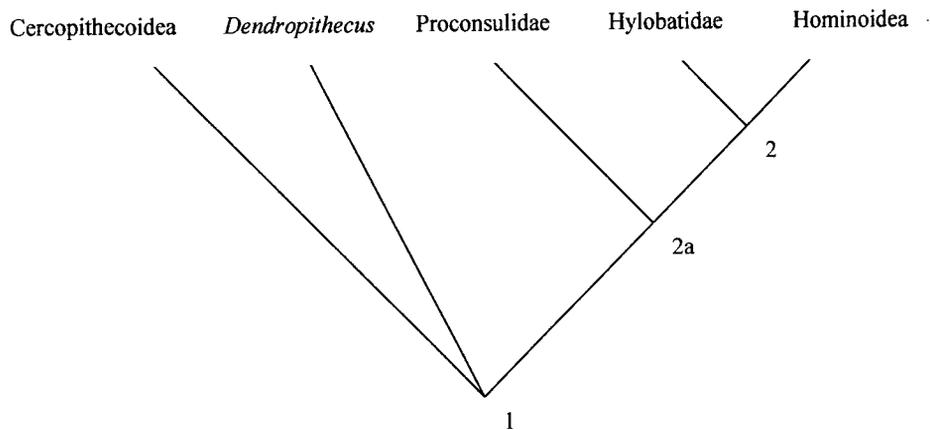
interpretation is twofold: firstly, the inferred condition characterizing ancestral morphotypes of the principle groups of living anthropoids is defined differently by both researchers since *Proconsul* not only occupies different nodes, but as a consequence, it groups with different clades or groups of primates; and secondly, the number of changes upper premolar cusp heteromorphy undergoes across catarrhine phylogeny, differs for both researchers.

As a result, the derived condition of a reduction in cusp heteromorphy is interpreted as a hominoid synapomorphy by Andrews (1985, 1992; Andrews and Martin, 1987b), thereby accommodating the hominoid status of *Proconsul*. Conversely, a reduction in cusp heteromorphy is interpreted as a hominid synapomorphy by Harrison (1987; Harrison and Rook, 1997), who has consistently argued that “there is no convincing morphological evidence to firmly place *Proconsul*...as the sister group of the Hominoidea” (Harrison, 1987:70). The only point on which both researchers agree is that the primitive catarrhine morphotype is characterized by extreme cusp heteromorphy of the upper premolars.

### **REDUCTION IN UPPER PREMOLAR CUSP HETEROMORPHY AS A HOMINOID SYNAPOMORPHY**

Andrews (1985) considers the primitive catarrhine morphotype to be characterized by upper premolars in which there is a marked difference in height between the paracone and protocone, while extant hominoids and *Proconsul* exhibit the derived condition characterized by a reduction in cusp heteromorphy. According to Andrews (1985), reduced cusp heteromorphy on the upper premolars is one of eight hominoid synapomorphies present in *Proconsul*, but

because this fossil taxon shares no character exclusively with the Hominidae, it is considered to represent the sister group of the extant hominoid families (= basal hominoid). Andrews's (1985) phylogenetic hypothesis predicts, therefore, that a reduction in cusp heteromorphy on the upper premolars characterizes both the Proconsulidae and members of the living Hominoidea to the exclusion of *Dendropithecus*, since this fossil taxon retains the primitive condition in all eight features designated by the author as characteristic of the ancestral hominoid morphotype (Figure 2.7).



**Figure 2.7 Cladogram depicting Andrews's (1985:18) proposed phylogenetic position of the Proconsulidae within the Hominoidea.** Characters defining nodes 1 and 2a include: upper premolars with heteromorphic cusps (node 1), and reduction in cusp heteromorphy on the upper premolars (node 2a).

Andrews (1992) later reiterated this, listing a reduction in upper premolar cusp heteromorphy as one of eight characters distinguishing the Proconsulidae (node 0 in Figure 2.5), some of which are also considered characteristic of the Hominoidea (node 1 in Figure 2.5), thereby substantiating the hominoid status of *Proconsul*. Andrews's (1992) Proconsulidae (node 0 in Figure 2.5) includes the following fossil genera: *Proconsul*, *Rangwapithecus*, *Nyanzapithecus*, and *Kamoyapithecus*,

though there is no discussion as to whether *Dendropithecus* is again excluded from this clade. In addition, presumably to accommodate the retention of “varying degrees of cusp heteromorphy” characteristic of some members of the Dryopithecinae, Andrews (1992:642) included two premolar cusp morphologies in the Afropithecini characterization: one in which *Afropithecus* and *Morotopithecus* exhibit strong cusp heteromorphy on the anterior upper premolar (seemingly *Heliopithecus* is also included in this arrangement), and one in which *Equatorius* displays cusps that are more nearly equal in size.

Andrews and Martin’s (1987a) interpretation of the primitive hominoid condition as including upper premolars in which the cusps *are* heteromorphic appears to be a slight deviation not only from Andrews’s (1985) previous work, but also from the authors’ collective study that appeared in the same year (Andrews and Martin, 1987b). Andrews and Martin’s (1987a:388) interpretation is based on the “widespread occurrence” of this character condition among early catarrhines (such as *Propliopithecus* and *Dendropithecus*) as well as early Miocene hominoids (such as *Proconsul* and *Heliopithecus*), and the subsequent absence of cusp heteromorphy “throughout the living catarrhines”.

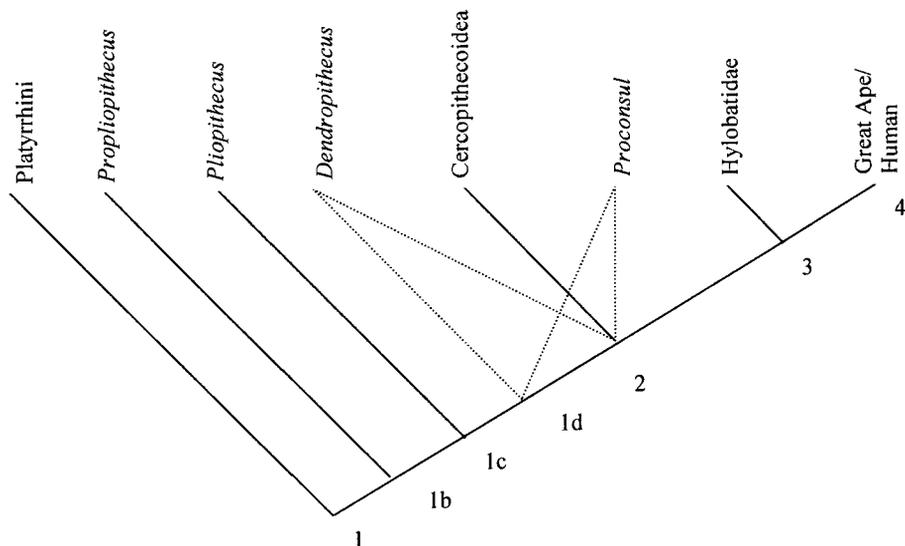
Andrews and Martin (1987a) reported that *Heliopithecus* retained a greater degree of cusp heteromorphy than that seen in both *Equatorius* and *Dryopithecus* (a primitive character that it shares with *Proconsul*), and hence, argued for the intermediate phylogenetic position of *Heliopithecus* between the hominoid and hominid ancestral conditions. Thus, although *Proconsul* is still regarded by Andrews and Martin (1987a:383) as possessing “some hominoid synapomorphies” (here the reader is referred to Andrews, 1985), in this paper, *Proconsul* is characterized by the ancestral hominoid pattern of cusp

heteromorphy. It is possible that with the discovery of a new fossil hominoid that Andrews and Martin (1987a) interpreted as resembling *Proconsul* in the primitive retention of cusp heteromorphy while being linked to the great ape and human clade in other derived dental characters (such as upper premolar enlargement and molar enamel thickening), it became necessary to characterize the ancestral hominoid pattern by upper premolar cusp heteromorphy to maintain the hominoid status of *Proconsul* and accommodate the 'intermediate' phylogenetic position of the newly discovered *Heliopithecus*.

### **REDUCTION IN UPPER PREMOLAR CUSP HETEROMORPHY AS A HOMINID SYNAPOMORPHY**

Harrison (1987), however, has argued that not only does *Proconsul* exhibit a marked discrepancy in height between the buccal and lingual cusps of the upper third and fourth premolars, this difference is more pronounced than that seen in any extant catarrhine species, with the exception of hylobatids and some cercopithecoids. Partly on the basis that the marked cusp heteromorphy seen in *Proconsul* more closely resembles the primitive catarrhine condition rather than the more derived pattern of extant great apes, Harrison (1987) considers *Proconsul* to represent the sister taxon of all extant catarrhines (= basal catarrhine). In Harrison's (1987) phylogenetic scheme, upper premolar cusp height evolution undergoes two changes: the ancestral anthropoid morphotype is characterized by upper premolars with the buccal cusp only slightly higher than the lingual cusp, the primitive catarrhine morphotype is described as upper premolars in which the buccal cusp much higher than the lingual cusp, and the great ape/human clade is defined by the derived reversal in which the buccal cusp

is nearly the same height as the lingual cusp (Figure 2.8). Thus, Harrison (1987) argues that the hylobatids, *Proconsul*, and *Dendropithecus* (along with some members of the Cercopithecoidea) exhibit marked cusp heteromorphy, while only the extant great apes are characterized by a reduction in the disparity in height between the paracone and the protocone.



**Figure 2.8 Cladogram depicting Harrison's (1987:72) inferred position of *Proconsul* relative to extant and extinct catarrhines.** Characters defining nodes 1, 1b, and 4 include: upper premolars with the buccal cusp only slightly higher than the lingual cusp (node 1), upper premolars with the buccal cusp much higher than the lingual cusp (node 1b), and upper premolars with the buccal and lingual cusps of more or less equal height (node 4).

Harrison and Rook (1997) later corroborated this with evidence they gleaned from measuring the relative height of the cusps on the upper premolars<sup>6</sup> of six extant hominoid genera as well as four fossil taxa: *Oreopithecus*, *Proconsul*, *Dendropithecus*, and *Propitopithecus*. The authors found that “hylobatids and proconsulids are more primitive in retaining a greater differential between the two

<sup>6</sup> Harrison and Rook's (1997:348) index for calculating the relative height of cusps on the upper premolars is height of protocone x 100/height of paracone.

cusps”, while the extant hominids are characterized by upper premolars in which the paracone is only slightly more elevated than the protocone (Harrison and Rook, 1997:348). Thus, their data show that a reduction in upper premolar cusp heteromorphy (more so on the third premolar rather than the fourth) is exclusively an hominid synapomorphy.

### **UPPER PREMOLAR CUSP HETEROMORPHY AS A DISTINGUISHING CHARACTER BETWEEN SPECIES**

Like relative upper premolar enlargement, upper premolar cusp heteromorphy has also been used as a character to distinguish between species in several diagnoses, including those of *P. africanus*, *P. heseloni*, *D. macinnesi*, and *H. leakeyi*. Indeed, Hopwood (1933a, b) first noted the pronounced disparity in height between the buccal and lingual cusps of the upper premolars in the holotype of *P. africanus*. In fact, Hopwood (1933b:455) considered the “tall, sharp-pointed buccal cusps of the premolars” among the ‘specialized’ characters of the upper dentition of this fossil species, since its expression in the third upper premolars was so marked so as to almost “make the teeth caniniform”. Hopwood (1933b) used the presence of a more caniniform third upper premolar as one of six characters distinguishing the primitive dentition of *P. africanus* from the chimpanzee - the presumed descendant of *P. africanus*.

More recently, however, this character has been listed as a feature distinguishing the sample of *P. africanus* specimens known from the Tindereet sites (Koru and Songhor) from the small Rusinga Island *Proconsul* species assigned to *P. heseloni* by Walker *et al.* (1993); the “elongated buccal cusp of the P<sup>3</sup>” is given as a character distinguishing *P. africanus* from Rusinga *Proconsul*,

though in the species diagnosis of *P. heseloni* the authors list “premolar cusps slightly to markedly heteromorphic on P<sup>3</sup> and not at all on P<sup>4</sup>” as a diagnostic character (Walker *et al.*, 1993:51). In terms of upper premolar morphology, then, it seems the main difference between the species is that the buccal cusp of the fourth upper premolar in *P. africanus* is rather projecting, but not at all in *P. heseloni*.

What remains unclear, however, is whether upper premolar cusp heteromorphy is correlated with sexual dimorphism in extant primate species, such that species that exhibit marked sexual dimorphism in maximum canine crown length will also possess a pronounced discrepancy in the height of the paracone relative to the protocone or more simply, a more caniniform anterior upper premolar. If this is the case, then one would expect to find a correlation between canine crown length and upper premolar cusp heteromorphy in the males of species, and a reduction in premolar cusp heteromorphy in the females of species. This has interesting implications in terms of the specific distinction made by Walker *et al.* (1993) between the male-dominated *P. africanus* sample from Koru and Songhor, and the female-dominated *P. heseloni* sample from Rusinga Island. Walker *et al.* (1993:51), however, do recognize that differences between *P. africanus* and Rusinga *Proconsul* that include cusp heteromorphy on P<sup>3</sup>, “may be reduced by additional samples that correct for sex differences between the two sites”.

## **AIMS AND OBJECTIVES**

### **HYPOTHESES TO BE TESTED**

Both relative upper premolar enlargement and a reduction in upper premolar cusp heteromorphy have been used to argue for the alternative phylogenetic position of the proconsulids relative to recent hominoids, based on the *a posteriori* determination of character states of both the living and fossil taxa examined in the studies in question (Andrews, 1985, 1992; Andrews and Martin, 1987a; Harrison, 1987; Harrison and Rook, 1997). As such, to test whether these hypothesized synapomorphies diagnose the groups for which they are proposed, both dental characters must first be shown to support living primate clades. Specifically, relative upper premolar enlargement should support an extant great ape clade (Andrews, 1992; Andrews and Martin, 1987a; Harrison and Rook, 1997), and a reduction in upper premolar cusp heteromorphy should support either an extant ape clade (Andrews, 1985, 1992) or an extant great ape clade (Harrison, 1987; Harrison and Rook, 1997). If these character states are shown to be present at the internode directly below the last common ancestor of either the Hominoidea or the Hominidae for each character, we can then infer that these characters work well in resolving the relations among groups of living primates and therefore, can be applied to the fossil record.

## CHAPTER 3

### MATERIALS AND METHODS

#### MATERIALS

##### EXTANT SAMPLE

The range of the extant sample analyzed in the present study was intended to encompass the major divisions within the Anthroidea in order to “maximiz[e] the size variation across the interspecific sample” (Ravosa, 2000:308), since the fossil taxa range in body mass from 4,200g estimated for *Propliopithecus* to 50,000g estimated for both *P. major* and *Afropithecus* (Fleagle, 1999). The extant sample, therefore, comprises five families from the Ceboidea, Cercopithecoidea, and Hominoidea. Two species are represented from the Cebidae (*Cebus apella* and *Cebus olivaceus*), as well as two species from the Atelidae (*Ateles paniscus* and *Alouatta seniculus*) within the Ceboidea. Six species are represented from the Cercopithecinae (*Macaca nigra*, *Papio anubis*, *Cercopithecus nictitans*, *Cercopithecus cephus*, *Cercocebus torquatus*, and *Lophocebus albigena*) and two species from the Colobinae (*Colobus guereza*, and *Ptilocolobus badius*) within the Cercopithecoidea. Finally, two species are represented from the Hylobatidae (*Hylobates agilis* and *Symphalangus syndactylus*), as well as three species from the Hominidae (*Pongo pygmaeus*, *Gorilla gorilla*, and *Pan troglodytes*) within the Hominoidea.

In total, 163 anthropoid specimens were analyzed for the study (Table 3.1). Only wild-caught, adult specimens (based on the eruption of the third molars) that exhibited minimal occlusal wear were selected for the analysis and where the sample permitted, equal numbers of males and females were measured for each

species. The specimens analyzed derive from the following institutions: Rijksmuseum van Natuurlijke Historie, Leiden, Holland; Powell-Cotton Museum, Kent, England; and the Royal Ontario Museum, Toronto, Canada.

**Table 3.1 Summary of Extant Sample**

<b>Species</b>	<b>Males</b>	<b>Females</b>	<b>Total</b>
<b>Cebidae</b>			
<i>Cebus apella</i>	4	2	6
<i>Cebus olivaceus</i>	5	1	6
<b>Atelidae</b>			
<i>Ateles paniscus</i>	1	4	5
<i>Alouatta seniculus</i>	3	3	6
<b>Cercopithecinae</b>			
<i>Macaca nigra</i>	3	1	4
<i>Papio anubis</i>	7	2	9
<i>Cercopithecus nictitans</i>	5	5	10
<i>Cercopithecus cephus</i>	5	5	10
<i>Cercocebus torquatus</i>	7	3	10
<i>Lophocebus albigena</i>	5	5	10
<b>Colobinae</b>			
<i>Colobus guereza</i>	6	4	10
<i>Ptilocolobus badius</i>	5	5	10
<b>Hylobatidae</b>			
<i>Hylobates agilis</i>	6	4	10
<i>Symphalangus syndactylus</i>	4	2	6
<b>Hominidae</b>			
<i>Pongo pygmaeus</i>	4	5	9
<i>Gorilla gorilla</i>	12	10	22
<i>Pan troglodytes</i>	9	11	20

## **FOSSIL SAMPLE**

The fossil sample consists of 15 extinct species and 12 genera from at least four different families: Cercopithecidae, Propithecidae, Proconsulidae, and Hominidae. The majority of the fossil dental data were obtained from the literature, with the exception of data collected from eight original specimens

housed at the Natural History Museum, London (Table 3.2). Only fossil specimens that preserved associated maxillary premolars and molars were chosen for the analysis.

## **MEASUREMENTS**

Based on preservation, up to thirteen linear measurements were taken on each specimen: C<sup>1</sup> maximum buccal crown height; P<sup>3</sup> maximum mesiodistal and buccolingual crown length and width, respectively; P<sup>3</sup> maximum buccal and lingual cusp height; P<sup>4</sup> maximum mesiodistal and buccolingual crown length and width, respectively; P<sup>4</sup> maximum buccal and lingual cusp height; M<sup>1</sup> maximum mesiodistal and buccolingual crown length and width, respectively; and M<sup>2</sup> maximum mesiodistal and buccolingual crown length and width, respectively. The data were recorded with Mitutoyo ‘Absolute Digimatic’ digital calipers accurate to 0.1 mm, and whenever possible, the data were recorded from the left-hand side only to ensure consistency.

In the analysis of relative upper premolar enlargement, ‘occlusal size’ is based on two independent measurements of the same tooth (mesiodistal length and buccolingual width) to yield an ‘occlusal area’ that is a “more accurate measure of tooth size than that given by any single measurement” (Gingerich *et al.*, 1982:83).

## **CHARACTERS**

Seven metric characters were chosen for the analysis (see below). These characters were derived from indices presented in Harrison and Rook (1997:348-349) and Andrews and Martin (1987a:387) for the purpose of testing the efficacy with which both relative upper premolar enlargement and a reduction in upper premolar cusp heteromorphy can be shown to diagnose living ape and/or great ape clades based on the methodology used in these studies.

**Table 3.2 Summary of Fossil Sample**

Species	Specimen Number	Source
<i>P. africanus</i>	BM(NH) M.14084	Natural History Museum, London
<i>P. heseloni</i>	KNM-RU 1674 KNM-RU 1705 KNM-RU 2036 KNM-RU 16000	Andrews (1978) Andrews (1978) Andrews (1978) Teaford <i>et al.</i> (1988)
<i>P. nyanzae</i>	BM(NH) M.16647 KNM-RU 1677 KNM-RU 7290	Natural History Museum, London Andrews (1978) Andrews (1978)
<i>P. major</i>	KNM-SO 418 KNM-CA 387-391	Andrews (1978) Martin (1981)
<i>K. hamiltoni</i>	KNM-LS 18352	Leakey <i>et al.</i> (1995)
<i>R. gordonii</i>	KNM-SO 401 KNM-SO 700	Andrews (1978) Andrews (1978)
<i>D. macinnesi</i>	KNM-RU 1774 KNM-RU 1806 KNM-RU 1849 KNM-RU 1850 KNM-RU 2086	Andrews (1978) Andrews (1978) Andrews (1978) Andrews (1978) Andrews (1978)
<i>A. turkanensis</i>	KNM-WK 16999	Leakey <i>et al.</i> (1988b)
<i>H. leakeyi</i>	BM(NH) M.35145	Natural History Museum, London
<i>M. bishopi</i>	UMP 62-11	Andrews (1978)
<i>T. kalakolensis</i>	KNM-WK 16950	Leakey <i>et al.</i> (1988a)
<i>E. africanus</i>	BM(NH) M.16649	Natural History Museum, London
<i>P. chirobates</i>	DPC 1087 DPC 1015 DPC 1108	Kay <i>et al.</i> (1981) Kay <i>et al.</i> (1981) Kay <i>et al.</i> (1981)
<i>A. zeuxis</i>	CGM 40237 DPC 1014 DPC 1109	Kay <i>et al.</i> (1981) Kay <i>et al.</i> (1981) Kay <i>et al.</i> (1981)
<i>M. pentelicus</i>	BM(NH) M.8947 BM(NH) M.8948 BM(NH) M.8945 BM(NH) M.8949	Natural History Museum, London Natural History Museum, London Natural History Museum, London Natural History Museum, London

All metric data were converted into ratios (Table 3.3) since this has the advantage of revealing changes in relative size, independent of changes in absolute size (Rae, 1993, 1997).

**CHARACTER 1:** Cusp heteromorphy on upper third premolar

This character measures the height of the protocone relative to the paracone on P<sup>3</sup>. Both the lingual height of the protocone and the buccal height of the paracone were measured from the cervix of the tooth to the tip of the cusp.

**CHARACTER 2:** Upper third premolar enlargement relative to first molar

This character measures the size of the upper third premolar relative to the first molar. Rather than relying on a single linear measurement (such as mesiodistal length) to yield the occlusal size of both P<sup>3</sup> and M<sup>1</sup>, the maximum mesiodistal length and buccolingual width were measured on both teeth to derive the occlusal area for each tooth.

**CHARACTER 3:** Upper third premolar enlargement relative to second molar

This character measures the size of the upper third premolar relative to the second molar. Again, maximum mesiodistal length and buccolingual width were measured on both teeth to derive the occlusal area of each tooth.

**CHARACTER 4:** Cusp heteromorphy on upper fourth premolar

This character measures the height of the protocone relative to the paracone on P<sup>4</sup>. Both the lingual height of the protocone and the buccal height of the paracone were measured from the cervix of the tooth to the tip of the cusp.

**CHARACTER 5:** Upper fourth premolar enlargement relative to first molar

This character measures the size of the upper fourth premolar in relation to the first molar. Both the maximum mesiodistal length and buccolingual width of P<sup>4</sup> and M<sup>1</sup> were measured to derive the occlusal area of each tooth.

### **CHARACTER 6:** Upper fourth premolar enlargement relative to second molar

This character measures the size of the upper fourth premolar relative to the second molar. Again, both the maximum mesiodistal length and buccolingual width of P<sup>4</sup> and M<sup>2</sup> were measured to derive the occlusal area of each tooth.

### **CHARACTER 7:** Upper fourth premolar/first molar crown module ratio

This character measures the size of the upper fourth premolar relative to the first molar using the crown modules calculated for each tooth (Andrews and Martin, 1987a). This character was included in the analysis because it serves to test the fit of the data using an alternative method of measuring the relative change in size of P<sup>4</sup> in relation to M<sup>1</sup> and hence, the results can be compared to those derived from Harrison and Rook's (1997) index for Character 5.

**Table 3.3 Character Description**

<b>Character</b>	<b>Description</b>	<b>Calculation</b>
1	cuspid heteromorphy on P <sup>3</sup>	height of protocone x 100/height of paracone
2	P <sup>3</sup> enlargement relative to M <sup>1</sup>	occlusal area of P <sup>3</sup> x 100/occlusal area of M <sup>1</sup>
3	P <sup>3</sup> enlargement relative to M <sup>2</sup>	occlusal area of P <sup>3</sup> x 100/occlusal area of M <sup>2</sup>
4	cuspid heteromorphy on P <sup>4</sup>	height of protocone x 100/height of paracone
5	P <sup>4</sup> enlargement relative to M <sup>1</sup>	occlusal area of P <sup>4</sup> x 100/occlusal area of M <sup>1</sup>
6	P <sup>4</sup> enlargement relative to M <sup>2</sup>	occlusal area of P <sup>4</sup> x 100/occlusal area of M <sup>2</sup>
7	P <sup>4</sup> /M <sup>1</sup> crown module ratio	$\frac{\text{length} + \text{breadth of P}^4/2}{\text{length} + \text{breadth of M}^1/2}$

## **METHODS**

### **STATISTICAL ANALYSIS**

Analysis of the quantitative data (univariate statistics, tests of significance, regression) was carried out using the statistical software package SPSS 10.0 for

Windows. Once the metric data were converted into ratios, analysis of variance (One-Way ANOVA) revealed that statistically significant differences existed among the seventeen taxon means for each character at an alpha level of  $p < 0.05$ . To determine which taxon means were statistically significantly different from one another at an alpha level of  $p < 0.05$ , two *post hoc* pairwise multiple comparisons tests were employed. Due to the heterogeneity of variances, the Games-Howell test that does not assume equal variances was used for characters 1, 2, 3, and 6, and Hochberg's GT2 test in which equal variances are assumed was used for characters 4, 5, and 7. Since the sample sizes for each taxon are unequal, Hochberg's GT2 test used an harmonic mean sample size of 7.965. The use of multiple comparisons to determine statistically significant differences among taxon means is preferred because "areas of overlap in statistical significance can occur" (Rae, 1998:225) which in turn, allows for intermediate character states.

The results of these statistical tests of significance are displayed as matrixes in which the means for groups of taxa in homogeneous subsets are revealed. These matrixes were thus used to identify discrete character states among the seven metric characters, and were subsequently coded using the homogeneous subset coding method of Simon (1983). In this method, homogeneous subsets are created through the comparison of all taxon means with one another; only taxa that are shown to be statistically significantly different from exactly the same taxa form an homogeneous subset and receive an identical code (Rae, 1998). If an overlap in statistical significance occurs such that two taxa that are not significantly different from each other receive different codes, it is hypothesized that "some change has occurred, although it may only be in the distribution of individual variates" (Rae, 1998:226). Due to small sample sizes, it was not

feasible to statistically analyze the fossil sample. Thus, fossil taxa were assigned the same codes as extant taxa whose mean values most closely approximated those of the fossils. This method is favoured over other coding procedures because it is based on groups that are statistically significantly different from one another (Simon, 1983).

All seven characters were treated as ordered (Rae, 1993, 1997; Slowinski, 1993). Ordering character states, such that a change to an adjacent character state is considered more likely than a change to the extremes of the range, is highly recommended for metric characters in which there is a discernable morphocline from small to medium to large (Rae, 1997; Slowinski, 1993).

## **PHYLOGENETIC ANALYSIS**

The Macintosh-based computer programme MacClade, version 3.01 (Maddison and Maddison, 1992) was employed in order to reconstruct ancestral nodes using the phylogenetic method of character optimization. The extant primate topology within which the seven metric characters were analyzed is taken from Fleagle (1999); this phylogeny is considered to be an accurate reflection of the currently known phylogenetic relationships among extant anthropoid taxa. This phylogeny recognizes the two superfamilies of the infraorder Catarrhini, with the Cercopithecoidea branching off before the Hominoidea. Within the Hominoidea, the dichotomy consisting of *Pan* and *Gorilla* with *Pongo* as the sister group to this clade, is also recognized. For the purpose of providing a comprehensive phylogenetic framework within which the fossil taxa could be analyzed, two families of the infraorder Platyrrhini were also included to function as a “phylogenetic lower boundary” in the analyses (Rae, 1993:171).

Rather than being a cladogram-finding programme such as PAUP (Swofford, 1993), MacClade focuses on the analysis of character evolution and allows the researcher to investigate alternative hypotheses under the same cladogram (Maddison and Maddison, 1987). Using parsimony algorithms, MacClade assigns character states to the branching points of the cladogram after first making a pass from the terminal branches to the root of the tree in what is termed the 'DownPass', and then reevaluates these designations in a pass from the root to the terminal branches of the tree in the 'UpPass' (Maddison and Maddison, 1987; Wiley *et al.*, 1991). Thus, the state estimated for a node combines information both from above and below the node. In tracing the evolution of a particular character, MacClade shades the branch of a tree the colour of the character state assigned to the terminal taxon of the branch, while the internodes assume the colour of the state reconstructed at the node directly above it; equivocal assignments result from the fact that more than one state could be placed at certain branches of the tree (Maddison and Maddison, 1992).

The algorithms of MacClade are "exact" in that they attempt to assign the most parsimonious character states for each node on the tree (Maddison and Maddison, 1987). The ordered parsimony algorithm of MacClade used in the present study to optimize the character distributions at the hypothetical ancestral nodes is based on the algorithm of Farris (1970), which was ultimately completed by Swofford and Maddison (1987), and treats character states as linearly ordered (Maddison and Maddison, 1987).

## CHAPTER 4

### RESULTS

#### EXTANT SAMPLE

#### STATISTICAL RESULTS

All seven characters were first tested for positive correlations (thus, a 1-tailed test was considered sufficient) with mean species (mixed sex) body masses (g) taken from Fleagle (1999). The mean species body weights were log transformed to base e (the LN function) to make the variation constant across all levels of the series, and then regressed against each character. None of the characters were shown to be statistically significantly positively correlated ( $p < 0.05$ ) with mean species body mass (Table 4.1). Thus, mean character values do not significantly increase as body mass increases.

T-tests for equality of means of males and females were also performed on Character 1 for all extant species included in the data set. The results of these tests failed to show significant differences ( $p < 0.05$ ) in cusp heteromorphy on  $P^3$  between males and females (Table 4.2).

**Table 4.1 Pearson Correlations for Character Means vs Ln Body Mass (g)**

Character	Pearson Correlation (r)	R square ( $r^2$ )	Significance (1-tailed)
1	-0.132	0.017	0.307
2	0.044	0.002	0.433
3	-0.107	0.011	0.342
4	0.067	0.005	0.399
5	-0.299	0.090	0.122
6	-0.278	0.077	0.140
7	-0.282	0.080	0.136

**Table 4.2 T-tests for Equality of Means of Males and Females (Character 1)**

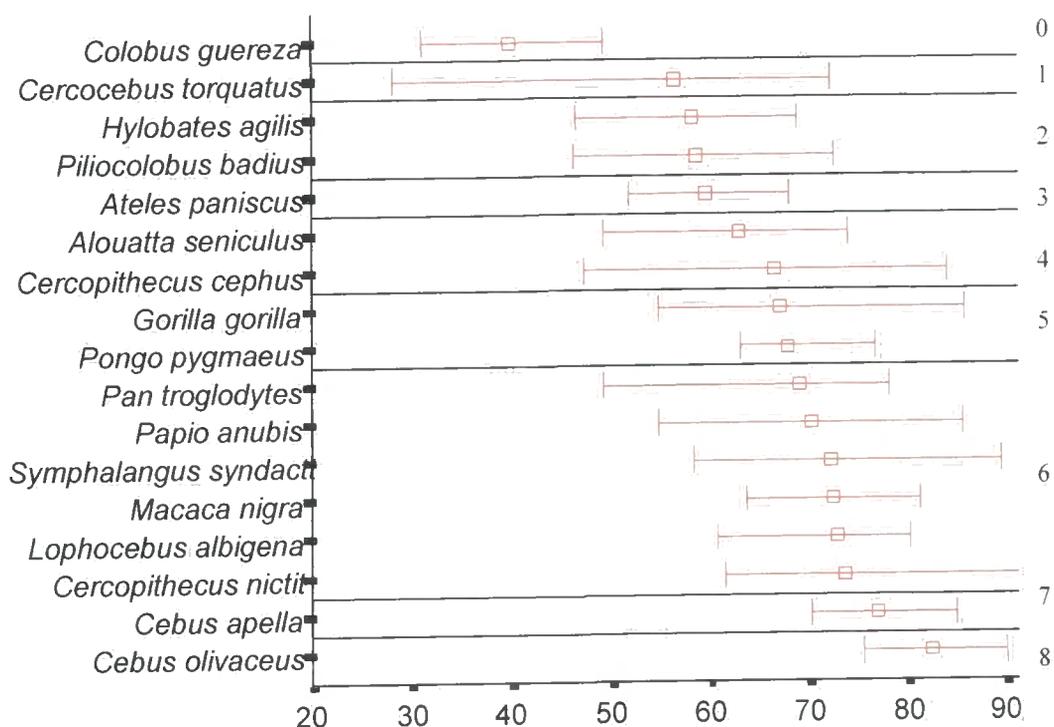
<b>Taxon</b>	<b>t</b>	<b>Sig. (2-tailed)</b>
<i>Hylobates agilis</i>	-1.864	0.105
<i>Symphalangus syndactylus</i>	0.314	0.769
<i>Pongo pygmaeus</i>	1.104	0.306
<i>Macaca nigra</i>	1.374	0.303
<i>Alouatta seniculus</i>	0.742	0.500
<i>Gorilla gorilla</i>	0.944	0.356
<i>Pan troglodytes</i>	1.324	0.202
<i>Colobus guereza</i>	1.330	0.220
<i>Ptilocolobus badius</i>	0.169	0.870
<i>Papio anubis</i>	1.134	0.294
<i>Lophocebus albigena</i>	-0.872	0.409
<i>Cercopithecus nictitans</i>	-0.715	0.495
<i>Cercopithecus cephus</i>	-0.837	0.427
<i>Cercocebus torquatus</i>	1.324	0.222
<i>Ateles paniscus</i>	0.860	0.453
<i>Cebus apella</i>	1.557	0.194
<i>Cebus olivaceus</i>	-1.230	0.286

The results of the univariate statistics performed for all seven characters are presented in Figures 4.1 - 4.7. These charts also delineate the groups of taxa found to be statistically significantly different from one another.

### **CHARACTER 1**

Both the lesser apes and great apes have previously been described as exhibiting a P<sup>3</sup> in which the protocone and paracone are more or less equal in height (Andrews, 1985, 1992). In contrast, Harrison (1987; Harrison and Rook, 1997) has maintained that *only* the great apes are defined by a P<sup>3</sup> in which the protocone is slightly less elevated than the paracone, and that the hylobatids and some cercopithecoids are characterized by a marked difference in height between both cusps. This assertion is rather curious in light of the fact that the data of Harrison and Rook (1997) show the mean value of the relative height of the cusps on P<sup>3</sup> for *Symphalangus syndactylus* (mean value is 67.0) to be virtually

## Cusp Heteromorphy on Upper Third Premolar



**Figure 4.1 Cusp heteromorphy on upper third premolar (Character 1).** This chart displays the change in height of the protocone relative to the paracone on P<sup>3</sup> across extant anthropoid taxa. Values that fall closer to the lower end of the scale indicate extreme cusp heteromorphy, while values that fall nearer to the upper end of the scale indicate cusps of more or less equal height. In this and all subsequent charts, the red box represents the mean value and the red line is the range of values for each taxon, bracketed by the lowest and highest values, respectively. The solid black lines divide the taxa into groups shown to be statistically significantly different from one another. The numbers to the right are the codes assigned to each homogeneous subset of taxa, for use in phylogenetic analysis.

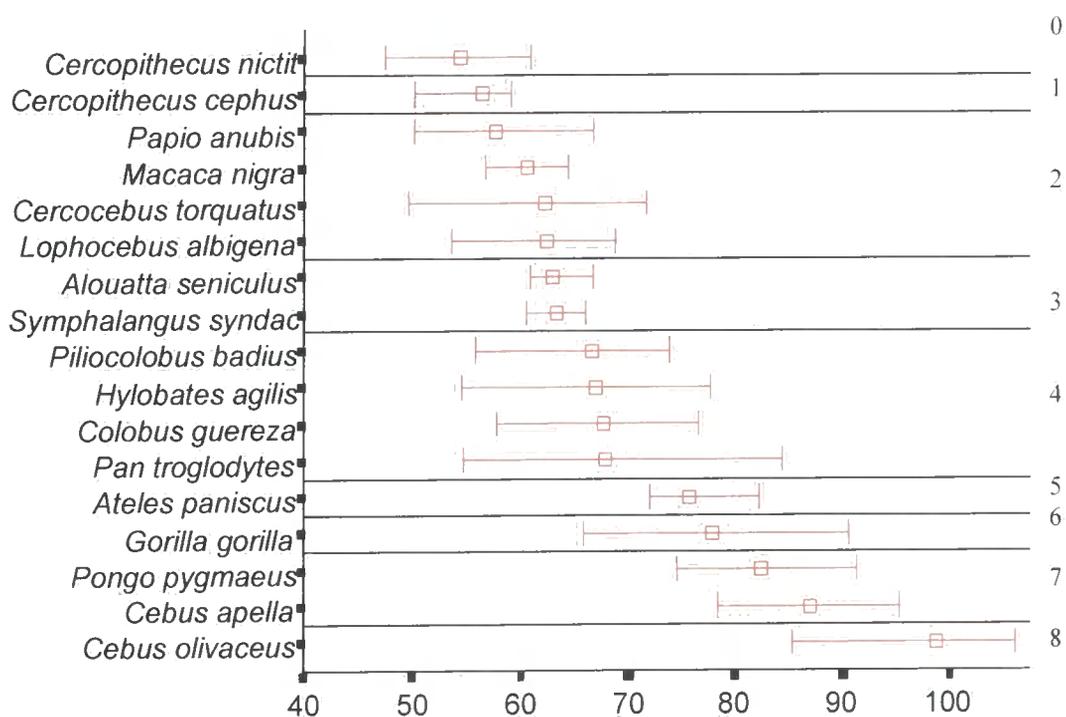
equivalent to that of *Pongo pygmaeus* (mean value is 67.4), and close to that of *Pan troglodytes* (mean value is 69.1).

Figure 4.1 shows that neither hypothesis is supported by the data. The species that exhibits the greatest reduction in upper third premolar cusp heteromorphy is *Cebus olivaceus*, along with *Cebus apella*. *Pan troglodytes* groups with four cercopithecoid taxa and the lesser ape *Symphalangus syndactylus*; all six taxa are characterized by a greater reduction in P<sup>3</sup> cusp heteromorphy than both *Pongo pygmaeus* and *Gorilla gorilla*. Interestingly, the means of the latter two taxa fall within the upper range of *Hylobates agilis*, but outside the ranges of both *Cebus olivaceus* and *Cebus apella*. The most extreme differential in height between the protocone and paracone is exhibited by *Colobus guereza*.

## **CHARACTER 2**

Extant great apes have previously been characterized by enlargement of the upper third premolar relative to the first molar (Andrews and Martin, 1987a; Andrews, 1992). The data displayed in Figure 4.2, however, do not support an hypothesis of relative upper third premolar enlargement as an hominid synapomorphy. Although *Gorilla gorilla* and *Pongo pygmaeus* exhibit relatively large P<sup>3</sup>s with mean values falling nearer to the upper end of the scale (mean values are 77.9 and 82.4, respectively), relative upper third premolar enlargement not only fails to group all three extant great ape taxa together, it is also shown not to be a trait exclusive to the extant hominids. In fact, *Cebus olivaceus* and *Cebus apella* exhibit the greatest enlargement of P<sup>3</sup> relative to M<sup>1</sup> across all seventeen taxa. While *Pongo pygmaeus* groups with *Cebus apella* at the top end of the scale, *Pan troglodytes* is shown to group with three other taxa including *Hylobates agilis* and two colobine taxa; all of which are shown to possess relatively small

## Upper Third Premolar Enlargement Relative to First Molar



**Figure 4.2 Upper third premolar enlargement relative to first molar (Character 2).** This chart displays the enlargement of the occlusal area of P<sup>3</sup> relative to the occlusal area of M<sup>1</sup> across extant anthropoid taxa. Values that fall closer to the lower end of the scale indicate a small P<sup>3</sup> relative to M<sup>1</sup>, while values that fall nearer to the upper end of the scale indicate upper third premolar enlargement relative to M<sup>1</sup>.

upper third premolars (mean values range from 66.9 for *Hylobates agilis* to 67.8 for *Pan troglodytes*). Species that exhibit the smallest P<sup>3</sup>s relative to M<sup>1</sup> include *Cercopithecus nictitans* and *Cercopithecus cephus*.

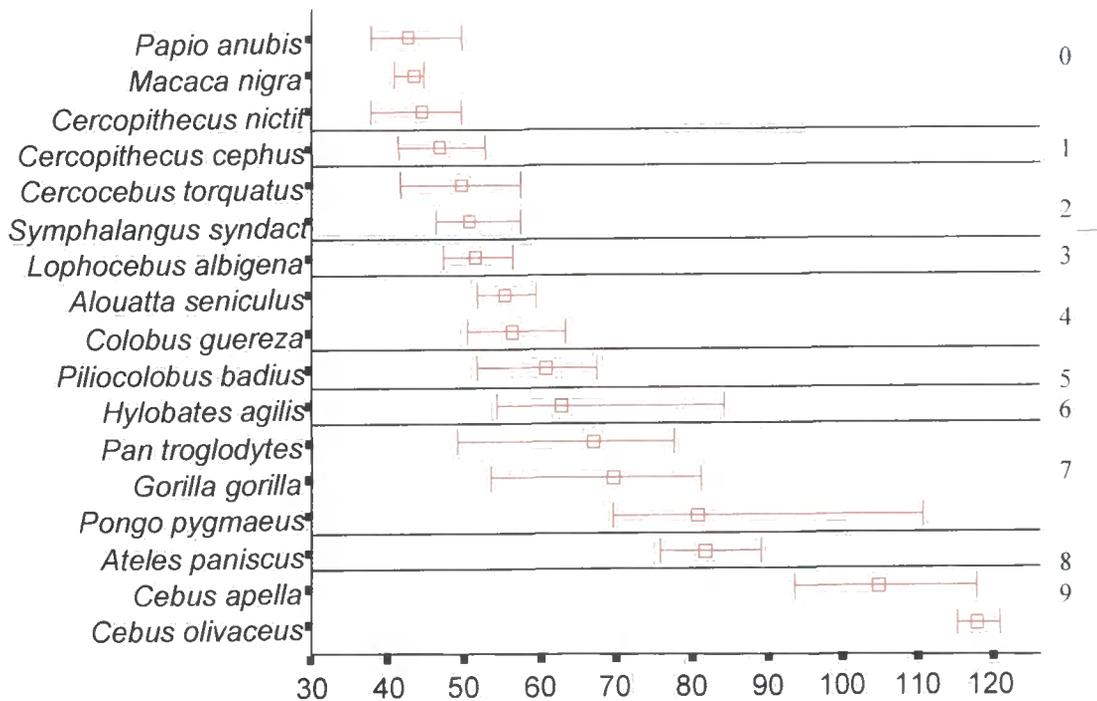
### **CHARACTER 3**

As with the previous character, extant great apes have been characterized by enlargement of the third premolar relative to the second molar, such that they can be readily distinguished from the hylobatids that exhibit “relatively much smaller premolars” (Harrison and Rook, 1997:348).

In contrast to the previous character, however, upper third premolar enlargement relative to the second molar groups the extant hominid taxa *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus* together. But like Character 2, Figure 4.3 shows relative enlargement of P<sup>3</sup> to be characteristic of other New and Old World Monkey taxa. In fact, the data indicate that other cebid (*Ateles paniscus*) and colobine (*Colobus guereza* and *Piliocolobus badius*) taxon means fall comfortably within the ranges of *Pongo pygmaeus*, and both *Pan troglodytes* and *Gorilla gorilla*, respectively. Once again, both New World Monkey taxa, *Cebus olivaceus* and *Cebus apella*, exhibit the greatest increase in relative upper third premolar size of all the seventeen taxa sampled, and interestingly, the mean of *Cebus apella* again fits within the range of *Pongo pygmaeus*.

Further, not only do the data show that *Hylobates agilis* exhibits relatively larger upper third premolars than all other cercopithecoids sampled in the present study but *contra* Harrison and Rook (1997), the size of P<sup>3</sup> in relation to M<sup>2</sup> of *Hylobates agilis* (mean value is 62.7) is similar to that of the extant hominids, especially *Pan troglodytes* (mean value is 67.1). It should be noted, however, that *Symphalangus syndactylus* exhibits relatively much smaller P<sup>3</sup>s, with a mean

## Upper Third Premolar Enlargement Relative to Second Molar



**Figure 4.3 Upper third premolar enlargement relative to second molar (Character 3).** This chart displays the enlargement of the occlusal area of P<sup>3</sup> relative to the occlusal area of M<sup>2</sup> across extant anthropoid taxa. Values that fall closer to the lower end of the scale indicate a small P<sup>3</sup> relative to M<sup>2</sup>, while values that fall nearer to the upper end of the scale indicate enlargement of the upper third premolar relative to M<sup>2</sup>.

value falling much closer to the lower end of the scale than any values given for the other living hominoids. Taxa that exhibit the smallest upper third premolars relative to  $M^2$  are *Papio anubis*, *Macaca nigra*, and *Cercopithecus nictitans*.

#### **CHARACTER 4**

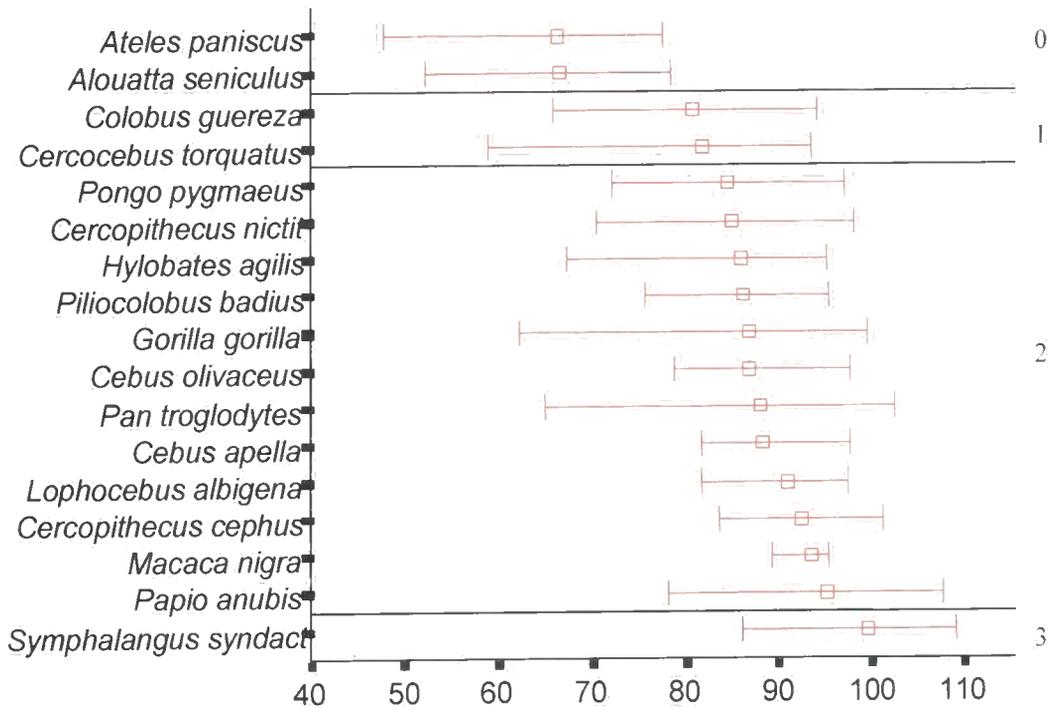
Reduction in cusp heteromorphy on the upper fourth premolar has variously been described as an hominoid synapomorphy (Andrews, 1985, 1992) or an hominid synapomorphy (Harrison, 1987; Harrison and Rook, 1997). Harrison and Rook (1997:348) argue that a reduction in cusp heteromorphy characterizes *only* the extant hominids since hylobatids “are more primitive in retaining a greater differential between the two cusps”. Curiously, as with  $P^3$  heteromorphy, this assertion is made despite the fact that their data reveal a mean value of the relative height of the cusps on  $P^4$  for *Symphalangus syndactylus* (mean value is 89.7) that is intermediate between *Pongo pygmaeus* (mean value is 87.6) and *Gorilla gorilla* (mean value is 91.5).

As with Character 1, a reduction in cusp heteromorphy on the upper fourth premolar fails to distinguish extant apes or great apes (Figure 4.4). In fact, the majority of taxon mean values fall between 80 and 95, grouping all three hominid taxa together with *Hylobates agilis*, two cebids, and six cercopithecoid taxa. Both *Ateles paniscus* and *Alouatta seniculus* exhibit the most pronounced cusp heteromorphy, while the lesser ape *Symphalangus syndactylus* possesses upper fourth premolars in which there is the greatest reduction in disparity between the height of the protocone and paracone of all seventeen anthropoid taxa examined.

#### **CHARACTER 5**

The data displayed in Figure 4.5 do not support the hypothesis of relative upper fourth premolar enlargement as a hominid synapomorphy, espoused by Andrews

## Cusp Heteromorphy on Upper Fourth Premolar



**Figure 4.4 Cusp heteromorphy on upper fourth premolar (Character 4).** This chart displays the change in height of the protocone relative to the paracone on  $P^4$  across extant anthropoid taxa. Values that fall closer to the lower end of the scale indicate extreme cusp heteromorphy, while values that fall nearer to the upper end of the scale indicate cusps of more or less equal height.

and Martin (1987a). In effect, the data do not distinguish any coherent extant anthropoid groups. Once again, New World Monkey taxa are shown to possess the largest upper premolars relative to  $M^1$ , with *Cebus olivaceus* exhibiting the greatest degree of relative upper fourth premolar enlargement. Unexpectedly, *Pan troglodytes* is shown to possess relatively very small upper fourth premolars, and *Gorilla gorilla* is shown to group with *Alouatta seniculus* near the middle of the range of mean values. Expectedly, however, the mean value of *Pongo pygmaeus* falls within the range of *Cebus apella*, towards the upper end of the scale.

*Hylobates agilis* exhibits the smallest upper fourth premolars relative to  $M^1$  of all seventeen taxa sampled.

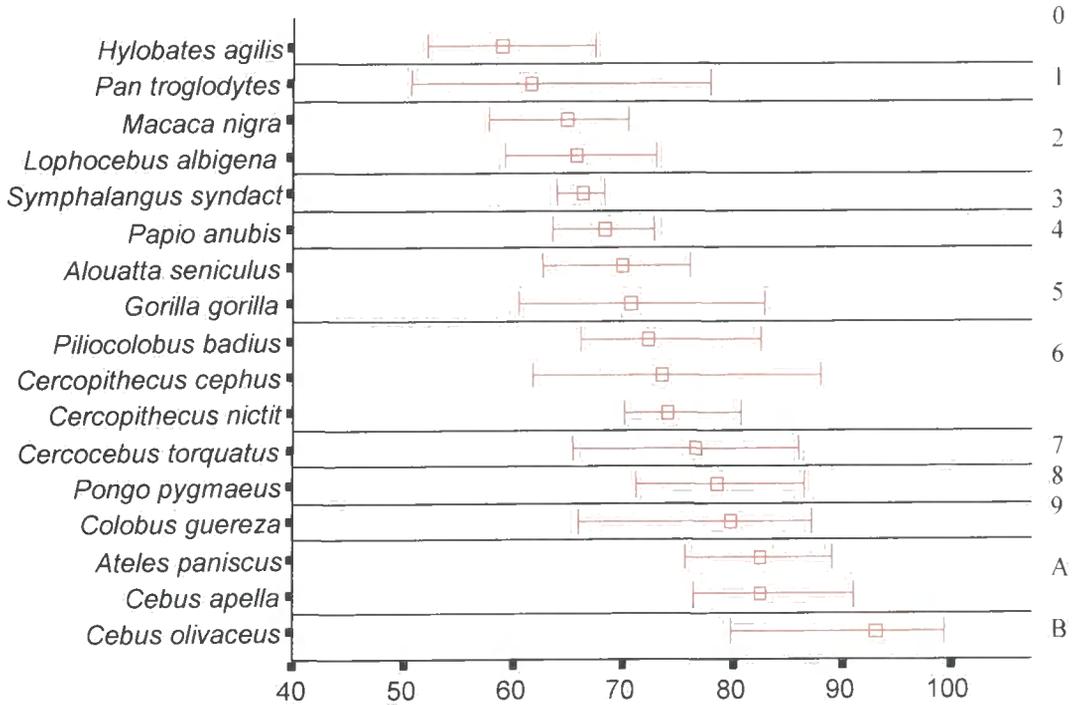
#### **CHARACTER 6**

Again, Figure 4.6 shows relative upper fourth premolar enlargement not to be an hominid synapomorphy as previously advanced by Harrison and Rook (1997). Although the lesser apes do exhibit relatively smaller upper fourth premolars in comparison with the great apes, this character cannot be shown to distinguish living hominids. As with characters 2, 3, and 5, *Cebus olivaceus* and *Cebus apella* exhibit the greatest degree of relative upper premolar enlargement of all seventeen taxa analyzed, and *Pongo pygmaeus* has the largest upper premolars relative to the molars of the extant hominids. *Pan troglodytes* groups with three other cercopithecoid taxa (*Cercopithecus nictitans*, *Cercopithecus cephus*, and *Cercocebus torquatus*) and one ateline (*Alouatta seniculus*), all of which are shown to possess relatively very small upper fourth premolars.

#### **CHARACTER 7**

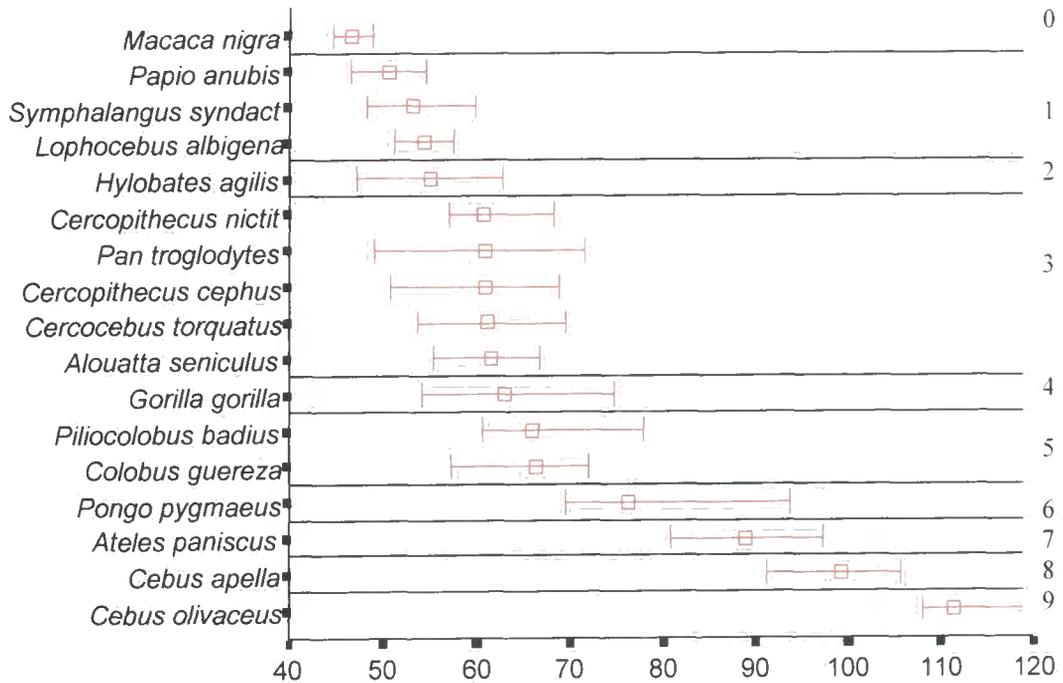
The data displayed in Figure 4.7 show that the method of measuring the relative change in size of  $P^4$  using Andrews and Martin's (1987a) crown module

## Upper Fourth Premolar Enlargement Relative to First Molar



**Figure 4.5** Upper fourth premolar enlargement relative to first molar (Character 5). This chart displays the change in size of the upper fourth premolar relative to the first molar. Values that fall closer to the lower range of the scale indicate a small upper fourth premolar relative to M<sup>1</sup>, while values that fall nearer to the upper end of the scale indicate relative upper fourth premolar enlargement.

## Upper Fourth Premolar Enlargement Relative to Second Molar

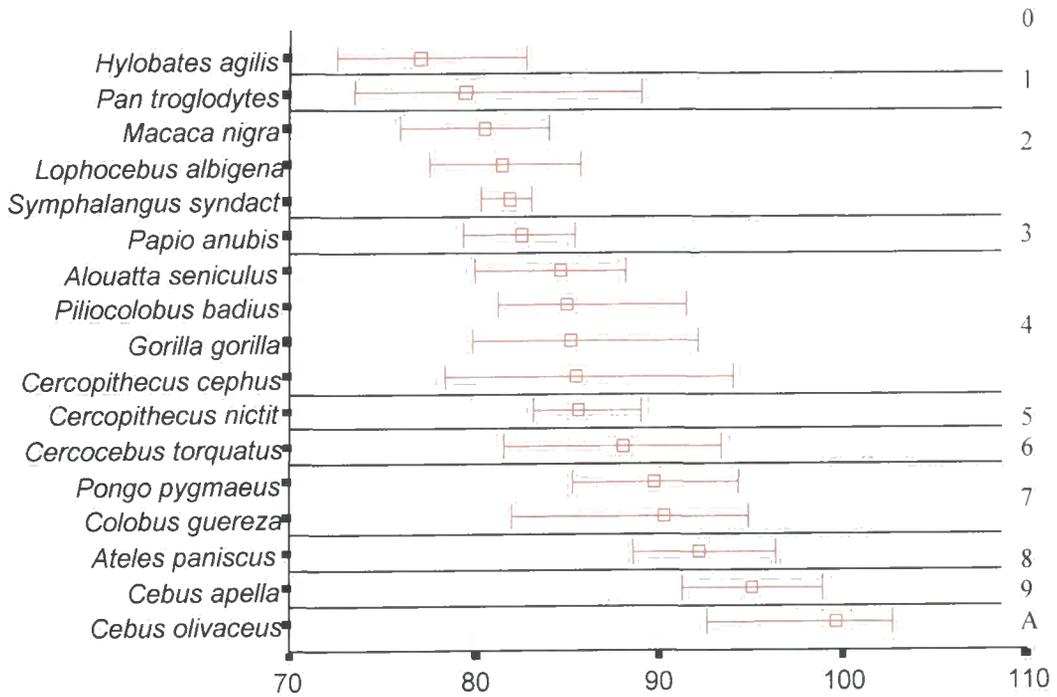


**Figure 4.6 Upper fourth premolar enlargement relative to second molar (Character 6).** This chart displays the change in size of the upper fourth premolar relative to the second molar. Values closer to the lower end of the scale indicate a small upper fourth premolar in relation to  $M^2$ , while values nearer to the upper end of the scale indicate relative upper fourth premolar enlargement.

ratio yields virtually the same results as those derived from Harrison and Rook's (1997) index for Character 5 (see Figure 4.5). The taxa are ranked almost identically, with only the positions of *Gorilla gorilla* and *Ptilocolobus badius* being reversed. The taxa are grouped slightly differently, however, and Character 7 includes one less character state than Character 5. *Gorilla gorilla* and *Alouatta seniculus* assume identical codes according to both Characters 5 and 7, but Character 5 separates *Pongo pygmaeus* and *Colobus guereza* whereas Character 7 groups them together. Another difference is seen in the grouping of the New World Monkey taxa *Ateles paniscus*, *Cebus apella*, and *Cebus olivaceus*; Character 7 codes all three species differently, whereas Character 5 groups *Ateles paniscus* with *Cebus apella*, and gives *Cebus olivaceus* a different code.

As with Character 5, Figure 4.7 shows relative enlargement of the upper fourth premolar not to be an hominid synapomorphy. In fact, not only does *Pongo pygmaeus* (which displays the greatest degree of relative P<sup>4</sup> enlargement of all three hominid taxa) group with *Colobus guereza*, the mean value of its P<sup>4</sup>/M<sup>1</sup> size ratio does not even fall within the upper range of *Pan troglodytes*. The latter taxon, together with *Hylobates agilis*, displays the smallest upper fourth premolars relative to M<sup>1</sup> of all taxa examined in this study.

## Upper Fourth Premolar/First Molar Crown Module Ratio



**Figure 4.7 Upper fourth premolar/first molar crown module ratio (Character 7).** This chart displays the change in size of the upper fourth premolar relative to the first molar, using the crown modules calculated for each tooth (length + breadth/2). Values that fall closer to the lower end of the scale indicate a small upper fourth premolar relative to M<sup>1</sup>, while values that fall nearer to the upper end of the scale indicate relative enlargement of P<sup>4</sup>.

## PHYLOGENETIC RESULTS

The results of converting the metric data into discrete codes for phylogenetic analysis using the homogeneous subset coding method of Simon (1983) are given in the data matrix of Table 4.3. The results of optimizing character distributions at the hypothetical ancestral nodes for each character using MacClade, version 3.01 (Maddison and Maddison, 1992) are displayed in Figures 4.8 - 4.11.

Character distributions show that the hypothesized synapomorphies of Andrews (1985, 1992; Andrews and Martin, 1987a) and Harrison (1987; Harrison and Rook, 1997) were found not to diagnose the groups of living taxa for which they were proposed. Of the seven characters tested, only upper third premolar enlargement relative to second molar (Character 3) was shown to diagnose extant great apes as a clade. This result, however, cannot be interpreted as a definite hominid synapomorphy due to the fact that the node representing the ancestral anthropoid condition (or the outgroup node) is shown to be ambiguous (Figure 4.9). Furthermore, none of the remaining characters tested in the present study can be interpreted as having a synapomorphous condition within the Hominoidea since the data present one of two results: 1) ambiguity at the outgroup node as well as at the base of the Hominoidea and/or the Cercopithecoidea (Characters 2, 5, and 6; Figures 4.8 and 4.10), or 2) retention of the plesiomorphic anthropoid or catarrhine condition at the base of the Hominoidea (Characters 1, 4, and 7; Figures 4.8, 4.9, and 4.11).

Most of the character distribution trees display a considerable amount of homoplasy as evidenced by the number of steps actually required for each character, in relation to the number of possible character state changes; Table 4.4

**Table 4.3 Data Matrix for Extant Anthropoids**

Taxon	Character						
	1	2	3	4	5	6	7
<i>Hylobates agilis</i>	2	4	6	2	0	2	0
<i>Symphalangus syndactylus</i>	6	3	2	3	3	1	2
<i>Pongo pygmaeus</i>	5	7	7	2	8	6	7
<i>Macaca nigra</i>	6	2	0	2	2	0	2
<i>Alouatta seniculus</i>	4	3	4	0	5	3	4
<i>Gorilla gorilla</i>	5	6	7	2	5	4	4
<i>Pan troglodytes</i>	6	4	7	2	1	3	1
<i>Colobus guereza</i>	0	4	4	1	9	5	7
<i>Ptilocolobus badius</i>	2	4	5	2	6	5	4
<i>Papio anubis</i>	6	2	0	2	4	1	3
<i>Lophocebus albigena</i>	6	2	3	2	2	1	2
<i>Cercopithecus nictitans</i>	6	0	0	2	6	3	5
<i>Cercopithecus cephus</i>	4	1	1	2	6	3	4
<i>Cercocebus torquatus</i>	1	2	2	1	7	3	6
<i>Ateles paniscus</i>	3	5	8	0	A	7	8
<i>Cebus apella</i>	7	7	9	2	A	8	9
<i>Cebus olivaceus</i>	8	8	9	2	B	9	A

Characters are as follows: 1) cusp heteromorphy on upper third premolar; 2) upper third premolar enlargement relative to first molar; 3) upper third premolar enlargement relative to second molar; 4) cusp heteromorphy on upper fourth premolar; 5) upper fourth premolar enlargement relative to first molar; 6) upper fourth premolar enlargement relative to second molar; and 7) upper fourth premolar/first molar crown module ratio.

gives the consistency indices (CI)<sup>7</sup> calculated for each character tree. All characters (except Character 4), exhibit a substantial degree of homoplasy among the taxa examined. For the most part, the great apes share a reduction in upper premolar cusp heteromorphy and relative enlargement of the upper premolars convergently with cercopithecines and, both platyrrhines and cercopithecoids, respectively. In Figure 4.8, the character state optimization of Character 1 (cusp heteromorphy on upper third premolar) shows that *Pan troglodytes* together with the lesser ape *Symphalangus syndactylus* share the condition in which the

<sup>7</sup> The consistency index (CI) is a ratio of the minimum amount of steps (or changes) on a particular tree and the amount of actual change or tree length (Wiley *et al.*, 1991).

paracone is only slightly more elevated than the protocone on P<sup>3</sup> convergently with four other species of cercopithecines. Interestingly, *Pan troglodytes* and *Symphalangus syndactylus* share the condition of a greater reduction in P<sup>3</sup> cusp heteromorphy to the exclusion of both *Gorilla gorilla* and *Pongo pygmaeus*. Character 1 also indicates that the cebids show the greatest reduction in P<sup>3</sup> cusp heteromorphy, while *Colobus guereza* possesses the greatest disparity in height between the protocone and paracone.

In contrast, the character state optimization of Character 4 (cusp heteromorphy on upper fourth premolar) shows virtually no homoplasy (Figure 4.9). All of the great apes together with most of the cercopithecoids and cebids, retain the plesiomorphic anthropoid condition in which the cusps of the upper fourth premolar are of more or less equal height. The atelines are unique among anthropoids in possessing upper fourth premolars with heteromorphic cusps.

**Table 4.4 Consistency Indices for Extant Character Trees**

Character	Consistency Index (1= no homoplasy)
1	0.35
2	0.50
3	0.38
4	0.60
5	0.31
6	0.41
7	0.33

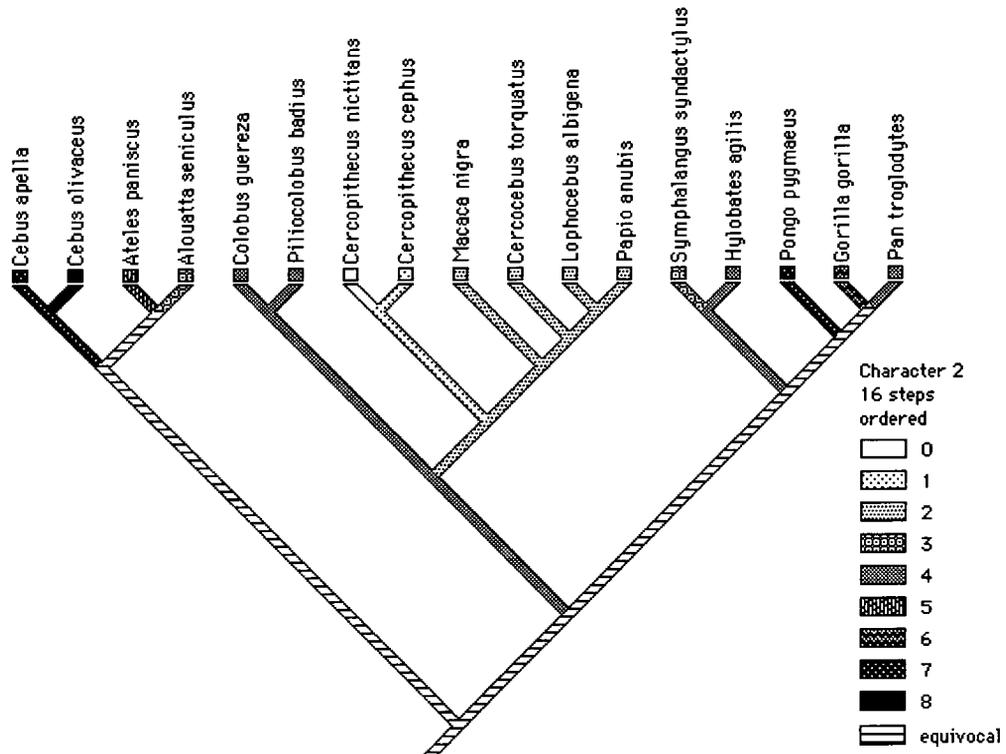
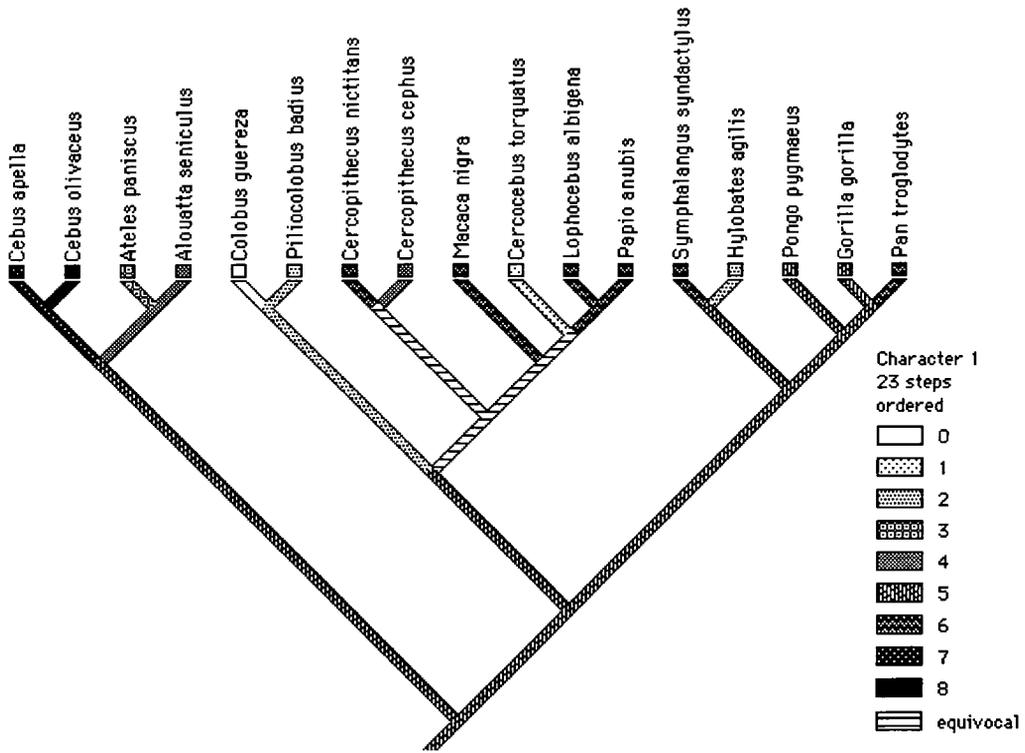
Characters 2, 5, 6, and 7 show relative enlargement of the upper premolars to be extremely homoplasious, evolving independently in several lineages. In Figure 4.8, the results suggest that both *Pongo pygmaeus* and *Cebus apella* evolved a greatly enlarged P<sup>3</sup> relative to M<sup>1</sup> convergently, while *Pan troglodytes* and *Hylobates agilis* independently share a relatively small P<sup>3</sup> with the colobines

(Character 2). In Figure 4.10, *Gorilla gorilla* is shown to share moderate enlargement of the upper fourth premolar relative to M<sup>1</sup> convergently with *Alouatta seniculus* (Character 5). The character state optimization of Character 7 (for which the change in relative size of P<sup>4</sup> was calculated using crown module ratios), also indicates that moderate enlargement of P<sup>4</sup> relative to M<sup>1</sup> arose independently in both *Gorilla gorilla* and *Alouatta seniculus* (Figure 4.11). The difference, however, is that Character 7 shows this character state also evolved independently in two additional lineages: one species of the Cercopithecinae (*Cercopithecus cephus*) and one species of the Colobinae (*Piliocolobus badius*). Furthermore, according to both characters, *Pongo pygmaeus* displays the greatest enlargement of P<sup>4</sup> relative to M<sup>1</sup> of all the extant great apes sampled. Only Character 7, however, shows that *Pongo pygmaeus* evolved this character state in parallel with *Colobus guereza*.

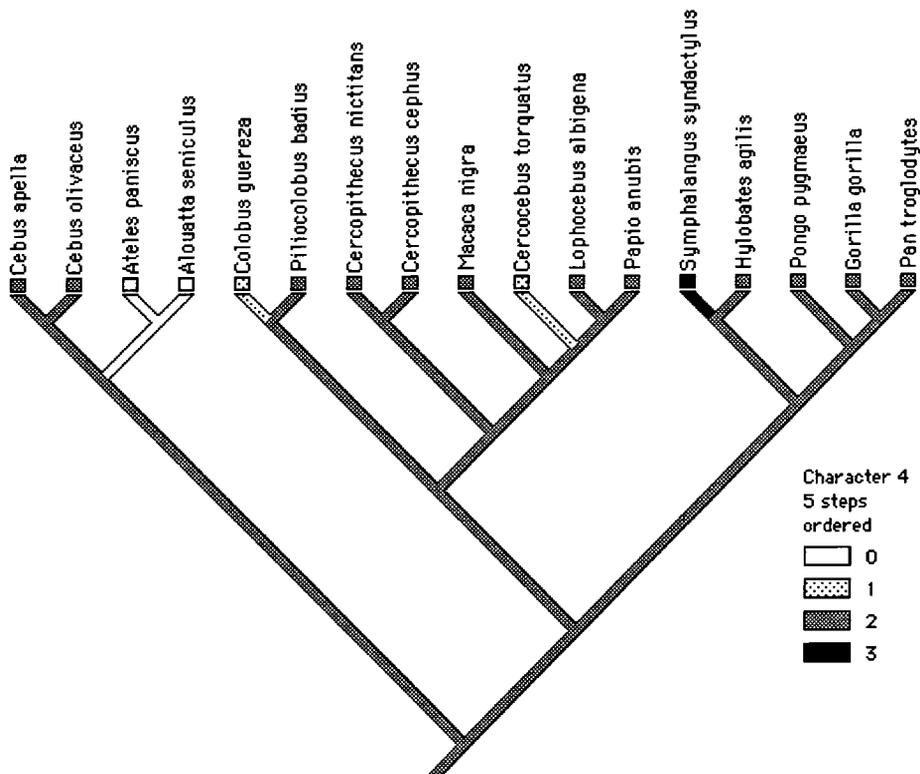
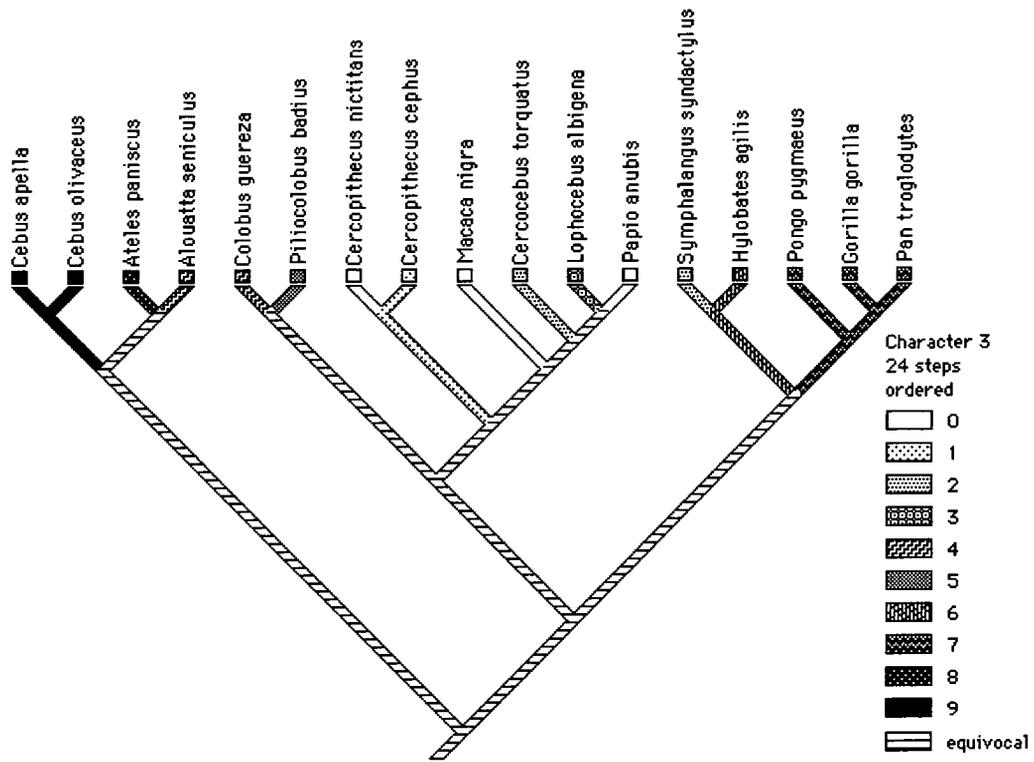
As with enlargement of the upper premolars relative to the first molar, Character 6 shows that moderate enlargement of P<sup>4</sup> relative to the second molar (Figure 4.10), evolved in several different lineages including: one species of the Hominidae (*Pan troglodytes*), three species of the Cercopithecinae (*Cercopithecus nictitans*, *Cercopithecus cephus*, and *Cercocebus torquatus*), and one species of the Atelinae (*Alouatta seniculus*). It is noteworthy that *Cebus olivaceus* and *Cebus apella* consistently yielded the greatest degree of enlargement of the upper premolars relative to both the first and second molars in all analyses.

It is clear, therefore, that the characters tested in the present study are uninformative phylogenetically due to the failure of most characters to reconstruct the hypothetical ancestral condition at the outgroup node and at the base of the Hominoidea and the Cercopithecoidea. Only one hominid synapomorphy (upper

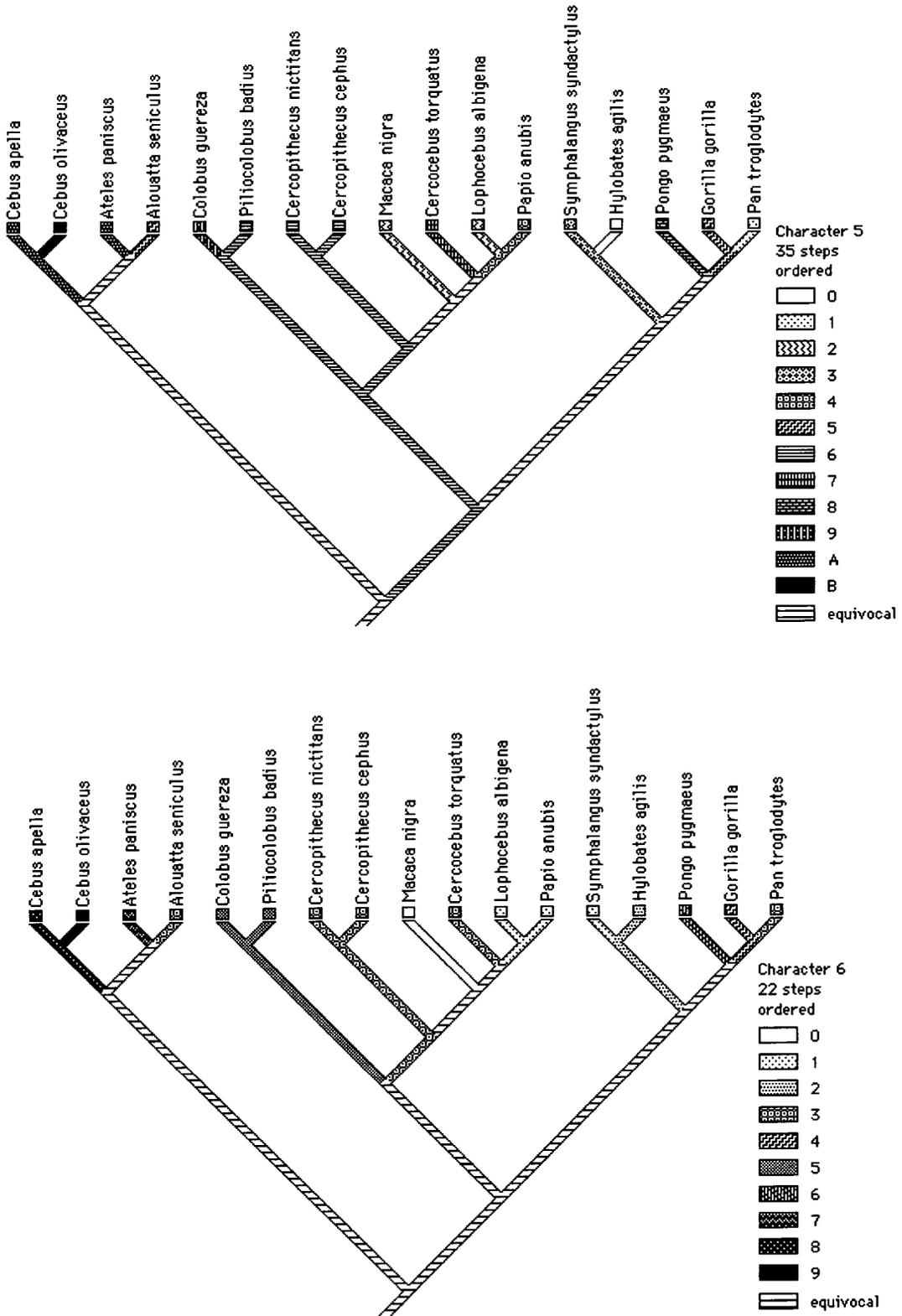
third premolar enlargement relative to second molar - Character 3) is supported by the data, and even as such, this result is tenuous due to ambiguity at the outgroup node.



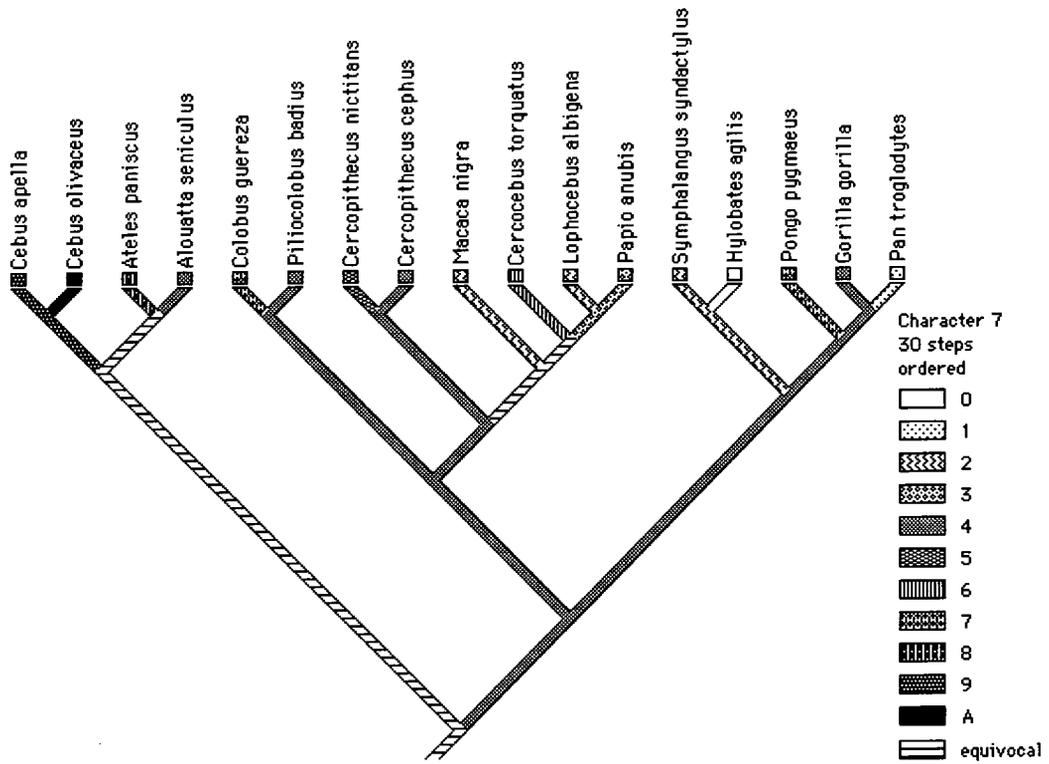
**Figure 4.8** Character distributions for Characters 1 and 2: cusp heteromorphy on upper third premolar (top) and upper third premolar enlargement relative to first molar (bottom).



**Figure 4.9** Character distributions for Characters 3 and 4: upper third premolar enlargement relative to second molar (top) and cusp heteromorphy on upper fourth premolar (bottom).



**Figure 4.10** Character distributions for Characters 5 and 6: upper fourth premolar enlargement relative to first molar (top) and upper fourth premolar enlargement relative to second molar (bottom).



**Figure 4.11** Character distribution for Character 7: upper fourth premolar/first molar crown module ratio.

## FOSSIL SAMPLE

### CHARACTER STATE ASSIGNMENT

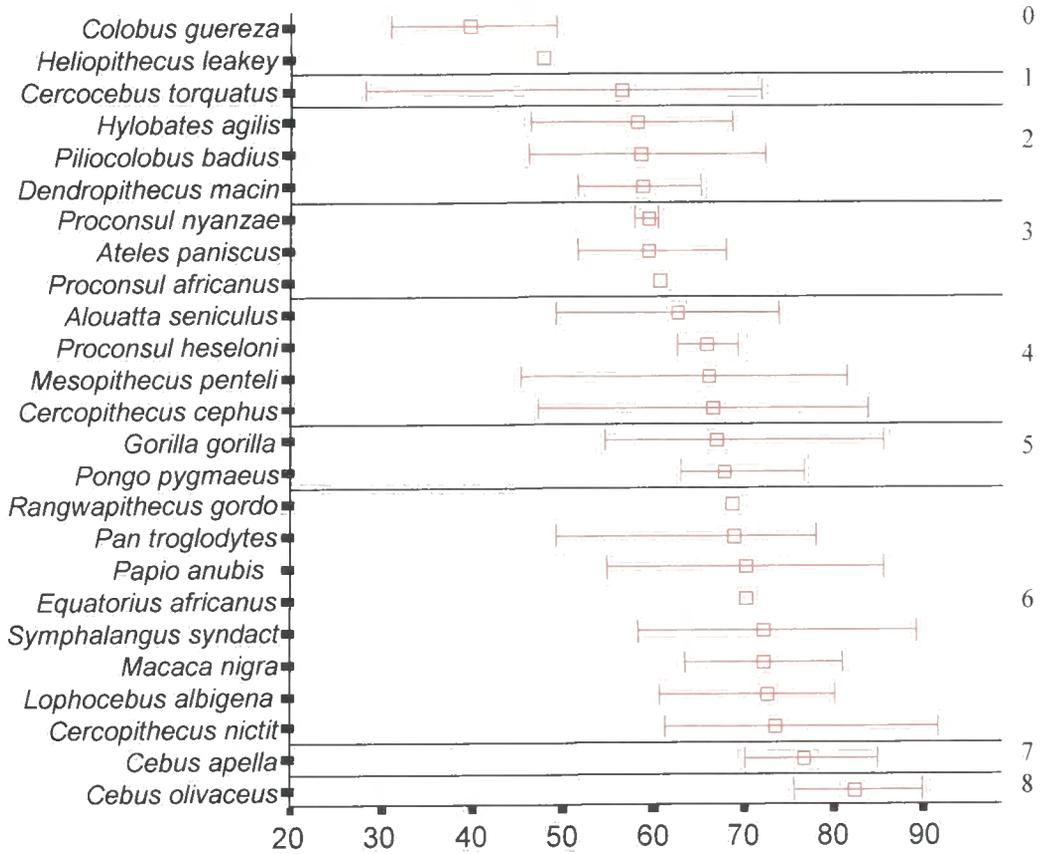
The comparison of mean values of the fossil taxa with extant distributions for all seven characters is presented in Figures 4.12 – 4.18. Following the presentation used in the previous section, these charts delineate groups of extant taxa shown to be statistically significantly different from one another; fossil taxa are grouped with extant taxa whose mean values most closely approximated those of the fossils.

### CHARACTER 1

*Proconsul* and the extant hominoids have previously been characterized by a reduction in cusp heteromorphy on the upper third premolar to the exclusion of *Dendropithecus*, in which the primitive catarrhine condition of cusp heteromorphy on P<sup>3</sup> is retained (Andrews, 1985). Harrison (1987:68) countered that not only does *Proconsul* and other fossil catarrhines such as *Dendropithecus* exhibit marked cusp heteromorphy on P<sup>3</sup>, this condition is “more pronounced than in any extant catarrhines, with the exception of the hylobatids and some cercopithecoids”.

Figure 4.12 shows that neither hypothesis is supported by the data. While *P. nyanzae*, *P. africanus*, and *P. heseloni* are all shown to possess P<sup>3</sup>s that are statistically significantly more cusp heteromorphic than those of the extant hominoids and the lesser ape *Symphalangus syndactylus*, the mean values of all three fossil taxa fall very comfortably within the ranges of *Gorilla gorilla* and *Pan troglodytes*. In fact, the condition of moderate cusp heteromorphy observed in *P. heseloni* (mean value is 65.9) very closely approximates the condition characterizing both *Gorilla gorilla* (mean value is 66.9) and *Pongo pygmaeus*

## Cusp Heteromorphy on Upper Third Premolar



**Figure 4.12 Cusp heteromorphy on upper third premolar (Character 1).** This chart displays the change in height of the protocone relative to the paracone on P<sup>3</sup> across extant and extinct anthropoid taxa. Values that fall closer to the lower end of the scale indicate extreme cusp heteromorphy, while values that fall nearer to the upper end of the scale indicate cusps of more or less equal height.

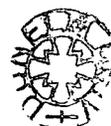
(mean value is 67.7). Furthermore, *Dendropithecus* shares with *Hylobates agilis* (and *Piliocolobus badius*) greater cusp heteromorphy on P<sup>3</sup> than that observed in *P. nyanzae*, *P. africanus*, *P. heseloni*, and the extant great apes.

The fossil species that displays the most extreme cusp heteromorphy is *Heliopithecus*, with a value (47.6) falling well below those given for all three species of *Proconsul*, *Dendropithecus*, and the living great apes, but within the range of *Colobus guereza*. Unexpectedly, the early Miocene catarrhine *Rangwapithecus* is shown to group with the middle Miocene hominoid *Equatorius* along with *Pan troglodytes*, *Symphalangus syndactylus*, and four cercopithecoid taxa; all eight taxa are shown to possess a P<sup>3</sup> in which the paracone is only slightly more elevated than the protocone.

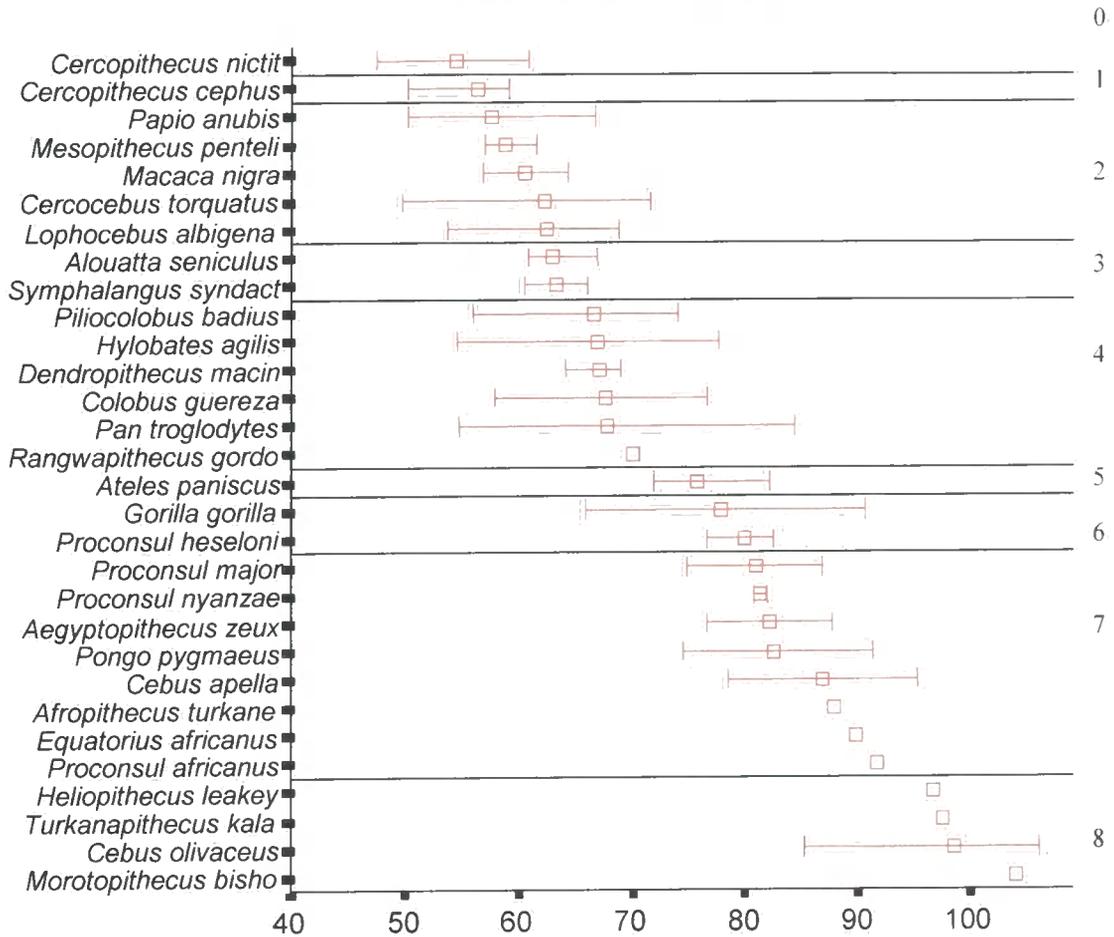
## CHARACTER 2

The fossil taxa *Afropithecus*, *Heliopithecus*, *Morotopithecus*, and *Equatorius* have previously been linked to the Hominidae through relative upper third premolar enlargement (Andrews and Martin, 1987a; Andrews, 1992). Specifically, Andrews and Martin (1987a) reported that *Afropithecus*, *Heliopithecus*, *Morotopithecus*, and *Equatorius* all exhibited a P<sup>3</sup> that was more similar in relative size to the extant African great apes than to *Pongo pygmaeus* and other Miocene hominoids, including *Proconsul*.

The data displayed in Figure 4.13 show relatively large upper third premolars not to be a trait linking *Afropithecus*, *Heliopithecus*, *Morotopithecus*, and *Equatorius* exclusively to the African great apes. Not only do the values given for *Afropithecus* and *Equatorius* fall within the *Pongo pygmaeus* range and outside of the *Pan troglodytes* range, the former two fossil taxa are also shown to group with three species of *Proconsul*: *P. major*, *P. nyanzae*, and *P. africanus*. This group



## Upper Third Premolar Enlargement Relative to First Molar



**Figure 4.13 Upper third premolar enlargement relative to first molar (Character 2).** This chart displays the enlargement of the occlusal area of P<sup>3</sup> relative to the occlusal area of M<sup>1</sup> across extant and extinct anthropoid taxa. Values that fall closer to the lower end of the scale indicate a small P<sup>3</sup> relative to M<sup>1</sup>, while values that fall nearer to the upper end of the scale indicate upper third premolar enlargement relative to M<sup>1</sup>.

(also unexpectedly including the stem catarrhine *Aegyptopithecus*) is characterized by relatively great enlargement of the upper third premolar, of which *P. africanus* displays the highest value (91.7). It is noteworthy that the mean values of all fossil taxa included in this group can be accommodated within the *Cebus apella* range.

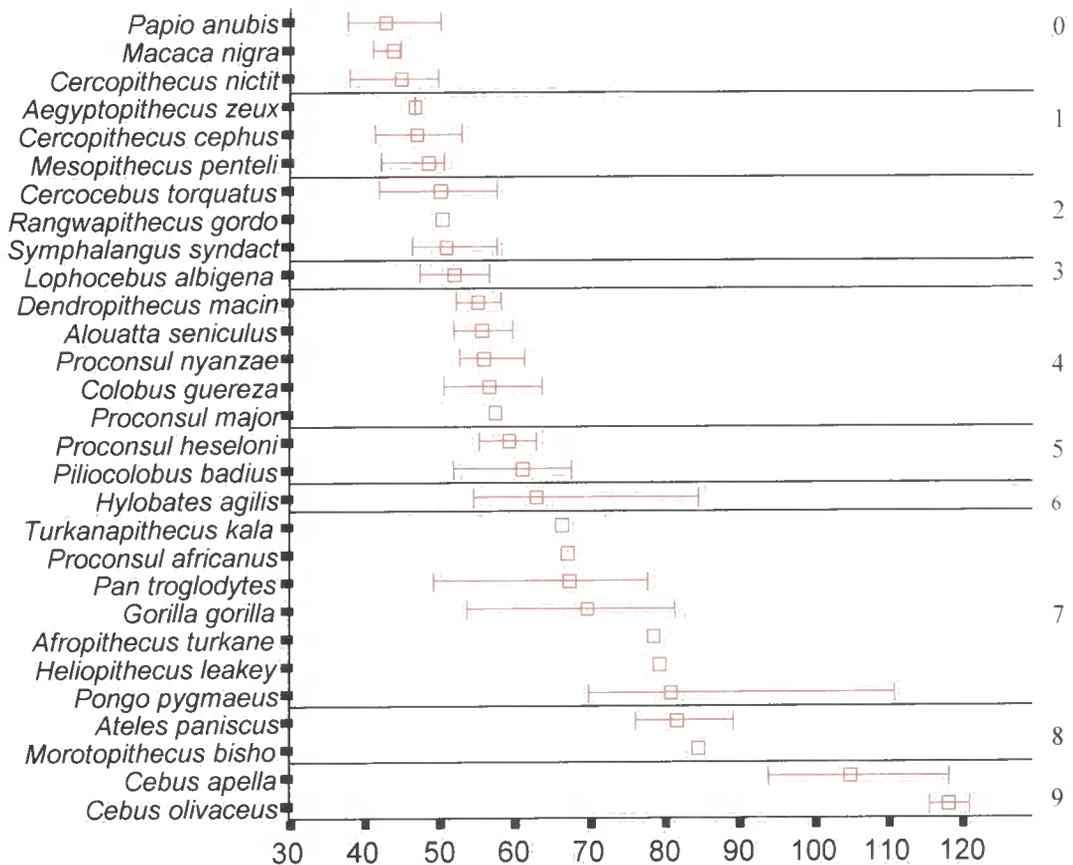
*Heliopithecus* and *Morotopithecus* are shown to be characterized by even more extreme enlargement of P<sup>3</sup> relative to M<sup>1</sup> than the former fossil taxa, and can be seen to group with *Cebus olivaceus* and *Turkanapithecus*. Interestingly, the values of both *Heliopithecus* and *Morotopithecus* (96.7 and 104.2, respectively) fall well beyond the upper limits of the ranges given not only for *Gorilla gorilla* and *Pan troglodytes*, but also for *Pongo pygmaeus*. Of the fossil taxa included within this group, *Morotopithecus* exhibits the most extreme relative enlargement of P<sup>3</sup>, with a value that does not even remotely approximate the upper limits of the ranges of all extant and extinct taxa examined in this study, except for that of *Cebus olivaceus*.

Another point of interest is seen in the grouping of *P. heseloni* with *Gorilla gorilla*, both of which are characterized by only moderate enlargement of P<sup>3</sup> relative to M<sup>1</sup>. Furthermore, *Dendropithecus* and *Rangwapithecus* group with *Pan troglodytes*, *Hylobates agilis*, and the two colobine taxa; all of which are clearly distinguished from the other fossil taxa examined in the present study by possessing relatively much smaller upper third premolars.

### **CHARACTER 3**

The proconsulids and hylobatids have previously been characterized by having relatively much smaller upper third premolars than the extant hominids, from which they can be readily distinguished (Harrison and Rook, 1997). The data

## Upper Third Premolar Enlargement Relative to Second Molar



**Figure 4.14** Upper third premolar enlargement relative to second molar (Character 3). This chart displays the enlargement of the occlusal area of P<sup>3</sup> relative to the occlusal area of M<sup>2</sup> across extant and extinct anthropoid taxa. Values that fall closer to the lower end of the scale indicate a small P<sup>3</sup> relative to M<sup>2</sup>, while values that fall nearer to the upper end of the scale indicate enlargement of the upper third premolar relative to M<sup>2</sup>.

displayed in Figure 4.14, however, show this not to be the case; the value of the relative size of P<sup>3</sup> given for *P. africanus* (66.9) is virtually identical to the mean value observed in *Pan troglodytes* (67.1), but less so than in *Gorilla gorilla* (69.5). This group also includes *Afropithecus*, *Heliopithecus*, and *Turkanapithecus*, and is characterized by great enlargement of P<sup>3</sup> relative to M<sup>2</sup>. The three other species of *Proconsul* are notably distinguished from *P. africanus* in that they exhibit only moderate enlargement of P<sup>3</sup>; mean values range from 55.6 for *P. nyanzae* to 58.9 for *P. heseloni*. Not only are these values substantially lower than the mean values calculated for all species of *Proconsul* for Character 2, the positions of all four fossil taxa seem to have shifted downwards from the upper end of the scale in Figure 4.13 towards the lower end of the scale in Figure 4.14, with the possible exception of *P. africanus*. The fossil taxon *Turkanapithecus* appears to make the most dramatic shift from the uppermost end of the scale (value is 97.5 for Character 2) to approximately mid-range of the scale (value is 66.1 for Character 3). This phenomenon appears to be a result of the fact that the upper second molar is the largest tooth in the molar series of many early Miocene hominoid taxa (including *Proconsul* spp., *Turkanapithecus*, and *Kamoyapithecus*), and hence, these taxa will exhibit a smaller ratio of premolar to molar occlusal area for Characters 3 and 6 when compared to Characters 2 and 5 (Begun, pers. comm.).

Of the fossil taxa sampled, *Aegyptopithecus* exhibits the smallest P<sup>3</sup>s relative to M<sup>2</sup>, grouping with *Cercopithecus cephus* and the Eurasian fossil colobine *Mesopithecus*. In addition, *Morotopithecus* again displays the greatest relative enlargement of P<sup>3</sup> of all the fossil taxa examined in this study. The difference, however, is that though the value calculated for Character 3 for *Morotopithecus* falls beyond the upper limits of the ranges of the African great apes, it is

accommodated within the *Pongo pygmaeus* range and falls short of both ranges given for *Cebus apella* and *Cebus olivaceus*.

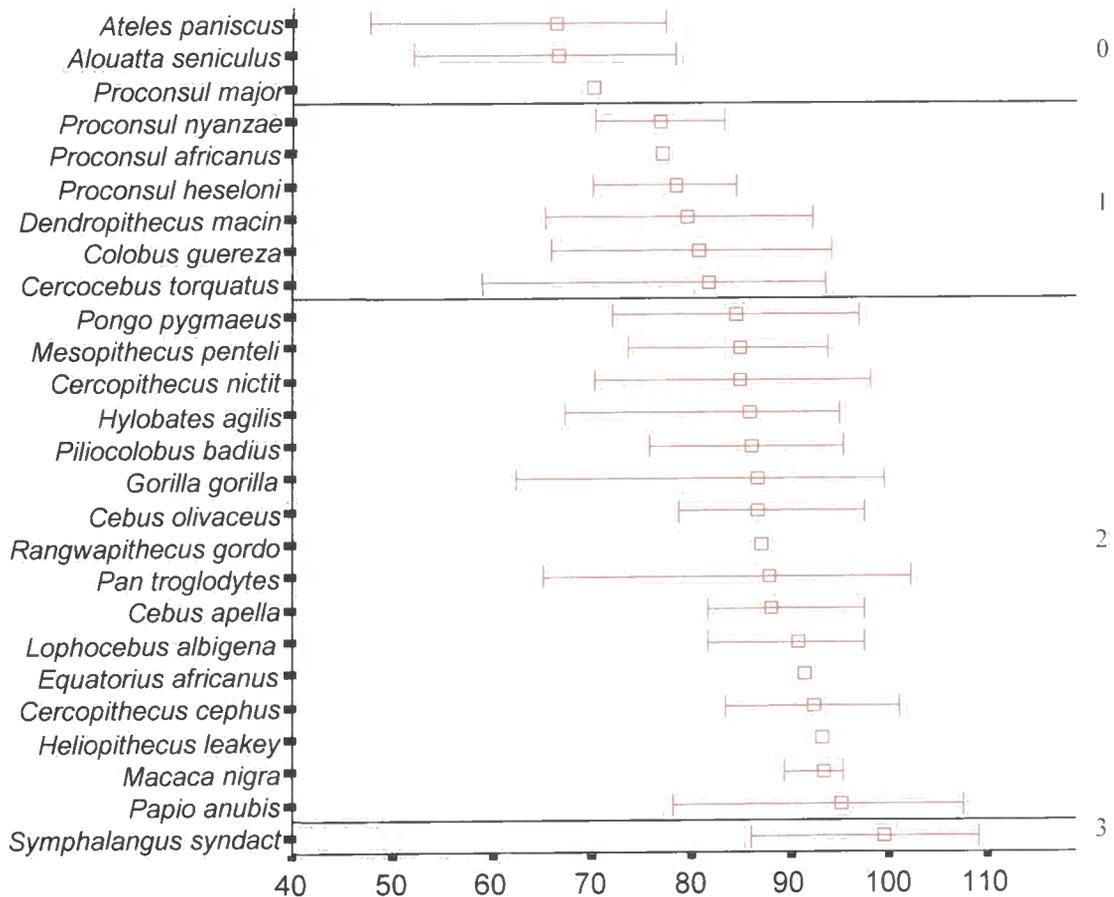
#### **CHARACTER 4**

As with Character 1, *Proconsul* has been characterized by a reduction in cusp heteromorphy on the upper fourth premolar to the exclusion of *Dendropithecus* (Andrews, 1985) or alternatively, by the retention of pronounced cusp heteromorphy on P<sup>4</sup>, that Harrison (1987) also considers to be characteristic of other fossil catarrhines. Figure 4.15 shows that neither hypothesis can be supported by the data. Although *P. nyanzae*, *P. africanus*, *P. heseloni*, and *Dendropithecus* exhibit moderately cusp heteromorphic P<sup>4</sup>s, the mean values of all four fossil taxa fall within the ranges of the extant great apes and *Hylobates agilis*. *P. major* is distinguished from the former four fossil taxa by possessing slightly more heteromorphic cusps on P<sup>4</sup>; a condition that it is seen to share with *Ateles paniscus* and *Alouatta seniculus*.

*Heliopithecus*, *Equatorius*, and *Rangwapithecus* share P<sup>4</sup>s in which the cusps are of more or less equal height with a wide range of extant anthropoid taxa including six species of cercopithecoids, two cebids, and the great apes. Mean values for this group range between 84.4 for *Pongo pygmaeus* to 95.2 for *Papio anubis*, within which values given for *Heliopithecus* and *Equatorius* fall towards the upper end of the range at 93.1 and 91.3, respectively. Interestingly and in stark contrast to Character 1, *Heliopithecus* exhibits the least amount of cusp heteromorphy on P<sup>4</sup> of all fossil taxa examined.

Thus, in contrast to Character 1, the data show that the majority of both fossil and extant taxa examined in the present study are characterized by upper fourth premolars in which the protocone and paracone are of more or less equal height.

## Cusp Heteromorphy on Upper Fourth Premolar



**Figure 4.15 Cusp heteromorphy on upper fourth premolar (Character 4).**

This chart displays the change in height of the protocone relative to the paracone on P<sup>4</sup> across extant and extinct anthropoid taxa. Values that fall closer to the lower end of the scale indicate extreme cusp heteromorphy, while values that fall nearer to the upper end of the scale indicate cusps of more or less equal height.

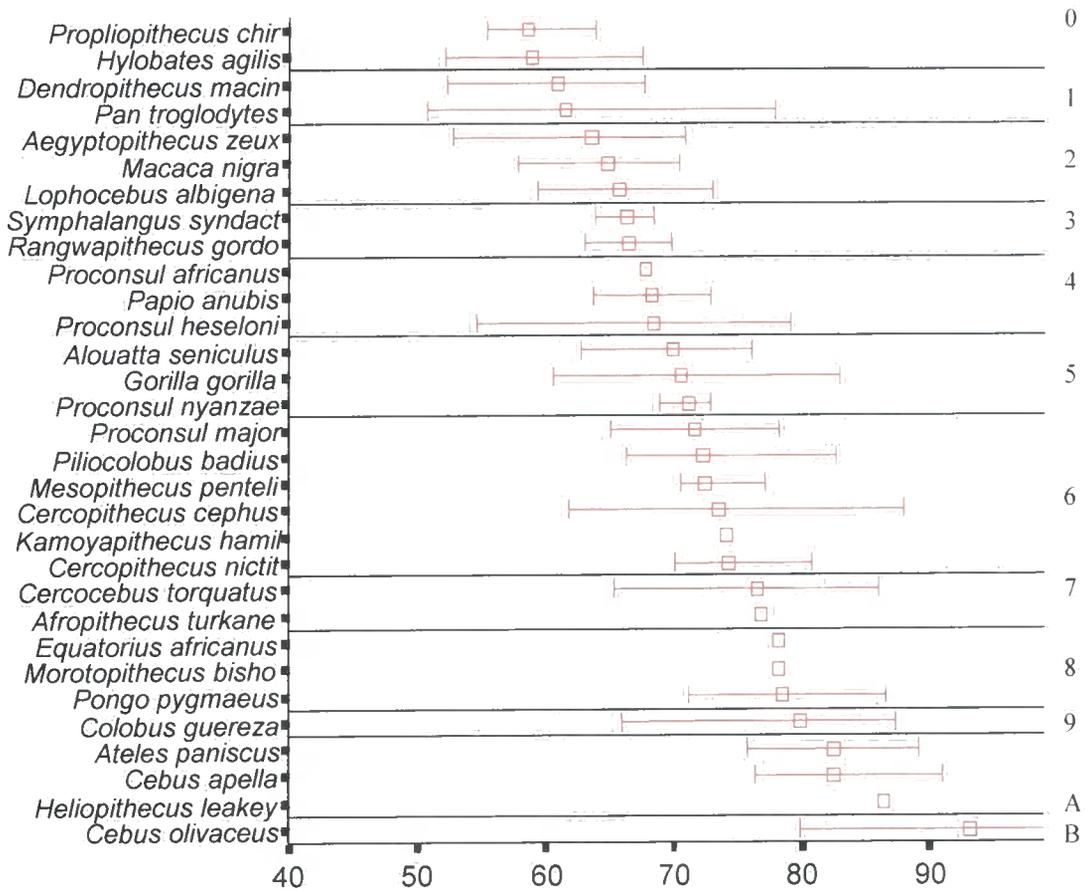
This is also apparent when the range of mean values are contrasted for both Characters 1 and 4; the lowest mean value given for Character 4 is 66.2, whereas the lowest value for Character 1 is given as 39.7. This indicates that Character 1 accommodates a disparity in height between the protocone and paracone on P<sup>3</sup> that is much more extreme than that contained within the range of Character 4. For Character 4, therefore, although fossil taxa such as *Proconsul* spp. and *Dendropithecus* are shown to exhibit more heteromorphic cusps on P<sup>4</sup> than the other seventeen taxa from which they can be distinguished, this distinction is slight.

### **CHARACTER 5**

Andrews and Martin (1987a) have argued that the fossil taxa *Afropithecus*, *Heliopithecus*, *Morotopithecus*, and *Equatorius* all share distinctive upper fourth premolar enlargement relative to the first molar that not only distinguishes them from extant great apes, but also from other Miocene hominoid genera including *Proconsul*. The data provided in Andrews and Martin's (1987a) study show that these four fossil taxa exhibit exceptionally large upper fourth premolars relative to M<sup>1</sup> such that they exceed all known extant and extinct hominoid size ranges.

The data collected for the present study (Figure 4.16), however, reveal quite a different scenario. *Heliopithecus* is the only taxon out of the four fossil hominoids identified by Andrews and Martin (1987a) that can be shown to exceed all known size ranges observed in both extant great apes and Miocene hominoids. In addition, the values given for *Equatorius* and *Morotopithecus* (78.1 and 78.2, respectively) are virtually identical to that of *Pongo pygmaeus* (mean value is 78.5). In fact, these values fall within the range of *Gorilla gorilla* and at the uppermost limits of the ranges given for *P. heseloni* and *P. major*, but outside the

## Upper Fourth Premolar Enlargement Relative to First Molar



**Figure 4.16 Upper fourth premolar enlargement relative to first molar (Character 5).** This chart displays the change in size of the upper fourth premolar relative to the first molar. Values that fall closer to the lower range of the scale indicate a small P<sup>4</sup> relative to M<sup>1</sup>, while values that fall nearer to the upper end of the scale indicate relative P<sup>4</sup> enlargement.

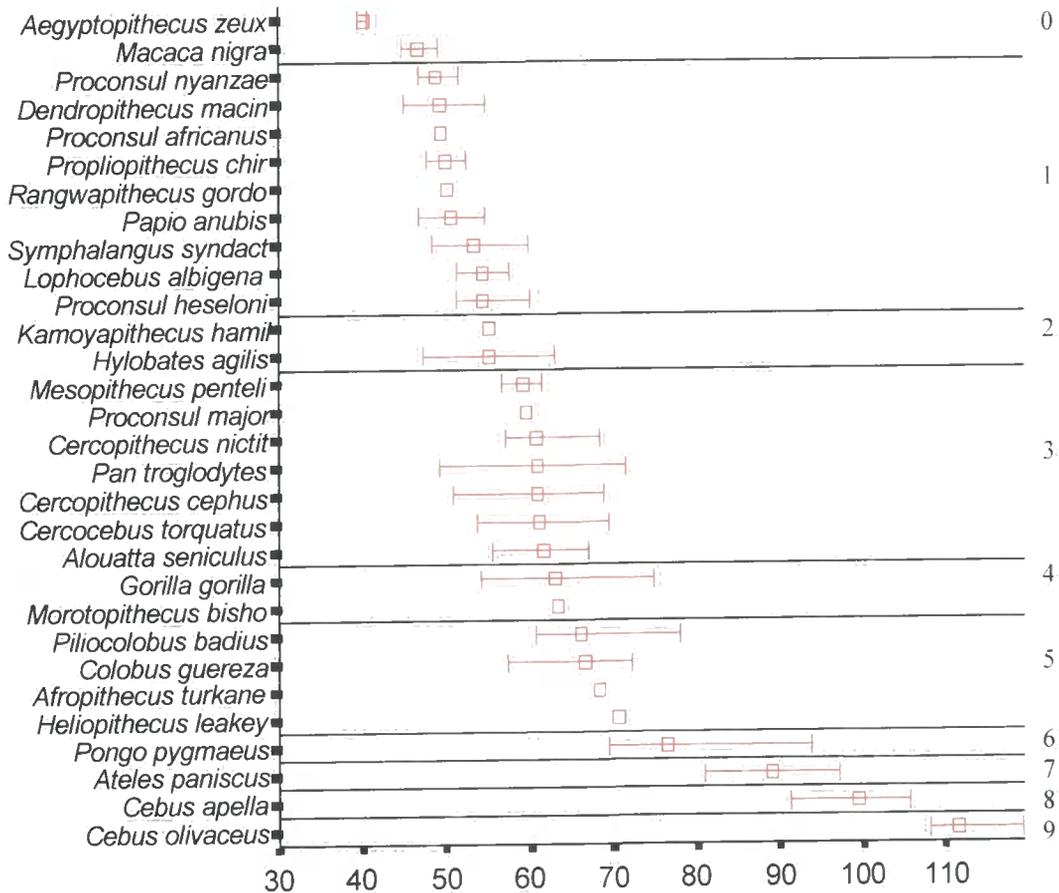
*Pan troglodytes* range. *Afropithecus*, on the other hand, is the only taxon out of the four fossil hominoids whose value falls within all three extant great ape taxon ranges, in addition to those of *P. heseloni* and *P. major*. *Afropithecus*, *Equatorius*, and *Morotopithecus* are all characterized by great enlargement of  $P^4$  relative to  $M^1$ , and *Heliopithecus* is distinguished from these taxa by even greater relative enlargement of  $P^4$ , which it shares with *Cebus apella* and *Ateles paniscus*.

The four species of *Proconsul* are characterized by moderate relative enlargement of  $P^4$ ; a condition that they also share in common with the late Oligocene hominoid *Kamoyapithecus*. Fossil taxa that are characterized by relatively small upper fourth premolars include *Propliopithecus*, *Dendropithecus*, *Aegyptopithecus*, and *Rangwapithecus*, of which *Propliopithecus* exhibits the smallest  $P^4$ s.

## **CHARACTER 6**

As with Character 3, Harrison and Rook (1997) have previously characterized the proconsulids and hylobatids as having much smaller upper fourth premolars (in relation to the second molars) than extant hominids. Figure 4.17 shows that this is not the case, as many proconsulid mean values (including those of *P. major*, *P. heseloni*, *Kamoyapithecus*, *Morotopithecus*, *Afropithecus*, and *Heliopithecus*) fall within the ranges of *Gorilla gorilla* and *Pan troglodytes*. Furthermore, by virtue of the fact that many early Miocene hominoid taxa possess larger upper second molars than first molars, this appears to have the effect of artificially deflating the ratio of premolar to molar occlusal area calculated for the upper second molar. Thus, in contrast to Character 5, the value of the ratio of  $P^4/M^2$  calculated for *Heliopithecus* positions this fossil taxon above extant taxa with which it had previously been grouped (such as *Cebus apella* and *Ateles*

## Upper Fourth Premolar Enlargement Relative to Second Molar



**Figure 4.17 Upper fourth premolar enlargement relative to second molar (Character 6).** This chart displays the change in size of the upper fourth premolar relative to the second molar. Values closer to the lower end of the scale indicate a small P<sup>4</sup> in relation to M<sup>2</sup>, while values nearer to the upper end of the scale indicate relative P<sup>4</sup> enlargement.

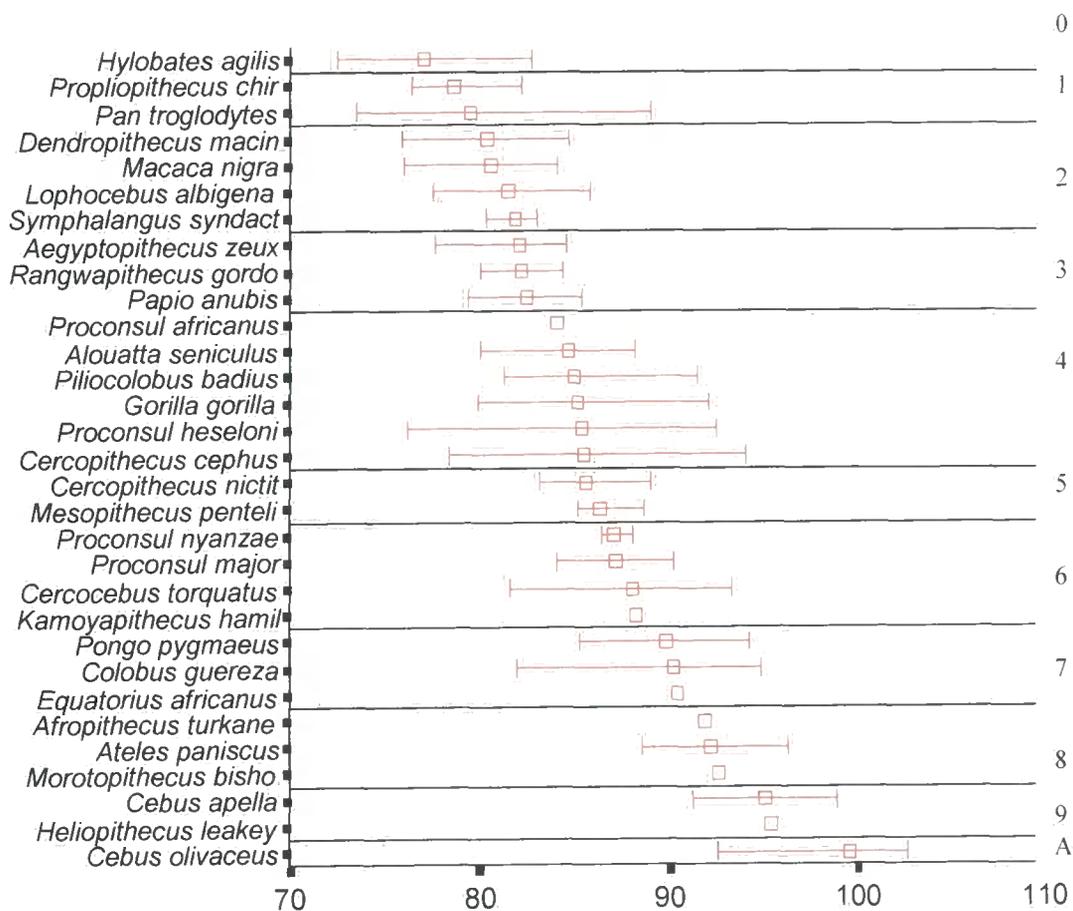
*paniscus*) or from which it had previously been distinguished by exhibiting relatively much larger  $P^4$ s in relation to  $M^1$  (such as *Pongo pygmaeus*). Despite the effect of this phenomenon, however, *Heliopithecus* again displays the greatest relative enlargement of  $P^4$  of all fossil taxa examined in this study. Another point of interest is the fact that *Heliopithecus* is the only fossil taxon examined whose value falls within the *Pongo pygmaeus* range; *Pongo pygmaeus* exhibits the greatest relative enlargement of  $P^4$  of all the living great apes sampled.

This phenomenon is also apparent in *Kamoyapithecus* and *Proconsul* spp.; *P. africanus*, *P. nyanzae*, and *Kamoyapithecus* are all shown to possess relatively much smaller upper fourth premolars in relation to  $M^2$  than the African great apes, when compared to the results calculated for Character 5 (see Figure 4.16). Similar to the results presented in Figure 4.16, the fossil taxa *Aegyptopithecus*, *Dendropithecus*, and *Propliopithecus* exhibit relatively very small upper fourth premolars, of which *Aegyptopithecus* possesses the smallest  $P^4$ s in relation to  $M^2$ .

#### **CHARACTER 7**

Using Andrews and Martin's (1987a) crown module ratio to calculate the relative change in size of  $P^4$  in relation to  $M^1$  again yields virtually the same results as those derived from Harrison and Rook's (1997) index for Character 5 (Figure 4.18). Furthermore, the  $P^4/M^1$  crown module ratios calculated for *Afropithecus*, *Morotopithecus*, and *Equatorius* have failed to distinguish these fossil taxa from the extant great apes and other Miocene hominoid genera, as advanced by Andrews and Martin (1987a). Like Character 5, only *Heliopithecus* is distinguished from the extant great apes and all fossil taxa examined in the present study by greatly enlarged  $P^4$ s relative to  $M^1$ ; a condition that it is also seen to share with *Cebus apella*.

## Upper Fourth Premolar/First Molar Crown Module Ratio



**Figure 4.18** Upper fourth premolar/first molar crown module ratio (Character 7). This chart displays the change in size of the upper fourth premolar relative to the first molar, using the crown modules calculated for each tooth (length + width/2). Values that fall closer to the lower end of the scale indicate a small P<sup>4</sup> relative to M<sup>1</sup>, while values that fall nearer to the upper end of the scale indicate relative enlargement of P<sup>4</sup>.

The values of both *Afropithecus* and *Equatorius* (91.8 and 90.4, respectively) fall within the ranges of *Gorilla gorilla* and *Pongo pygmaeus*, but outside the *Pan troglodytes* range. Unlike Character 5, however, *Morotopithecus* is shown to group with *Afropithecus* and its value just falls short of the uppermost limit of the *Gorilla gorilla* range. But like Character 5, the mean values of all four species of *Proconsul* fall within the ranges of *Pan troglodytes* and *Gorilla gorilla*, towards mid-range of the scale; *Proconsul* spp. is again characterized by moderate enlargement of P<sup>4</sup> relative to M<sup>1</sup>.

## PHYLOGENETIC RESULTS

Table 4.5 presents the results of converting the extant metric data into discrete codes for phylogenetic analysis using the homogeneous subset coding method of Simon (1983); fossil taxa are assigned the same codes as extant taxa whose mean values most closely approximated those of the fossils. The results of reconstructing the character distributions at the hypothetical ancestral nodes for each character using MacClade, version 3.01 (Maddison and Maddison, 1992) are displayed in Figures 4.19 - 4.33.

### UPPER PREMOLAR CUSP HETEROMORPHY

#### Upper Third Premolar

A reduction in cusp heteromorphy on P<sup>3</sup> cannot be interpreted as a definite hominoid synapomorphy (Andrews, 1985, 1992) due to ambiguity at the hypothetical ancestral hominoid node (Figure 4.19a,b). The character state optimization of Character 1 using Andrews's (1985) topology<sup>8</sup> reconstructs the ancestral catarrhine morphotype as being characterized by upper third premolars in which the paracone is higher than the protocone. *Contra* Andrews (1985), however, *Proconsul* spp. does not share the 'derived' condition of a reduction in cusp heteromorphy with the extant hominoids. In fact, according to this topology, *P. heseloni* retains the ancestral anthropoid/catarrhine condition of relatively cusp heteromorphic P<sup>3</sup>s, which it shares convergently with the fossil cercopithecoid taxon *Mesopithecus*, and two extant anthropoid taxa (*Cercopithecus cephus* and *Alouatta seniculus*). Furthermore, both *P. africanus* and *P. nyanzae* exhibit even greater cusp heteromorphy than *P. heseloni*, and they are seen to share this

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<sup>8</sup> It should be noted that *Heliopithecus* was not named at this time and therefore, not included in Andrews's (1985) study.

**Table 4.5 Data Matrix for Extant and Extinct Anthropoids**

Taxon	Character						
	1	2	3	4	5	6	7
<i>Hylobates agilis</i>	2	4	6	2	0	2	0
<i>Symphalangus syndactylus</i>	6	3	2	3	3	1	2
<i>Pongo pygmaeus</i>	5	7	7	2	8	6	7
<i>Macaca nigra</i>	6	2	0	2	2	0	2
<i>Alouatta seniculus</i>	4	3	4	0	5	3	4
<i>Gorilla gorilla</i>	5	6	7	2	5	4	4
<i>Pan troglodytes</i>	6	4	7	2	1	3	1
<i>Colobus guereza</i>	0	4	4	1	9	5	7
<i>Ptilocolobus badius</i>	2	4	5	2	6	5	4
<i>Papio anubis</i>	6	2	0	2	4	1	3
<i>Lophocebus albigena</i>	6	2	3	2	2	1	2
<i>Cercopithecus nictitans</i>	6	0	0	2	6	3	5
<i>Cercopithecus cephus</i>	4	1	1	2	6	3	4
<i>Cercocebus torquatus</i>	1	2	2	1	7	3	6
<i>Ateles paniscus</i>	3	5	8	0	A	7	8
<i>Cebus apella</i>	7	7	9	2	A	8	9
<i>Cebus olivaceus</i>	8	8	9	2	B	9	A
<i>Propithecus chirobates</i>	?	?	?	?	0	1	1
<i>Aegyptopithecus zeuxis</i>	?	7	1	?	2	0	3
<i>Proconsul africanus</i>	3	7	7	1	4	1	4
<i>Proconsul heseloni</i>	4	6	5	1	4	1	4
<i>Proconsul nyanzae</i>	3	7	4	1	5	1	6
<i>Proconsul major</i>	?	7	4	0	6	3	6
<i>Kamoyapithecus hamiltoni</i>	?	?	?	?	6	2	6
<i>Afropithecus turkanensis</i>	?	7	7	?	7	5	8
<i>Heliopithecus leakeyi</i>	0	8	7	2	A	5	9
<i>Morotopithecus bishopi</i>	?	8	8	?	8	4	8
<i>Turkanapithecus kalakolensis</i>	?	8	7	?	?	?	?
<i>Equatorius africanus</i>	6	7	?	2	8	?	7
<i>Mesopithecus pentelicus</i>	4	2	1	2	6	3	5
<i>Dendropithecus macinnesi</i>	2	4	4	1	1	1	2
<i>Rangwapithecus gordonii</i>	6	4	2	2	3	1	3

Characters are as follows: 1) cusp heteromorphy on upper third premolar; 2) upper third premolar enlargement relative to first molar; 3) upper third premolar enlargement relative to second molar; 4) cusp heteromorphy on upper fourth premolar; 5) upper fourth premolar enlargement relative to first molar; 6) upper fourth premolar enlargement relative to second molar; and 7) upper fourth premolar/first molar crown module ratio.

condition convergently with *Ateles paniscus*. Of the Proconsulidae, therefore, only *Rangwapithecus* is shown to share a relative reduction in cusp heteromorphy

on P<sup>3</sup> with living and fossil hominoids that include *Pan troglodytes*, *Symphalangus syndactylus*, and *Equatorius*. This character state, however, is also seen to have arisen independently in four additional species of extant cercopithecids including *Cercopithecus nictitans*, *Macaca nigra*, *Lophocebus albigena*, and *Papio anubis*.

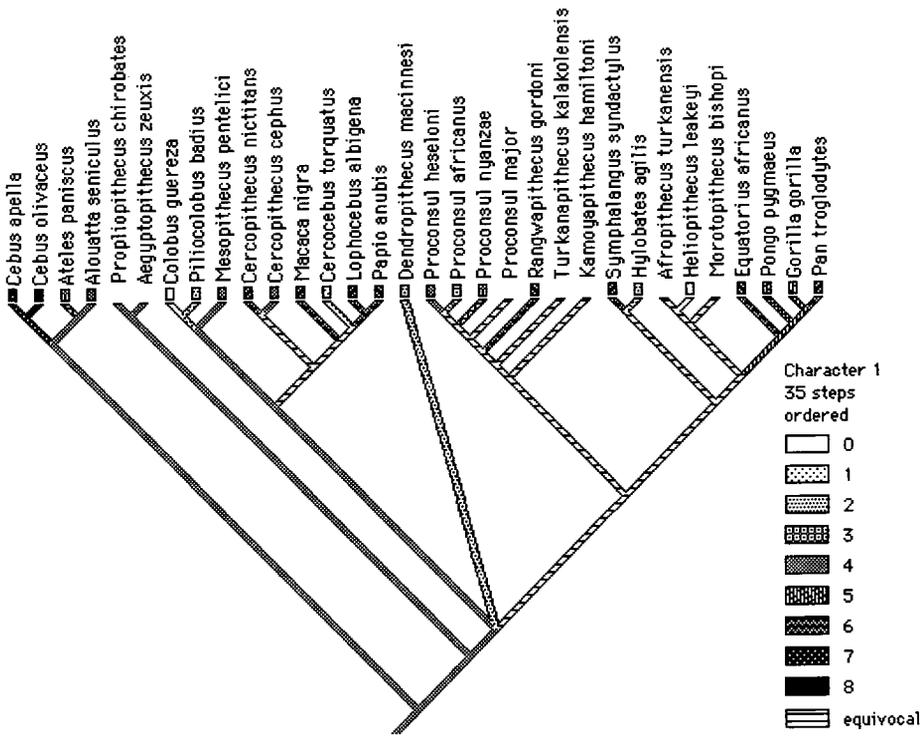
*Dendropithecus*, which was excluded from the Proconsulidae by Andrews (1985) on the basis of the retention of the ancestral catarrhine condition for several characters including cusp heteromorphy on P<sup>3</sup>, does exhibit relatively more cusp heteromorphic P<sup>3</sup>s than both *Proconsul* spp. and *Rangwapithecus*. The results presented in Figure 4.19a, however, show that the character state defining *Dendropithecus* is not a retention of the ancestral catarrhine condition and furthermore, it is seen to share relatively cusp heteromorphic P<sup>3</sup>s with the lesser ape *Hylobates agilis*.

Andrews's (1992) topology differs from the former in that *Equatorius* is included within the Afropithecini (Figure 4.19b). This appears to have the effect of causing ambiguity at the ancestral anthropoid and catarrhine nodes. The character distributions in both topologies are similar, however, in that they both reconstruct the ancestral hominid morphotype as being characterized by a reduction in cusp heteromorphy such that the paracone is only slightly more elevated than the protocone; *Equatorius* is seen to share even further reduction in cusp heteromorphy with *Pan troglodytes*.

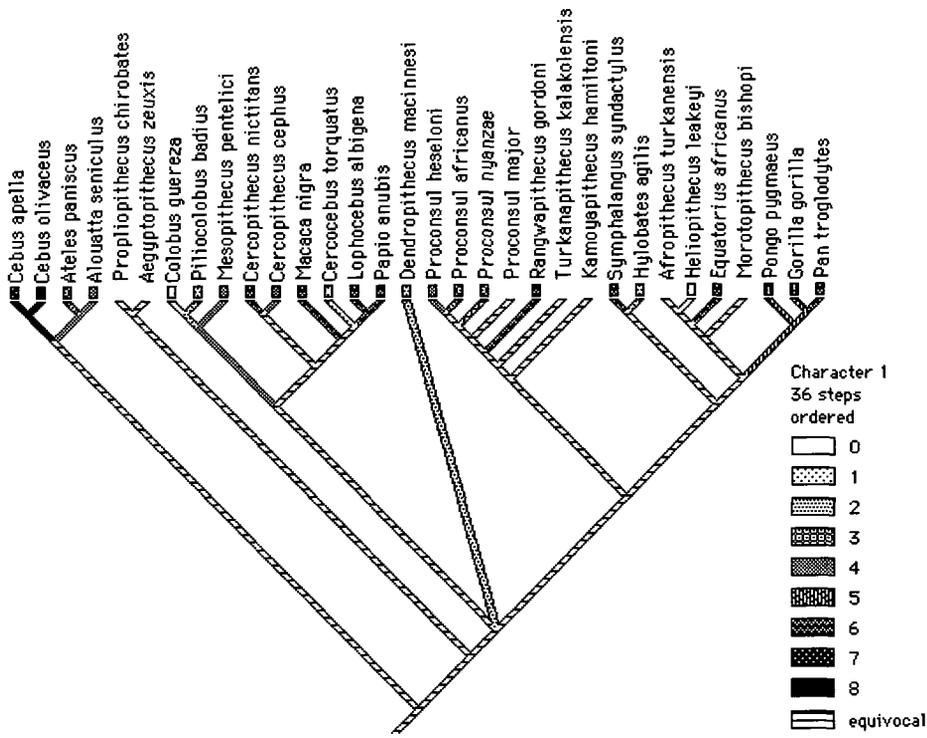
Using Harrison's (1987) topology<sup>9</sup>, the results of character optimization are virtually identical to those derived from Andrews's (1992) phylogeny, despite the

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<sup>9</sup> It should be noted that both *Heliopithecus* and *Equatorius* were not included in Harrison's (1987) study.



**Figure 4.19a** Character distribution for Character 1 (cusp heteromorphy on upper third premolar) using Andrews's (1985) topology.

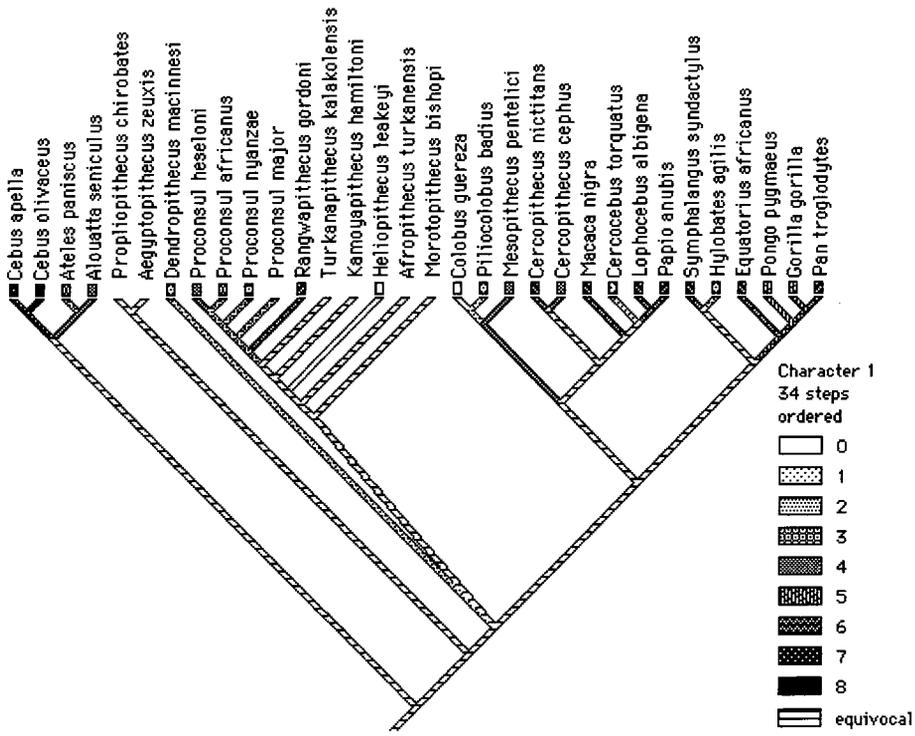


**Figure 4.19b** Character distribution for Character 1 (cusp heteromorphy on upper third premolar) using Andrews's (1992) topology.

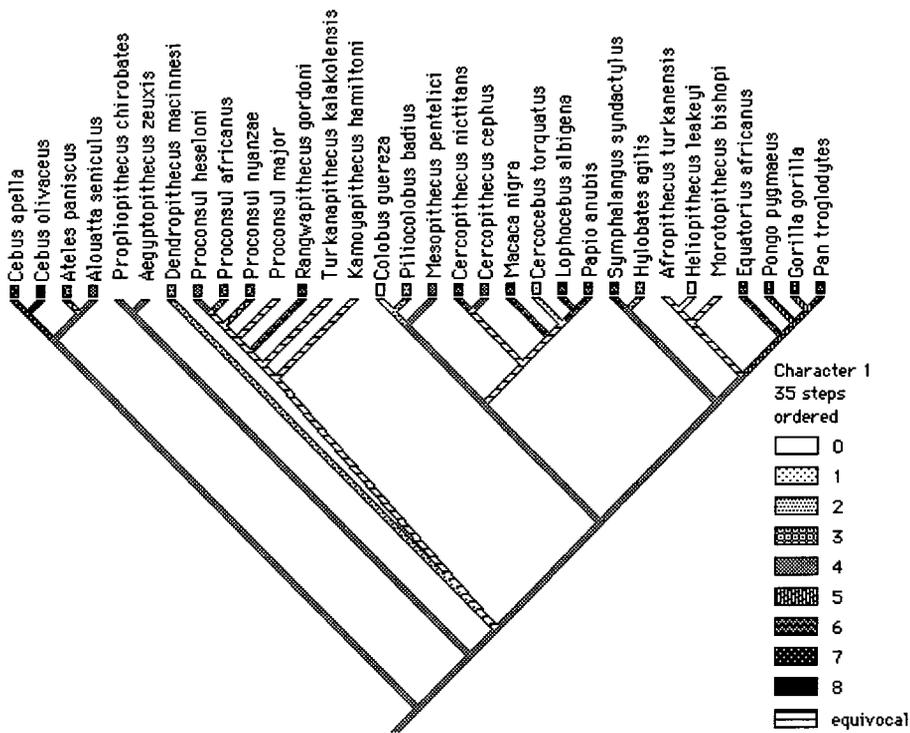
exclusion of the proconsulids from the Hominoidea (Figure 4.20a). As predicted by Harrison (1987), a reduction in cusp heteromorphy on P<sup>3</sup> can be seen to diagnose the extant hominids. Furthermore, two species of *Proconsul* (*P. africanus* and *P. nyanzae*) display cusp heteromorphy on P<sup>3</sup> that is more pronounced than that of the extant catarrhines, with the exception of some cercopithecoids (including the colobines and *Cercocebus torquatus*) and the lesser ape *Hylobates agilis*. Similar to the results derived from Andrews's (1992) topology, however, a reduction in cusp heteromorphy cannot be interpreted as a definite hominid synapomorphy due to ambiguity at the outgroup node as well as all subsequent nodes below it. In addition to this, the condition in which the paracone is only slightly more elevated than the protocone on P<sup>3</sup> can also be seen to have arisen independently in several additional extant cercopithecoid taxa.

In contrast to the results derived from Harrison's (1987) topology, the ancestral anthropoid condition of cusp heteromorphy is retained in the last common ancestor of the Hominoidea using Harrison and Rook's (1997) phylogeny (Figure 4.20b). As predicted by Harrison and Rook (1997), the extant hominids are characterized by subsequent reduction in cusp heteromorphy on P<sup>3</sup> relative to the proconsulids and hylobatids, and this character state is also seen to have arisen in the last common ancestor of a clade comprising *Equatorius* + the extant great apes. It is noteworthy that *Heliopithecus* displays the highest degree of cusp heteromorphy on P<sup>3</sup> of all fossil taxa examined using the four topologies, and it is seen to share this character state convergently only with *Colobus guereza*.

Interestingly, the inclusion of fossil taxa in character distributions for Character 1 has the effect of creating more ambiguity at the hypothetical ancestral nodes



**Figure 4.20a** Character distribution for Character 1 (cusp heteromorphy on upper third premolar) using Harrison's (1987) topology.



**Figure 4.20b** Character distribution for Character 1 (cusp heteromorphy on upper third premolar) using Harrison and Rook's (1997) topology.

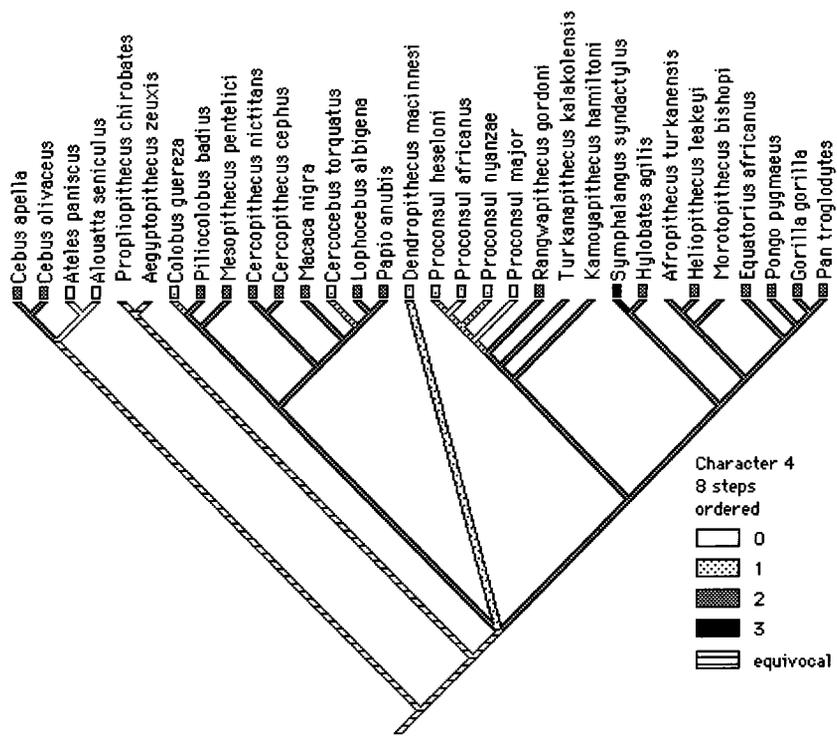
rather than clarifying the character states characterizing various branching points (compare with Figure 4.8). Furthermore, in Andrews's (1985) and Harrison and Rook's (1997) respective topologies, the ancestral anthropoid morphotype is reconstructed as being characterized by relative cusp heteromorphy on P<sup>3</sup> rather than a reduction in the disparity in height between the paracone and protocone.

### **Upper Fourth Premolar**

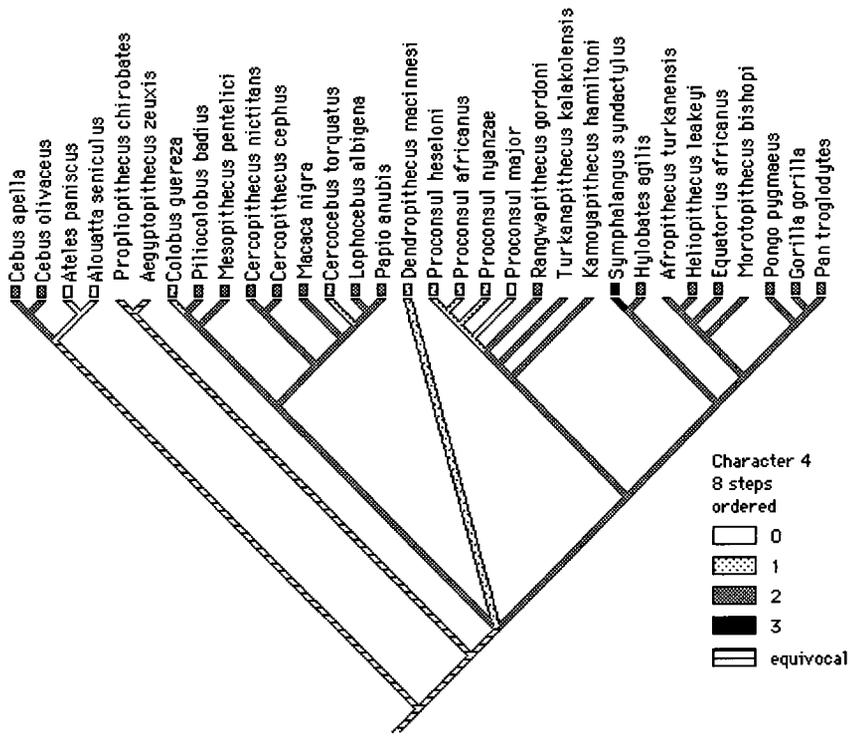
As with Character 1, a reduction in cusp heteromorphy on P<sup>4</sup> cannot be interpreted as a definite hominoid synapomorphy (Andrews, 1985, 1992) due to ambiguity at the outgroup node (Figure 4.21a,b). Although the results of character optimization for Character 4 derived from Andrews's (1985) topology reconstruct the ancestral hominoid morphotype as being characterized by P<sup>4</sup>s in which the cusps are of more or less equal height, it is impossible to conclude with any degree of certainty that a 'reduction' in cusp heteromorphy on P<sup>4</sup> is derived with regard to the ancestral anthropoid or catarrhine morphotype due to ambiguity at these nodes.

Furthermore, *contra* Andrews (1985), *Proconsul* does not share a 'reduction' in cusp heteromorphy on P<sup>4</sup> with the extant hominoids to the exclusion of *Dendropithecus*; *P. heseloni*, *P. africanus*, and *P. nyanzae* all exhibit moderately cusp heteromorphic P<sup>4</sup>s that, according to Andrews's (1985) topology, they share convergently with *Dendropithecus* and two species of extant cercopithecoid taxa (*Colobus guereza* and *Cercocebus torquatus*). *P. major* is further distinguished from its congeners by displaying a greater degree of cusp heteromorphy, and it shares this character state convergently with the atelines.

Of Andrews's (1985) Proconsulidae, therefore, only *Rangwapithecus* is shown to retain the ancestral hominoid condition of P<sup>4</sup>s in which the cusps are of more or



**Figure 4.21a** Character distribution for Character 4 (cusp heteromorphy on upper fourth premolar) using Andrews's (1985) topology.



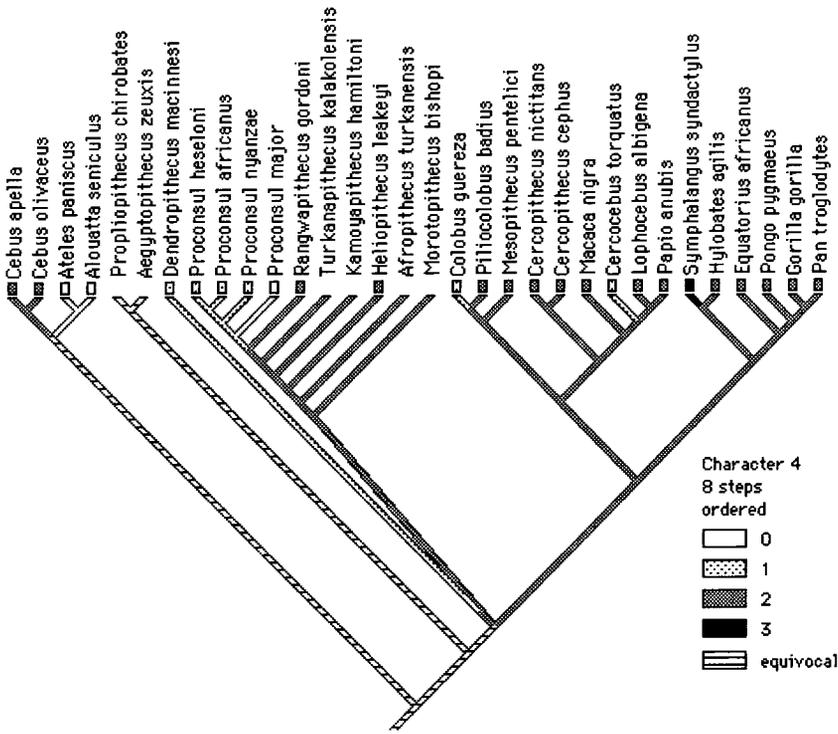
**Figure 4.21b** Character distribution for Character 4 (cusp heteromorphy on upper fourth premolar) using Andrews's (1992) topology.

less equal height; a condition that also characterizes the extant hominoids, with the exception of *Symphalangus syndactylus*. This character state, however, is also seen to have arisen independently in the majority of extant cercopithecoïd taxa and the two cebids examined in the present study.

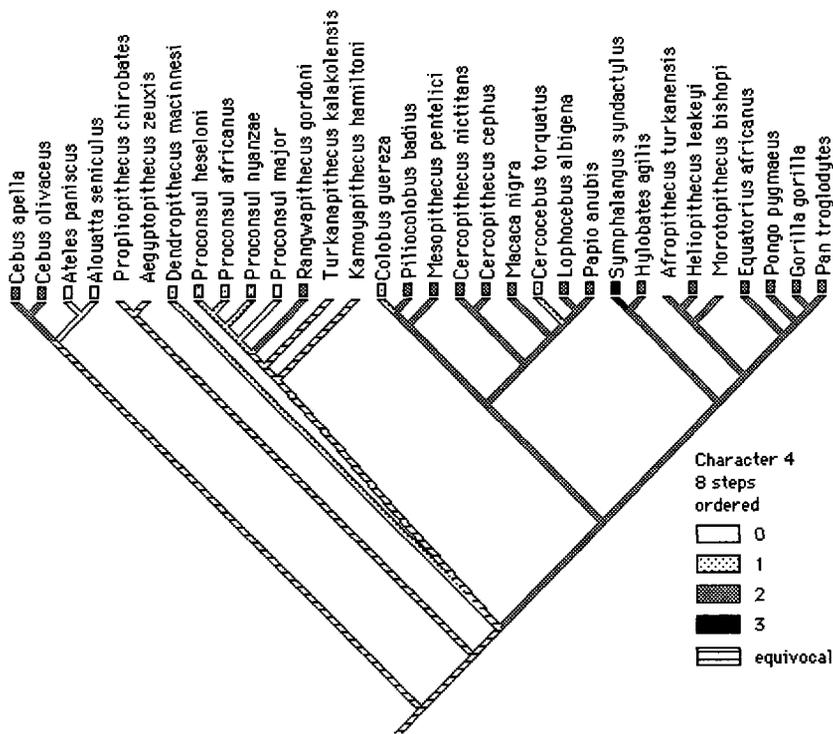
The results of character optimization using Andrews's (1992) topology are identical to those derived from Andrews's (1985) phylogeny, despite the inclusion of *Equatorius* in the Afropithecini rather than positioned as the direct sister group to the living great apes (Figure 4.21b). Both *Equatorius* and *Heliopithecus* retain the ancestral hominoid condition, seen also in the last common ancestor of a clade comprising the Afropithecini + the extant great apes.

A reduction in cusp heteromorphy on P<sup>4</sup> also cannot be interpreted as a definite hominid synapomorphy (Harrison, 1987; Harrison and Rook, 1997) since the results of character optimization for Character 4 using Harrison's (1987) topology reconstruct the ancestral hominid morphotype as being characterized by the same character state found at the ancestral cercopithecoïd and hominoid nodes (Figure 4.22a). Furthermore, because the ancestral anthropoid morphotype is ambiguous, it remains unclear as to whether the character state found in the hypothetical cercopithecoïd/hominoid/hominid ancestors is a retention of the plesiomorphic anthropoid condition, or if the condition of P<sup>4</sup>s with cusps of more or less equal height is derived relative to the ancestral anthropoid condition.

As predicted by Harrison (1987), however, *Proconsul* exhibits moderately more pronounced cusp heteromorphy on P<sup>4</sup> than the extant great apes and most cercopithecoïds examined in the present study, with the exception of *Colobus guereza* and *Cercocebus torquatus*. *Contra* Harrison (1987) and Harrison and Rook (1997), however, *Proconsul* cannot be seen to share the 'primitive'



**Figure 4.22a** Character distribution for Character 4 (cusp heteromorphy on upper fourth premolar) using Harrison's (1987) topology.



**Figure 4.22b** Character distribution for Character 4 (cusp heteromorphy on upper fourth premolar) using Harrison and Rook's (1997) topology.

condition of a greater differential between the height of the protocone and that of the paracone with the hylobatids (Figure 4.22a). Furthermore, due to ambiguity at the ancestral catarrhine node, it is impossible to speculate whether the condition characterizing *Proconsul* represents the primitive catarrhine condition (Harrison, 1987).

The results of character evolution using Harrison and Rook's (1997) topology are very similar to those derived from Harrison's (1987) phylogenetic scheme (Figure 4.22b). The only difference is that the proconsulid branch is equivocal, presumably due to the exclusion of the Afropithecidae from the Proconsuloidea.

Again, the inclusion of fossil taxa in character distributions for Character 4 have had the effect of causing ambiguity at all of the ancestral anthropoid and catarrhine nodes (as well as at two cercopithecoid nodes) of the four topologies examined (compare with Figure 4.9).

## **UPPER PREMOLAR ENLARGEMENT RELATIVE TO FIRST MOLAR**

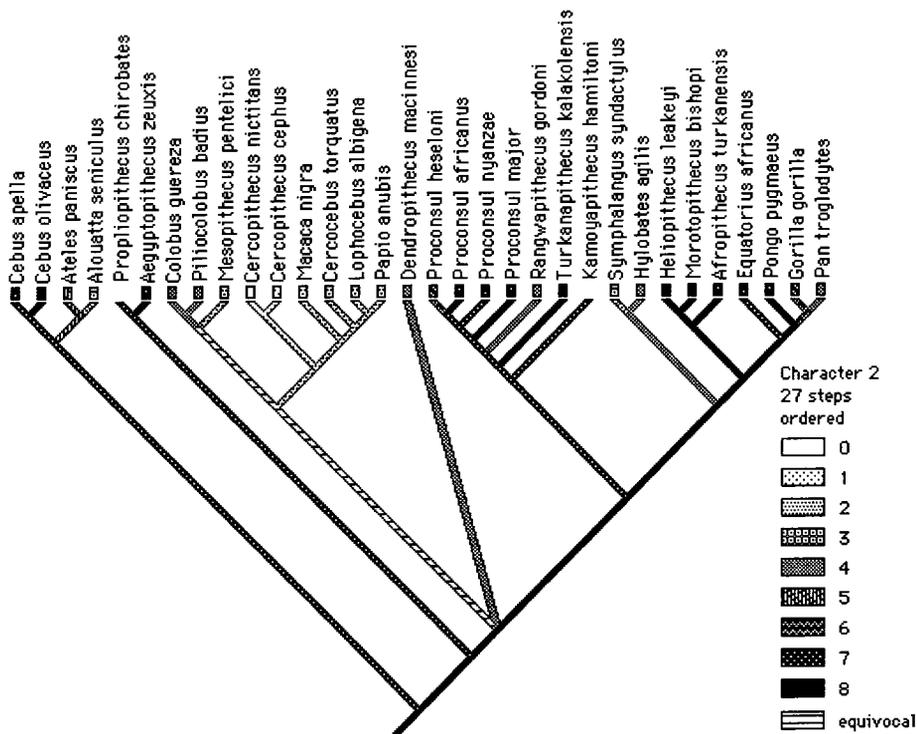
### **Upper Third Premolar**

The inclusion of fossil taxa in the character distributions for Character 2 have the effect of resolving ambiguity at virtually all of the hypothetical ancestral nodes (Figures 4.23 – 4.25; compare with Figure 4.8). Upper third premolar enlargement relative to the first molar, however, cannot be interpreted as a definite hominid synapomorphy (Andrews and Martin, 1987a; Andrews, 1992; Harrison and Rook, 1997), since the results show that the ancestral hominid morphotype is characterized by retention of the ancestral anthropoid condition of relatively greatly enlarged P<sup>3</sup>s in four of the five topologies examined.

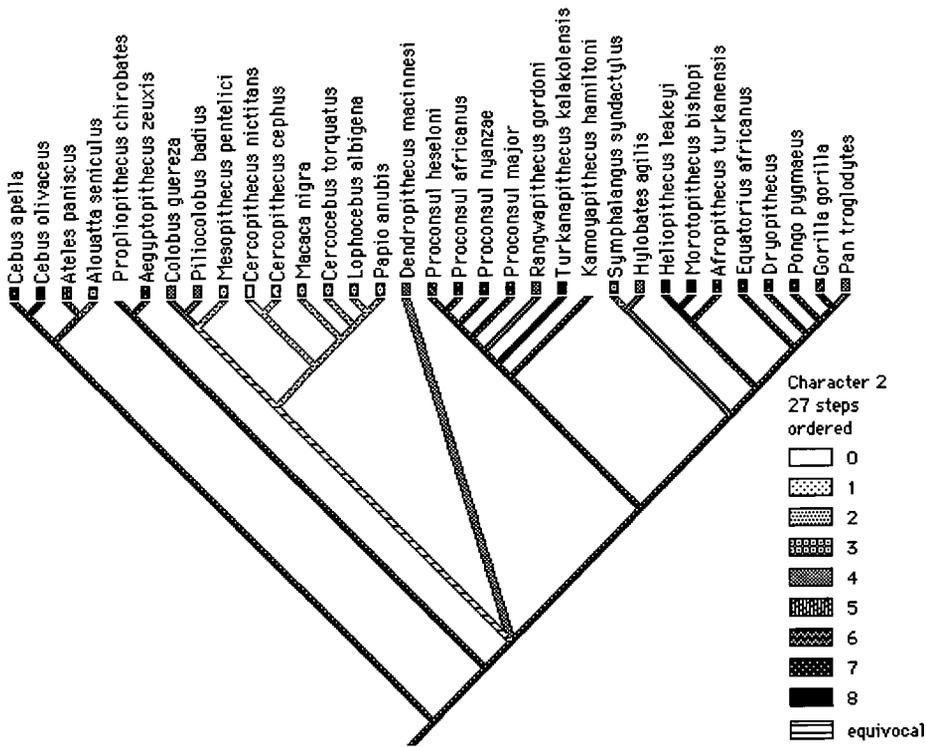
The results of character optimization using Andrews and Martin's (1987a) topology clearly show that upper third premolar enlargement relative to the first molar cannot be interpreted as a feature characteristic of the great ape and human clade (Figure 4.23a). In fact, the results show that, not only is the condition of relatively greatly enlarged P<sup>3</sup>s that characterizes the living Asian great apes a retention of the plesiomorphic anthropoid condition, but *Pongo pygmaeus* shares this character state with three fossil hominoids (including *P. africanus*, *P. nyanzae*, and *P. major*), the stem catarrhine *Aegyptopithecus*, and the extant platyrrhine *Cebus apella*.

Thus, *contra* Andrews and Martin (1987a), this character fails to distinguish *Proconsul* spp. from extant hominids and other early Miocene hominoids considered to be more closely related to the living great apes (such as *Equatorius*, *Heliopithecus*, and *Afropithecus*), in that *P. africanus*, *P. nyanzae*, and *P. major* are *not* characterized by retaining the primitive hominoid condition of relatively small upper premolars. In addition, of the extant hominids examined, only *Pongo pygmaeus* is characterized by relatively greatly enlarged P<sup>3</sup>s; *Pan troglodytes* shares relatively small P<sup>3</sup>s with *Hylobates agilis* and the fossil taxa *Rangwapithecus* and *Dendropithecus*; and *Gorilla gorilla* together with the fossil proconsulid *P. heseloni* share only moderate enlargement of P<sup>3</sup> relative to M<sup>1</sup>.

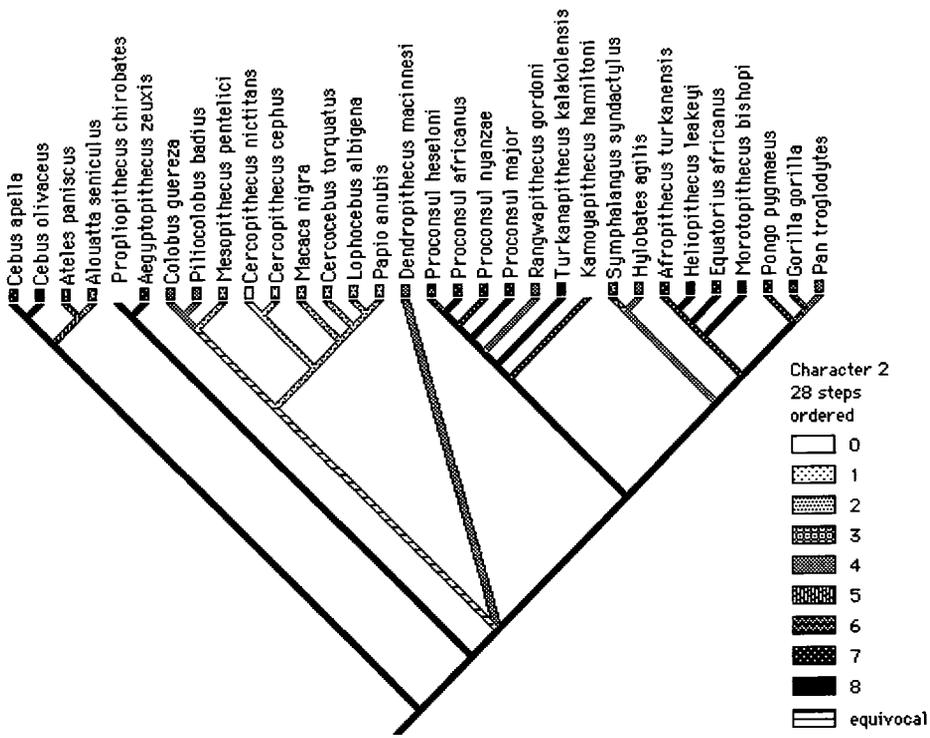
Furthermore, Figures 4.23a and 4.23b clearly show that *Afropithecus*, *Heliopithecus*, *Morotopithecus*, and *Equatorius* do not share a relatively larger P<sup>3</sup> only with the African great apes, to the exclusion of *Proconsul* and *Dryopithecus*. If the fossil taxon *Dryopithecus* is included in Andrews and Martin's (1987a)



**Figure 4.23a** Character distribution for Character 2 (upper third premolar enlargement relative to first molar) using Andrews and Martin's (1987a) topology.



**Figure 4.23b** Character distribution for Character 2 (upper third premolar enlargement relative to first molar) using Andrews and Martin's (1987a) topology, with *Dryopithecus* included.



**Figure 4.24** Character distribution for Character 2 (upper third premolar enlargement relative to first molar) using Andrews's (1992) topology.

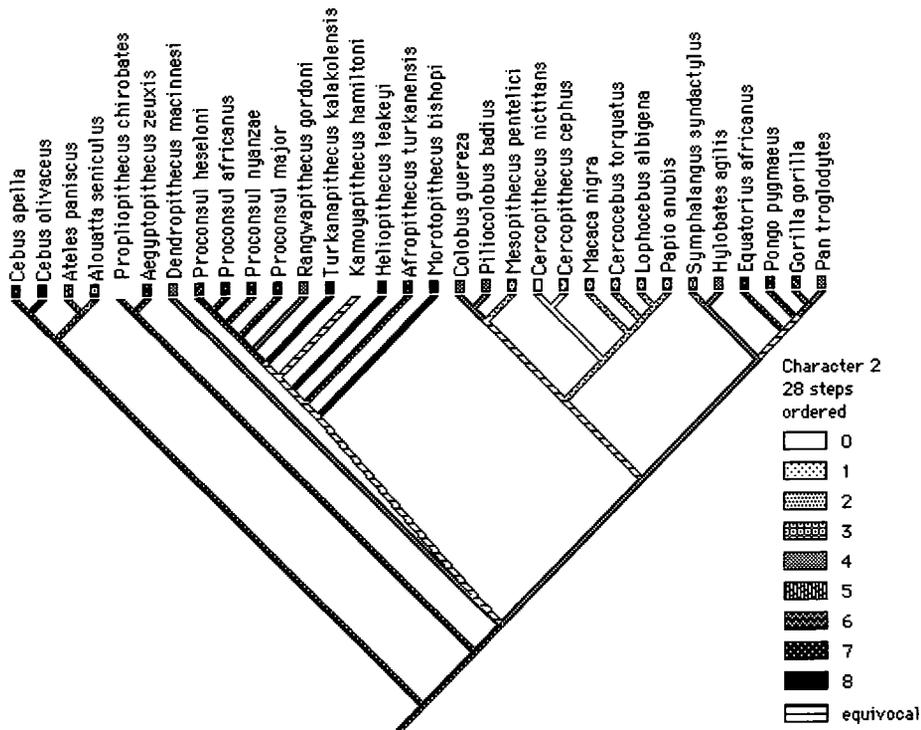
topology<sup>10</sup>, the reconstructed ancestral morphotypes are identical to those derived from the topology that excludes this fossil taxon, since *Dryopithecus* is seen to share greatly enlarged P<sup>3</sup>s relative to M<sup>1</sup> with *Afropithecus*, *Equatorius*, *P. africanus*, *P. nyanzae*, *P. major*, and *Pongo pygmaeus* (Figure 4.23b). In contrast to the results of Andrews and Martin's (1987a) study, Figures 4.23a and 4.23b show that both *Heliopithecus* and *Morotopithecus* are distinguished from all extant great apes by extreme enlargement of P<sup>3</sup> relative to M<sup>1</sup>; a condition that they are seen to share with the fossil hominoid *Turkanapithecus* and convergently with *Cebus olivaceus*.

The results of character optimization using Andrews's (1992) topology are identical to those previously discussed (Figure 4.24). The character state optimizations fail to diagnose a clade comprising the Afropithecini + the extant great apes by relative upper third premolar enlargement, though two members of the Afropithecini (*Heliopithecus* and *Morotopithecus*) are characterized by further enlargement of P<sup>3</sup>.

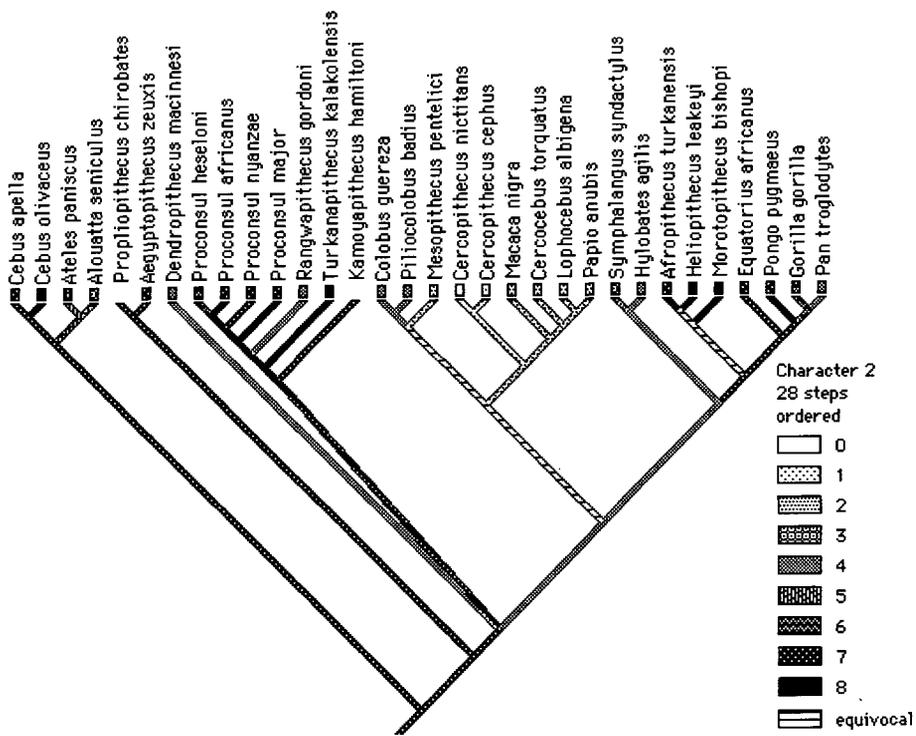
Harrison's (1987) topology, in which all proconsulids are positioned as stem catarrhines, yields quite different results than those derived from Andrews and Martin's (1987a) and Andrews's (1992) respective topologies (Figure 4.25a). Although the ancestral anthropoid and catarrhine morphotypes are characterized by relatively greatly enlarged P<sup>3</sup>s in relation to M<sup>1</sup>, both ancestral cercopithecoid and hominoid morphotypes are reconstructed as being characterized by upper third premolars that are relatively small in relation to M<sup>1</sup>. In addition, the

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<sup>10</sup> It should be noted that due to the absence of a reference referring the reader to the data from which the *Dryopithecus* range was derived, the median value for the range given in Andrews and Martin (1987a) was calculated and subsequently coded for phylogenetic analysis. The median value used was 86.5, which was coded as character state 7.



**Figure 4.25a** Character distribution for Character 2 (upper third premolar enlargement relative to first molar) using Harrison's (1987) topology.



**Figure 4.25b** Character distribution for Character 2 (upper third premolar enlargement relative to first molar) using Harrison and Rook's (1997) topology.

ancestral hominid morphotype is shown as equivocal. Thus, according to this phylogenetic scheme, the relatively great enlargement of P<sup>3</sup> characterizing both *Equatorius* and *Pongo pygmaeus* represents a reversal to the plesiomorphic anthropoid condition, and the presence of this character state in *Afropithecus*, *Aegyptopithecus*, and three species of *Proconsul* represents retention of the plesiomorphic anthropoid condition, which is also seen to be present in the last common ancestor of the Catarrhini.

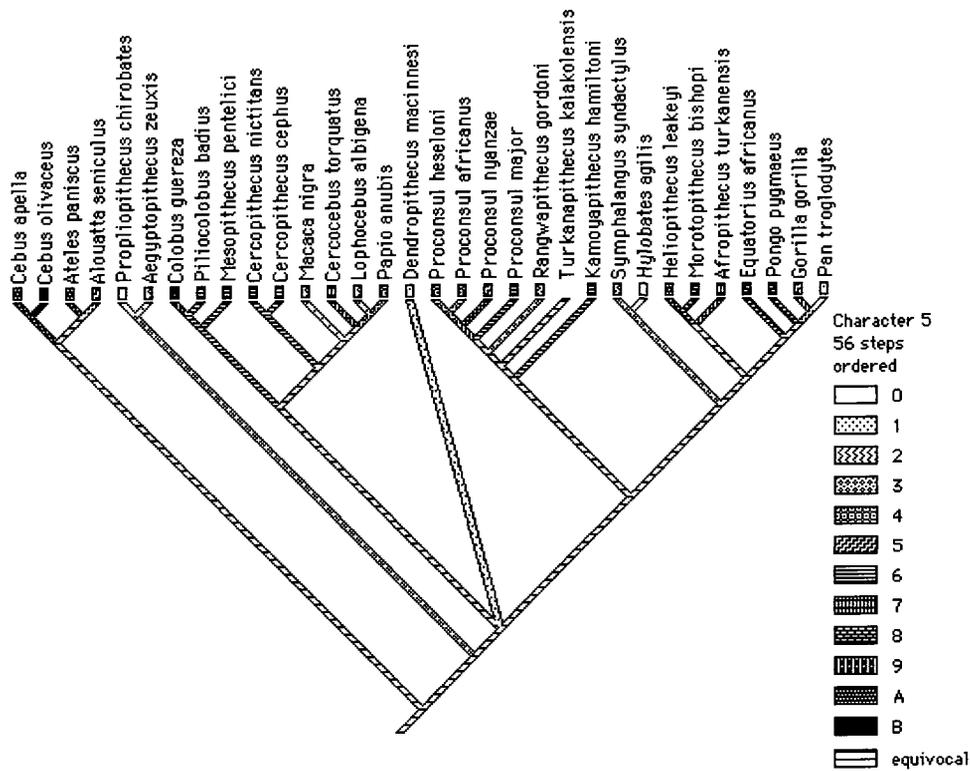
With the inclusion of the Afropithecidae in the Hominoidea, results derived from Harrison and Rook's (1997) topology differ from those of Harrison (1987) in that the ancestral hominid morphotype is reconstructed as being characterized by relatively great enlargement of P<sup>3</sup> (Figure 4.25b). Thus, according to this phylogenetic scheme, a clade comprising the Afropithecidae + *Equatorius* as the sister group of extant great apes is characterized by a reversal to the plesiomorphic anthropoid condition. This result again highlights the fact that relative upper third premolar enlargement in relation to the first molar cannot be interpreted as having a synapomorphous condition within the Hominidae.

#### **Upper Fourth Premolar**

Using Harrison and Rook's (1997) index to calculate the size of P<sup>4</sup> in relation to M<sup>1</sup> fails to reconstruct any of the hypothetical ancestral nodes of either Andrews and Martin's (1987a) topology in which *Equatorius* is positioned as the direct sister group to the extant great apes, or Andrews's (1992) topology in which *Equatorius* is included in the Afropithecini (Figure 4.26a,b). *Contra* Andrews and Martin (1987a) therefore, this result indicates that relative enlargement of P<sup>4</sup> (in relation to M<sup>1</sup>) cannot be interpreted as a synapomorphy of the great ape and human clade, nor can *Heliopithecus*, *Equatorius*, *Afropithecus*, and

*Morotopithecus* collectively be distinguished from both living and fossil apes by possessing unusually large P<sup>4</sup>s. In fact, the results of character optimization for Character 5 using Andrews and Martin's (1987a) topology indicate that both *Equatorius* and *Morotopithecus* share relatively great enlargement of P<sup>4</sup> with *Pongo pygmaeus*. *Heliopithecus* is the only taxon of the four fossil hominoids designated by Andrews and Martin (1987a) that displays extreme enlargement of P<sup>4</sup> relative to M<sup>1</sup> such that it is distinguished from all living and fossil apes sampled; *Heliopithecus* is shown to share this character state convergently, however, with both *Cebus apella* and *Ateles paniscus*. Furthermore, *Afropithecus* is characterized by a lesser degree of P<sup>4</sup> enlargement than *Heliopithecus*, *Morotopithecus*, and *Equatorius*, and the results show that it shares this condition convergently with *Cercocebus torquatus*.

Of the remaining proconsulids, *P. heseloni* and *P. africanus* are shown to share moderate enlargement of P<sup>4</sup> convergently with *Papio anubis*, and *P. nyanzae* together with *Gorilla gorilla* are characterized by slightly greater enlargement of P<sup>4</sup> than the former two fossil taxa. Both *P. major* and *Kamoyapithecus* exhibit the largest P<sup>4</sup>s relative to M<sup>1</sup> of all members included in this clade; the condition of moderate enlargement characterizing these fossil taxa is also shown to have arisen independently in four other cercopithecoid taxa including *Cercopithecus nictitans*, *Cercopithecus cephus*, *Piliocolobus badius*, and the fossil colobine *Mesopithecus*. *Dendropithecus* shares relatively small P<sup>4</sup>s convergently with *Pan troglodytes* and interestingly, the stem catarrhine *Propliopithecus* shares the smallest P<sup>4</sup>s convergently with *Hylobates agilis* while *Rangwapithecus* and *Symphalangus syndactylus* are characterized by slightly larger P<sup>4</sup>s relative to M<sup>1</sup> than the former living and fossil taxa.



**Figure 4.26a** Character distribution for Character 5 (upper fourth premolar enlargement relative to first molar) using Andrews and Martin's (1987a) topology.

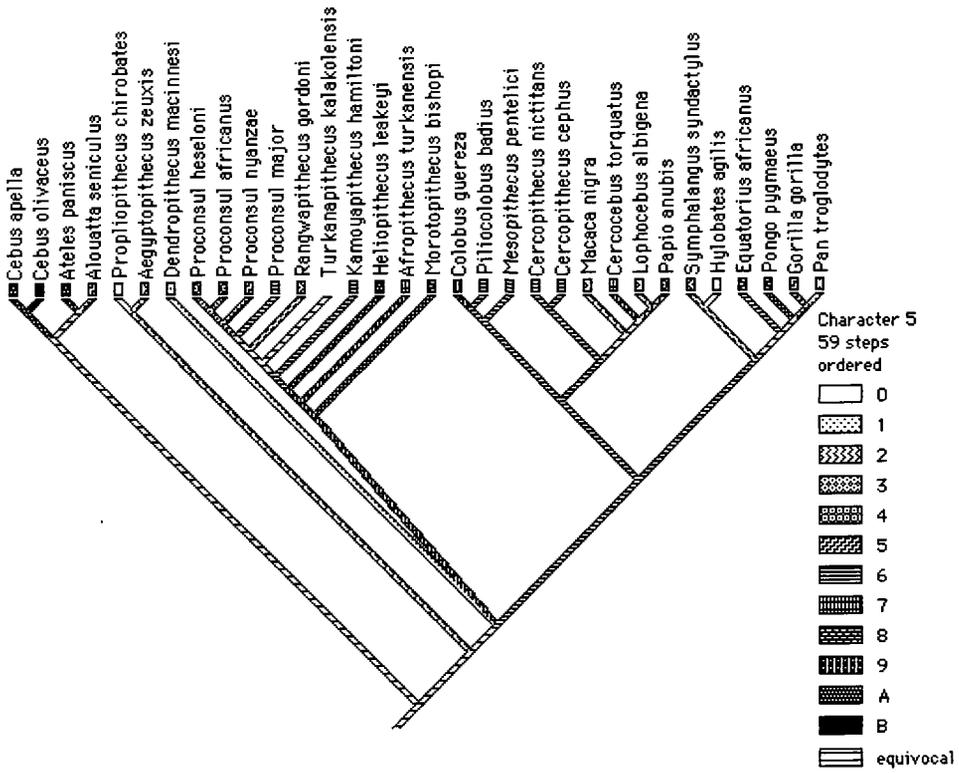


**Figure 4.26b** Character distribution for Character 5 (upper fourth premolar enlargement relative to first molar) using Andrews's (1992) topology.

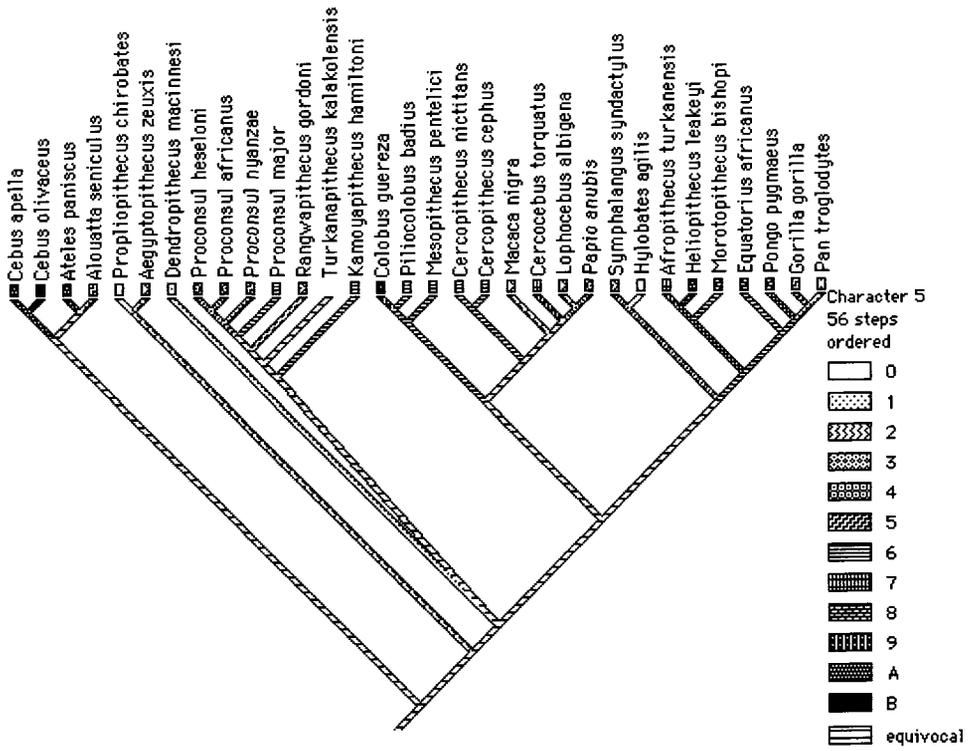
The results of character evolution analysis using Andrews's (1992) topology are virtually identical to those derived from Andrews and Martin's (1987a) phylogeny. The main difference is that the branch of the group comprising *Afropithecus*, *Heliopithecus*, *Equatorius*, and *Morotopithecus* is characterized by relatively great enlargement of  $P^4$  in relation to  $M^1$ . Due to ambiguity, however, at the internode below the clade comprising the Afropithecini + the extant great apes, as well as at the ancestral hominid node, it is not possible to conclude that the Afropithecini are in fact characterized by further enlargement of  $P^4$  relative to the extant great apes. Nor can relative enlargement of  $P^4$  in relation to  $M^1$  be interpreted as a definite hominid synapomorphy.

Harrison's (1987) topology that positions all proconsulids below the hominoid/cercopithecoid split yields quite different results in comparison to those previously discussed, in that both ancestral cercopithecoid and hominoid morphotypes are reconstructed as being characterized by  $P^4$ s that are moderately enlarged relative to  $M^1$  (Figure 4.27a). This result contradicts Andrews and Martin's (1987a) hypothesis that the primitive hominoid condition is characterized by small premolars relative to the molars. Due to ambiguity, however, at the outgroup node as well as at the ancestral hominid node, it is not possible to conclude that the extant hominids are characterized by a 'derived' condition in which the  $P^4$ s are enlarged relative to the condition characterizing the last common ancestor of the extant hominoids.

Using Harrison and Rook's (1997) topology, the results of character evolution analysis are yet more different from those derived from Harrison's (1987) phylogeny, presumably due to the inclusion of the Afropithecidae within the Hominoidea. Figure 4.27b shows that, according to this phylogenetic scheme,



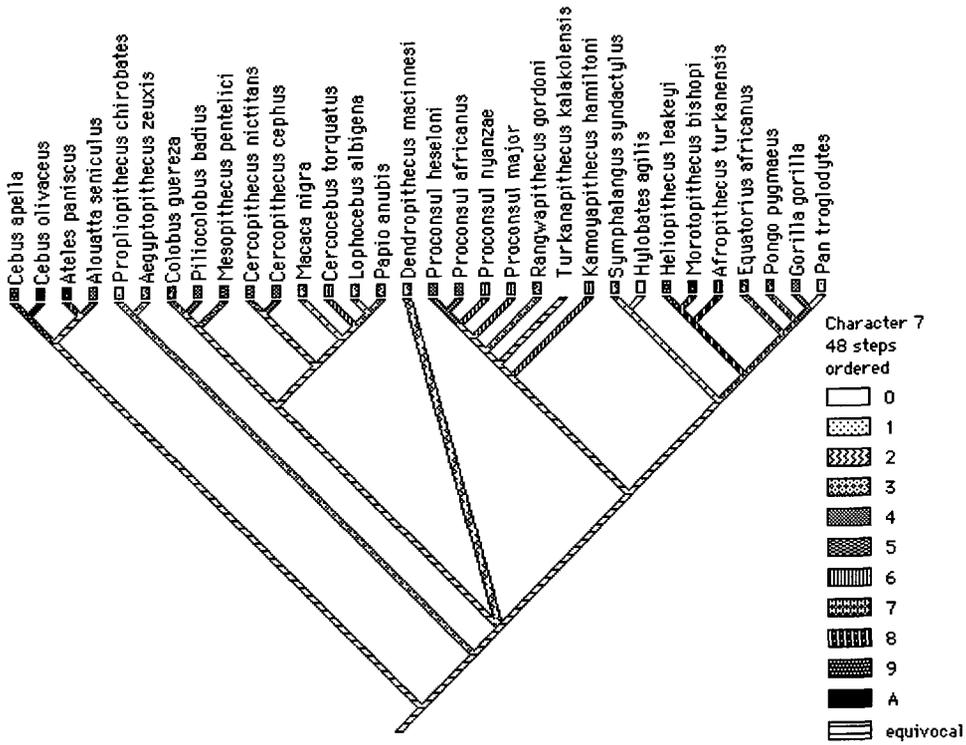
**Figure 4.27a** Character distribution for Character 5 (upper fourth premolar enlargement relative to first molar) using Harrison's (1987) topology.



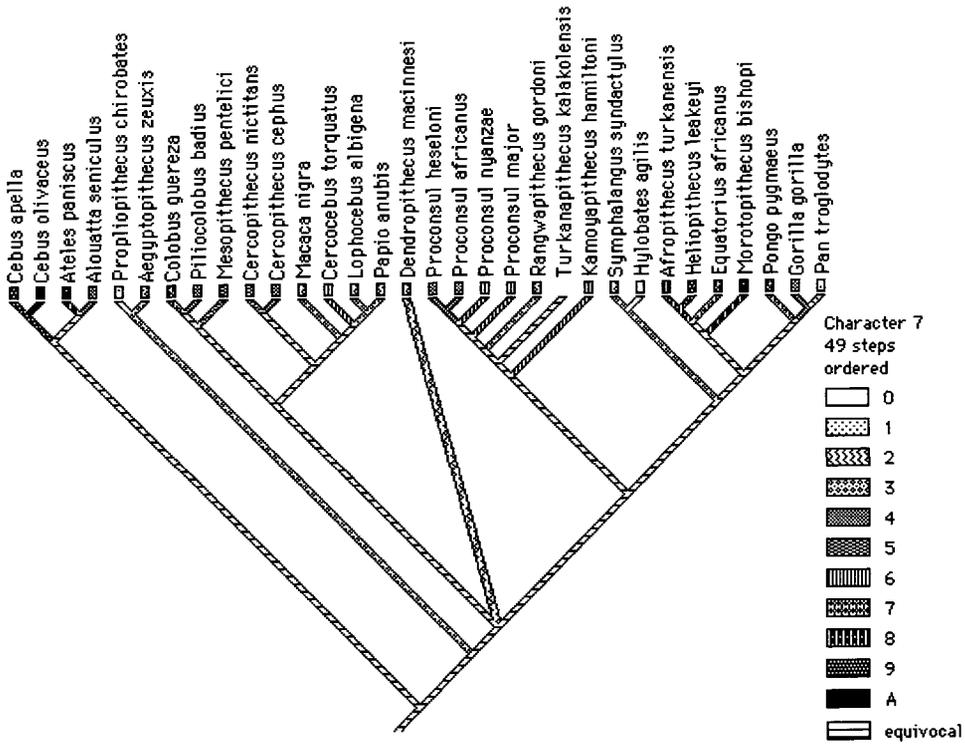
**Figure 4.27b** Character distribution for Character 5 (upper fourth premolar enlargement relative to first molar) using Harrison and Rook's (1997) topology.

relatively greatly enlarged P<sup>4</sup>s in relation to M<sup>1</sup> arose in the common ancestor of a clade comprising the extant hominids with the Afropithecidae and *Equatorius* as successive sister groups to this clade. This is the only topology examined for Character 5 in which relative enlargement of P<sup>4</sup> diagnoses extant hominids, and the presence of the same character state in *Morotopithecus* and *Equatorius* can be seen to link these taxa to the living great apes as advanced by Andrews and Martin (1987a) and Andrews (1992). As with the results derived from the previous topologies, however, relative P<sup>4</sup> enlargement cannot be interpreted as a definite hominid synapomorphy due to ambiguity at the outgroup node and all subsequent nodes below it.

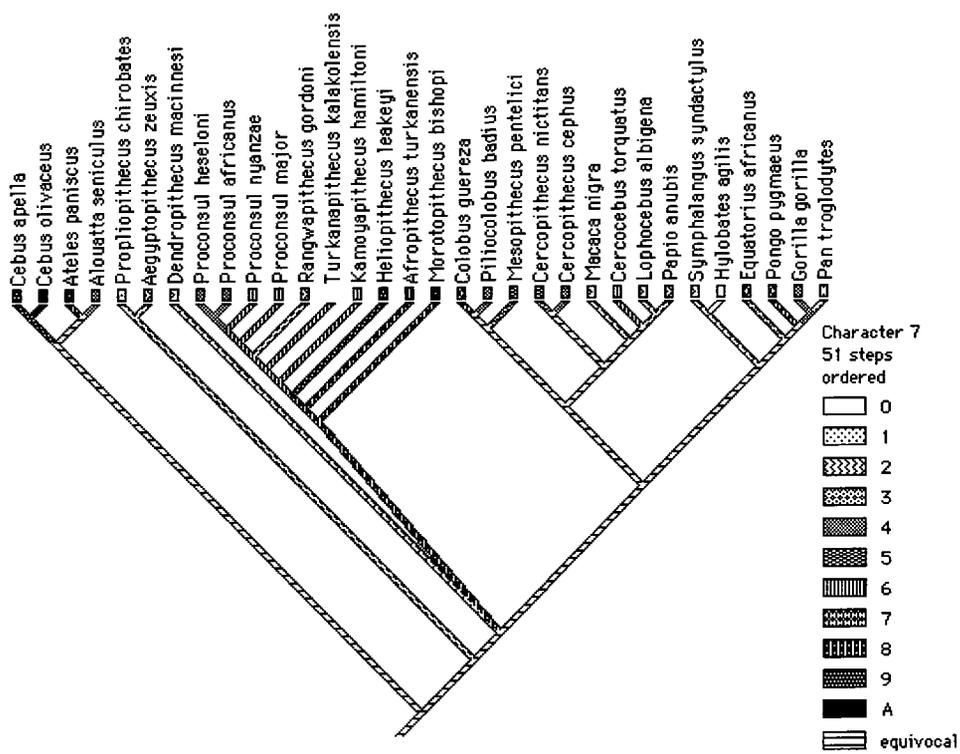
Using Andrews and Martin's (1987a) crown module ratio to calculate the size of P<sup>4</sup> in relation to M<sup>1</sup> (Character 7) yields different results than those derived for Character 5 using Harrison and Rook's (1997) index, in that two of the four topologies examined reconstruct the ancestral hominid morphotype as opposed to just one topology for Character 5 (Figures 4.28 – 4.29; compare with Figures 4.26 – 4.27). Both Andrews and Martin's (1987a) and Harrison and Rook's (1997) respective topologies reconstruct the last common ancestor of a clade comprising *Afropithecus*, *Heliopithecus*, and *Morotopithecus* as the more distant sister group to a clade comprising *Equatorius* + the extant hominids, as being characterized by relatively greatly enlarged P<sup>4</sup>s in relation to M<sup>1</sup>. The difference between both topologies is that while Harrison and Rook (1997) place the clade comprising *Proconsul* spp., *Rangwapithecus*, and *Kamoyapithecus* below the hominoid/cercopithecoid split, Andrews and Martin (1987a) position this clade as stem hominoids. Interestingly, however, both topologies require the same number of steps (48 steps); one step less than for Andrews's (1992) topology and three



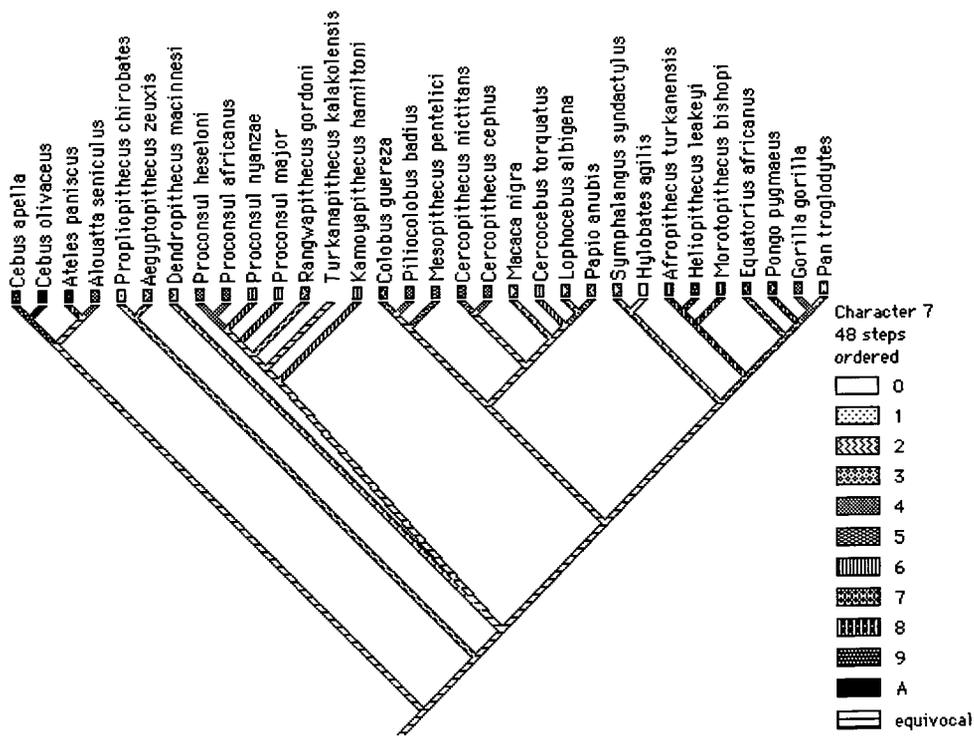
**Figure 4.28a** Character distribution for Character 7 (upper fourth premolar/first molar crown module ratio) using Andrews and Martin's (1987a) topology.



**Figure 4.28b** Character distribution for Character 7 (upper fourth premolar/first molar crown module ratio) using Andrews's (1992) topology.



**Figure 4.29a** Character distribution for Character 7 (upper fourth premolar/first molar crown module ratio) using Harrison's (1987) topology.



**Figure 4.29b** Character distribution for Character 7 (upper fourth premolar/first molar crown module ratio) using Harrison and Rook's (1997) topology.

steps less than for Harrison's (1987) topology. In addition, both character distribution trees show slightly less homoplasy than the trees derived for Character 5 using the equivalent topologies (CI is 0.21 for Character 7, and 0.20 for Character 5), and require eight fewer steps. These results are also interesting in light of the fact that, with the inclusion of fossil taxa in both topologies, the hypothetical ancestral hominid morphotype came to be characterized by relatively greatly enlarged P<sup>4</sup>s, rather than only moderate enlargement of P<sup>4</sup> in relation to M<sup>1</sup>, which in Figure 4.11 represented retention of the ancestral catarrhine condition.

As with the results presented for Character 5, however, relatively greatly enlarged P<sup>4</sup>s in relation to M<sup>1</sup> cannot be interpreted as a definite hominid synapomorphy due to ambiguity at the outgroup node as well as all subsequent nodes below it. Furthermore, the distinctive P<sup>4</sup> enlargement of *Heliopithecus*, *Equatorius*, *Afropithecus*, and *Morotopithecus* hypothesized by Andrews and Martin (1987a) to be a feature distinguishing these fossil taxa from both living and fossil apes cannot be wholly supported by the results presented in Figures 4.28 – 4.29. While relatively greater P<sup>4</sup> enlargement characterizes the clade comprising *Heliopithecus*, *Morotopithecus*, and *Afropithecus* and distinguishes them from the extant hominids as well as from other Miocene hominoids [using Andrews and Martin's (1987a) and Harrison and Rook's (1997) respective topologies], *Equatorius* is shown to share the same degree of relative P<sup>4</sup> enlargement with *Pongo pygmaeus*. Interestingly, when *Equatorius* is included in the Afropithecini (Andrews, 1992) or, conversely, positioned as the sister group to the extant great apes with *Heliopithecus*, *Afropithecus*, and *Morotopithecus* collectively included

within the Proconsuloidea (Harrison, 1987), this has the effect of rendering the ancestral hominid morphotype equivocal.

It should be stressed, however, that both Characters 7 and 5 do readily distinguish *Heliopithecus*, *Afropithecus*, *Morotopithecus*, and *Equatorius* from *Proconsul* spp., as hypothesized by Andrews and Martin (1987a). The former four fossil taxa consistently exhibit greater P<sup>4</sup> enlargement relative to M<sup>1</sup> than *Proconsul* spp. regardless of the method used to determine the relative size of P<sup>4</sup>. In addition, both Characters 7 and 5 clearly distinguish *Heliopithecus* from living and fossil hominoids in the extreme enlargement of P<sup>4</sup> relative to M<sup>1</sup>, and it is seen to share this character state convergently with *Cebus apella* (Character 7) or both *Cebus apella* and *Ateles paniscus* (Character 5).

Differences in the expression of character states across fossil taxa, however, do exist between Characters 7 and 5 such that fossil taxa are not shown to consistently group with the same extant anthropoid taxa for both characters. For example, in contrast to Character 5, *P. heseloni* and *P. africanus* share moderate P<sup>4</sup> enlargement with *Gorilla gorilla*, and *P. nyanzae* is seen to share slightly more enlarged P<sup>4</sup>s with *P. major* and *Kamoyapithecus* (and convergently with *Cercocebus torquatus*). Moreover, *Morotopithecus* shares relatively greatly enlarged P<sup>4</sup>s with *Afropithecus* (and convergently with *Ateles paniscus*) rather than with *Equatorius* and *Pongo pygmaeus*.

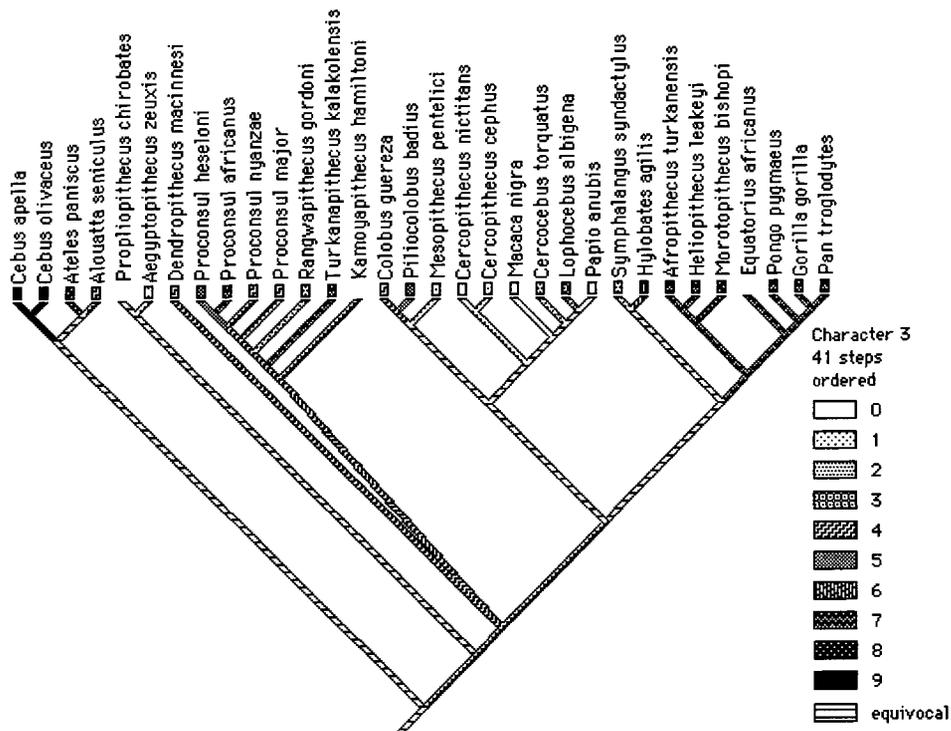
## **UPPER PREMOLAR ENLARGEMENT RELATIVE TO SECOND MOLAR**

### **Upper Third Premolar**

All four topologies examined reconstruct the ancestral hominid morphotype as being characterized by great enlargement of the upper third premolar relative to

the second molar (Figures 4.30 – 4.31); a result that is in agreement with the results presented in Figure 4.9 in which only extant taxa were analyzed. The three topologies in which the Afropithecidae (Harrison and Rook, 1997), the Afropithecini (Andrews, 1992), or a clade comprising *Heliopithecus*, *Afropithecus*, and *Morotopithecus* (Andrews and Martin, 1987a) are included within the Hominoidea, similarly reconstruct the condition found in the last common ancestor shared between these Miocene hominoids and the extant great apes by great enlargement of P<sup>3</sup> relative to M<sup>2</sup>. *Morotopithecus* is distinguished from these taxa by exhibiting even further relative enlargement of P<sup>3</sup> which it is seen to share convergently with *Ateles paniscus*.

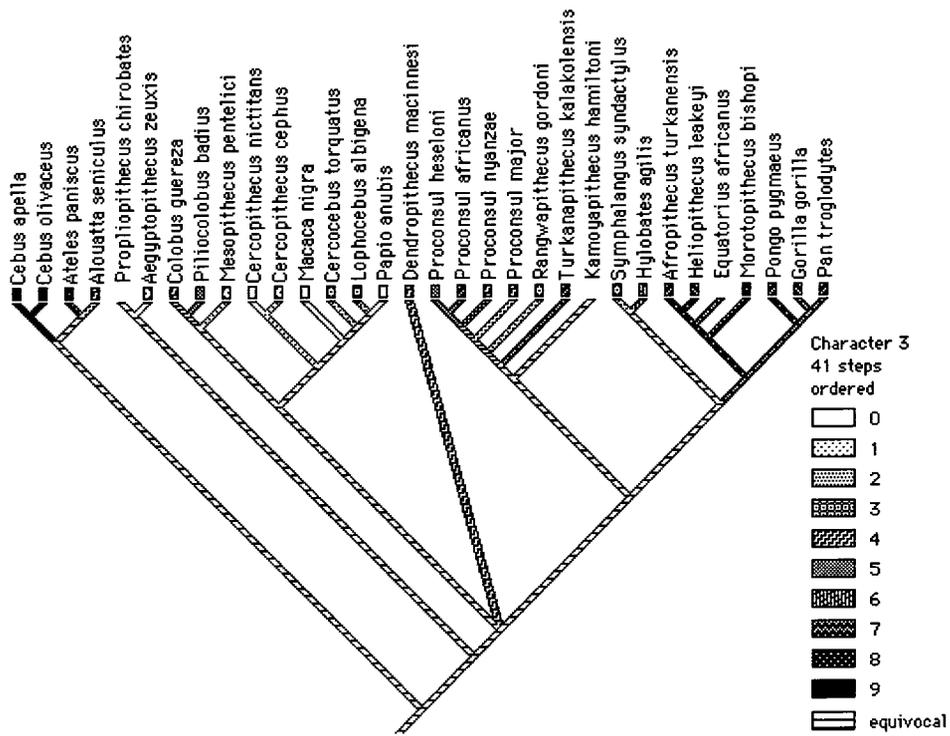
Of the four topologies examined, only that of Harrison and Rook (1997) reconstructs additional hypothetical ancestral nodes (Figure 4.30a). *Contra* Harrison and Rook (1997), however, the ancestral catarrhine and cercopithecoid morphotypes are characterized by moderate enlargement of P<sup>3</sup> relative to M<sup>2</sup>. Furthermore, the proconsulids are not distinguished from the extant hominids by having relatively much smaller premolars, since the results show that both *P. africanus* and *Turkanapithecus* convergently share (according to this phylogenetic scheme) great enlargement of P<sup>3</sup> relative to M<sup>2</sup> with *Pongo pygmaeus*, *Gorilla gorilla*, and *Pan troglodytes*. *P. heseloni*, *P. nyanzae*, *P. major*, and *Dendropithecus*, however, display only moderate enlargement of P<sup>3</sup> in relation to M<sup>2</sup>. The results show, therefore, that of the proconsulids examined, only *Rangwapithecus* possesses relatively much smaller P<sup>3</sup>s; a condition that it is seen to share convergently with *Cercocebus torquatus* and *Symphalangus syndactylus*. These results are quite different than those derived for Character 2 in which *P. africanus*, *P. nyanzae*, and *P. major* are all characterized by great enlargement of



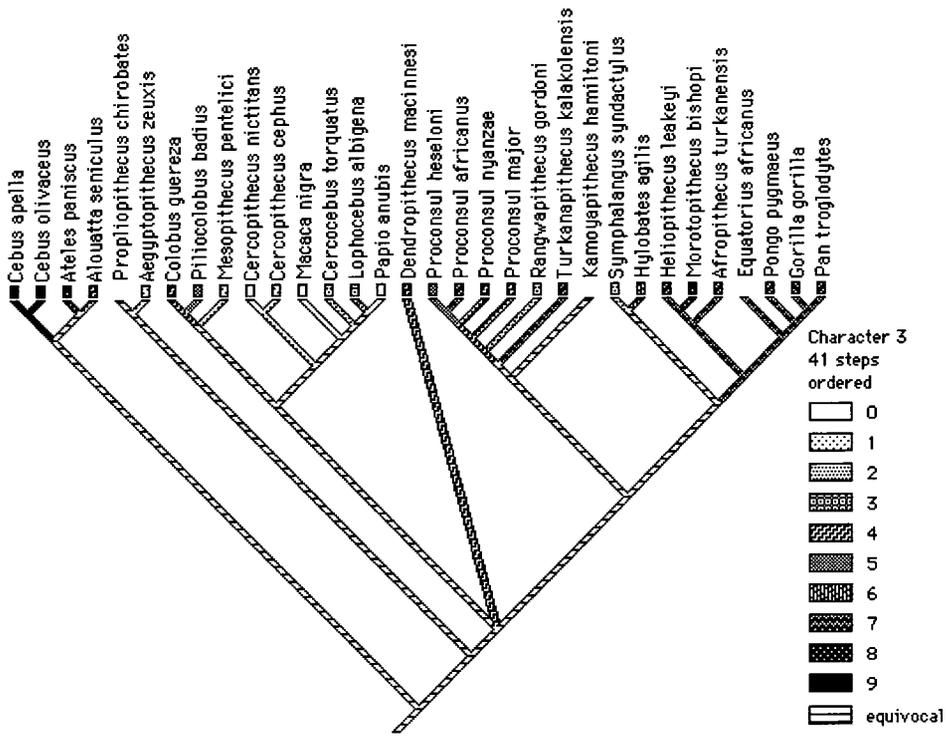
**Figure 4.30a** Character distribution for Character 3 (upper third premolar enlargement relative to second molar) using Harrison and Rook's (1997) topology.



**Figure 4.30b** Character distribution for Character 3 (upper third premolar enlargement relative to second molar) using Harrison's (1987) topology.



**Figure 4.31a** Character distribution for Character 3 (upper third premolar enlargement relative to second molar) using Andrews's (1992) topology.



**Figure 4.31b** Character distribution for Character 3 (upper third premolar enlargement relative to second molar) using Andrews and Martin's (1987a) topology.

P<sup>3</sup> relative to the first molar, and *Rangwapithecus* is characterized by moderate enlargement (see Figures 4.23 – 4.25).

The results of character state optimization using Andrews's (1992) and Andrews and Martin's (1987a) respective topologies are virtually identical to one another (Figure 4.31a,b). As with the results derived from Harrison and Rook's (1997) and Harrison's (1987) phylogenies, however, relatively great enlargement of P<sup>3</sup> in relation to M<sup>2</sup> cannot be interpreted as a definite hominid synapomorphy due to ambiguity at the outgroup node as well as at the ancestral hominoid node.

### **Upper Fourth Premolar**

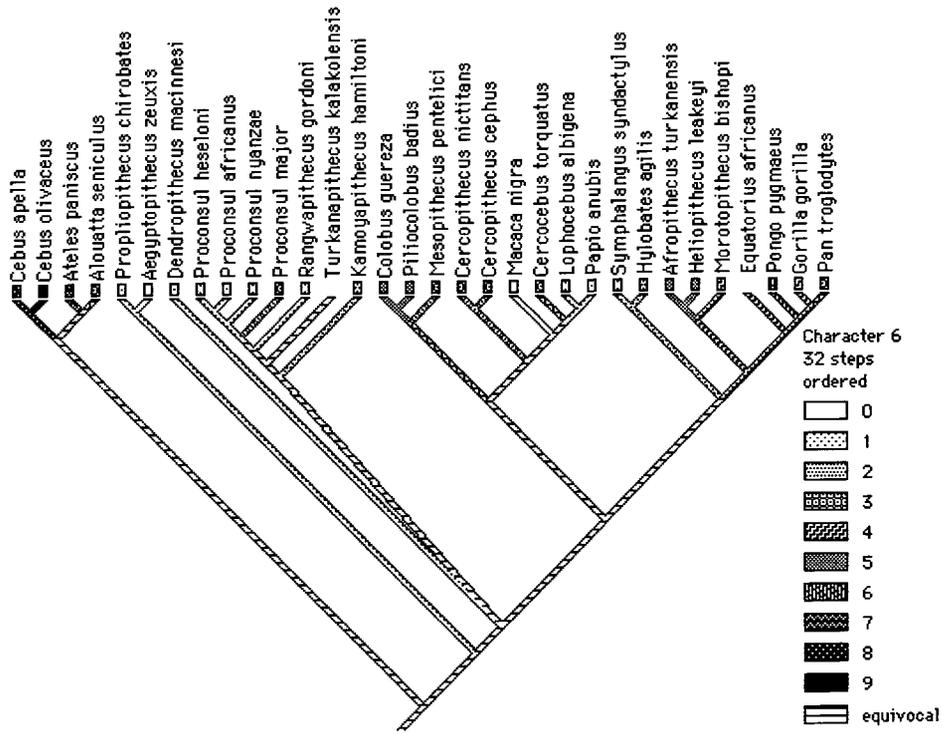
The addition of fossil taxa in character distribution trees derived for Character 6 have the effect of resolving ambiguity at the hypothetical ancestral hominid node in two of the four topologies examined (Figures 4.32 – 4.33; compare with Figure 4.10). Harrison and Rook's (1997) and Andrews's (1992) topologies both reconstruct the ancestral hominid morphotype as being characterized by moderate enlargement of P<sup>4</sup> relative to M<sup>2</sup>, which is also seen to characterize the last common ancestor shared between the clade comprising *Afropithecus*, *Heliopithecus*, and *Morotopithecus* and the extant hominids.

In contrast to the results derived from Andrews's (1992) topology, the results of character distribution using Harrison and Rook's (1997) phylogeny fail to reconstruct any additional hypothetical ancestral nodes (Figure 4.32a). The *Afropithecidae* is characterized by moderate enlargement of P<sup>4</sup> in relation to M<sup>2</sup>; within this clade, both *Afropithecus* and *Heliopithecus* are distinguished from *Morotopithecus* by further enlargement of P<sup>4</sup> that they are seen to share convergently with the extant colobines. Of the remaining proconsulids examined, only *P. major* is characterized by moderate enlargement of P<sup>4</sup> relative to M<sup>2</sup> and

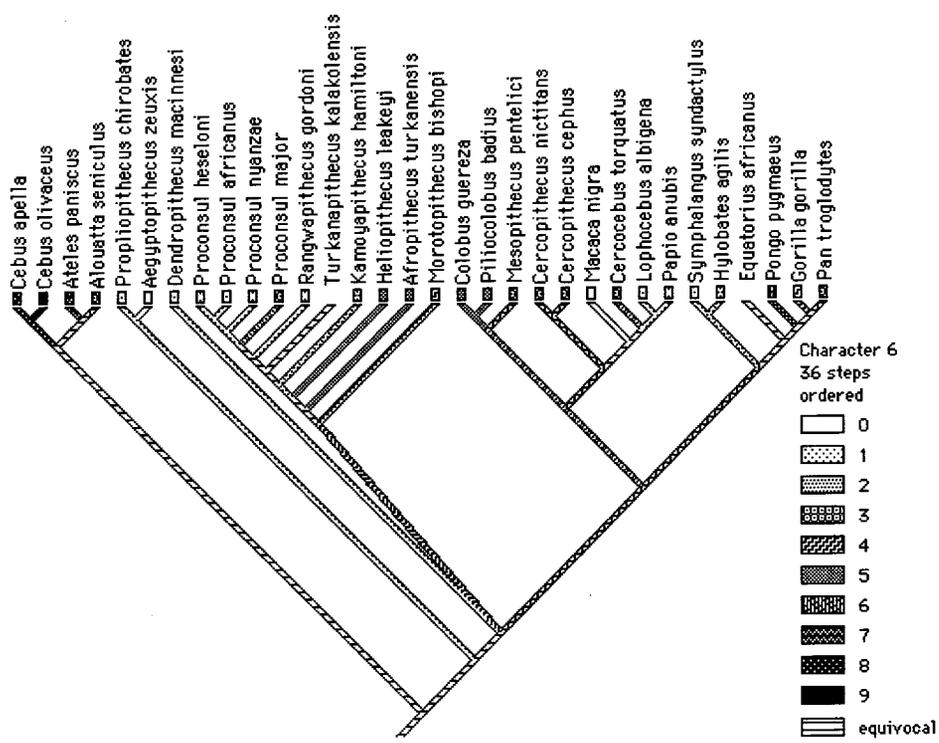
according to this phylogenetic scheme, it shares this character state convergently with *Pan troglodytes*, *Alouatta seniculus*, three species of cercopithecids (*Cercopithecus nictitans*, *Cercopithecus cephus*, and *Cercocebus torquatus*), and the fossil colobine *Mesopithecus*. *P. heseloni*, *P. africanus*, *P. nyanzae*, *Rangwapithecus*, and *Dendropithecus* are all characterized by relatively small P<sup>4</sup>s in relation to M<sup>2</sup>; a condition they are seen to share convergently with *Symphalangus syndactylus*, two species of cercopithecids (*Lophocebus albigena* and *Papio anubis*), and the stem catarrhine *Propliopithecus*. *Kamoyapithecus* is distinguished from this group of fossil taxa by slightly larger P<sup>4</sup>s relative to M<sup>2</sup>, and Figure 4.32a shows that this character state also arose independently in *Hylobates agilis*.

Thus, the results show that with the exception of *P. major*, members of Harrison and Rook's (1997) Proconsulidae and the extant hylobatids are characterized by relatively much smaller P<sup>4</sup>s in relation to M<sup>2</sup> that readily distinguishes them from the extant great apes. The moderate enlargement of P<sup>4</sup> characterizing extant hominids, however, cannot be interpreted as 'derived' relative to the proconsulids and hylobatids as hypothesized by Harrison and Rook (1997), due to ambiguity at the outgroup node and all subsequent nodes below it. Nor can the condition of relatively much smaller premolars in relation to the molars characterizing the proconsulids and hylobatids be interpreted as 'primitive' relative to the great apes.

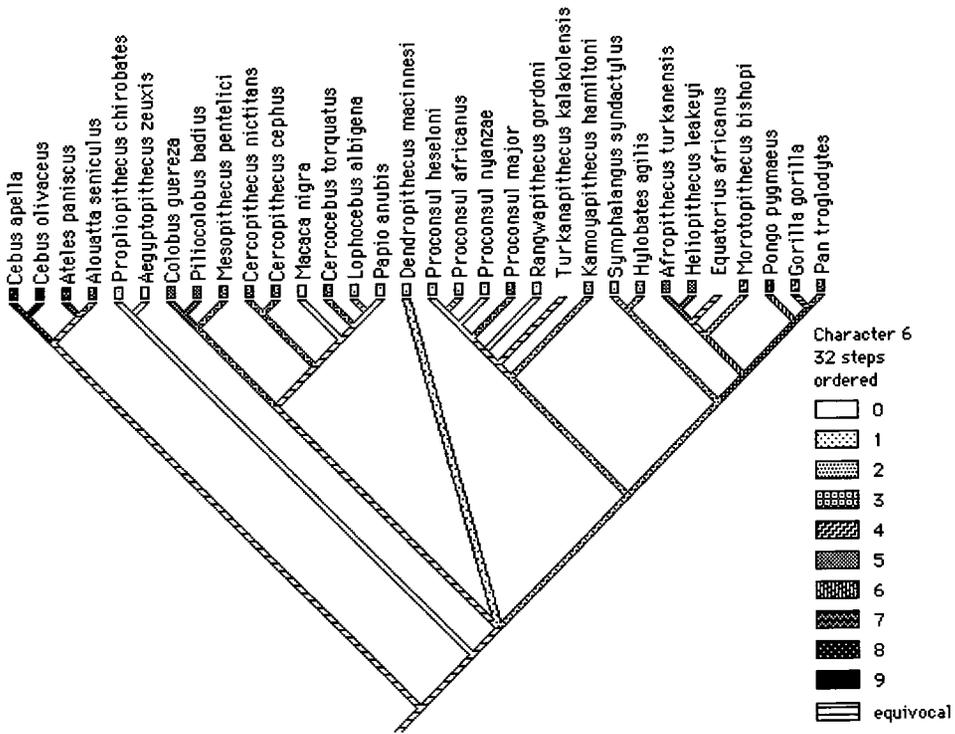
If *Heliopithecus*, *Afropithecus*, and *Morotopithecus* are included within the Proconsuloidea (Harrison, 1987), this has the effect of reconstructing both the hypothetical ancestral cercopithecoid and hominoid morphotypes, but fails to reconstruct the condition found in the last common ancestor of the extant great



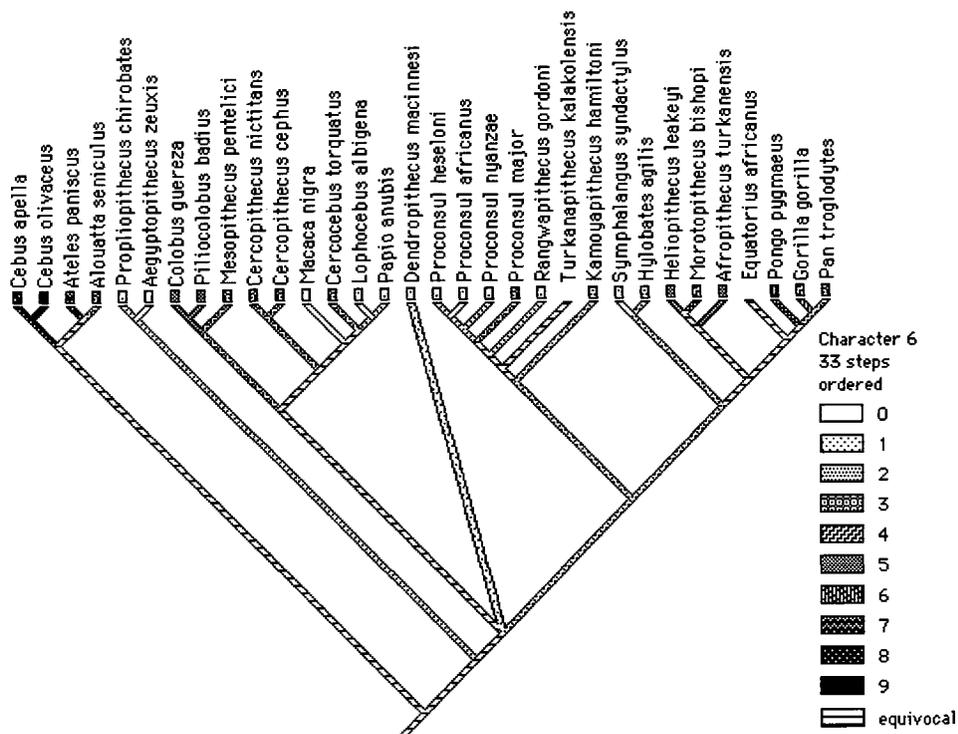
**Figure 4.32a** Character distribution for Character 6 (upper fourth premolar enlargement relative to second molar) using Harrison and Rook's (1997) topology.



**Figure 4.32b** Character distribution for Character 6 (upper fourth premolar enlargement relative to second molar) using Harrison's (1987) topology.



**Figure 4.33a** Character distribution for Character 6 (upper fourth premolar enlargement relative to second molar) using Andrews's (1992) topology.



**Figure 4.33b** Character distribution for Character 6 (upper fourth premolar enlargement relative to second molar) using Andrews and Martin's (1987a) topology.

apes (Figure 4.32b). The ancestral cercopithecoid and hominoid nodes are characterized by a lesser degree of  $P^4$  enlargement relative to  $M^2$  than that seen to characterize the hypothetical hominid ancestor reconstructed using Harrison and Rook's (1997) topology. But again, due to ambiguity at the outgroup node and at the ancestral hominid node, it is impossible to speculate as to whether this character state is 'primitive' relative to the extant great apes.

In stark contrast to these results, the results presented in Figures 4.33a and 4.33b show the ancestral hominoid morphotype to be characterized by small  $P^4$ s relative to  $M^2$  using Andrews's (1992) and Andrews and Martin's (1987a) topologies, in which all proconsulids are included within the Hominoidea. Not only do the results derived from Andrews's (1992) topology support Harrison and Rook's (1997) hypothesis, they also support premolar enlargement as a character defining a clade comprising the Afropithecini + the extant hominids (Andrews, 1992). Based on these results, therefore, it seems reasonable to regard relative  $P^4$  enlargement as a derived condition characterizing the extant great apes + the Afropithecini, and that the proconsulids and hylobatids are diagnosed by the primitive hominoid condition of relatively much smaller premolars. Yet again, however, ambiguity at the outgroup node precludes relative  $P^4$  enlargement from being interpreted as a definite hominid synapomorphy.

## CHAPTER 5

### DISCUSSION AND CONCLUSIONS

#### DISCUSSION

##### INTRODUCTION

The results of the present study raise several important issues that need to be addressed. Both relative upper premolar enlargement and a reduction in upper premolar cusp heteromorphy have failed to diagnose the groups of living taxa for which they were proposed by Andrews (1985, 1992; Andrews and Martin, 1987a) and Harrison (1987; Harrison and Rook, 1997); this indicates that the phylogenetic signal contained within these characters is comparatively weak.

Furthermore, the amount of variation in the expression of character states across the extant taxa examined, coupled with the numerous occurrences of convergent evolution, begs for a functional interpretation for an adaptation towards relative upper premolar enlargement and cusp heteromorphy on the upper premolars. Specifically, an hypothesis of relative premolar enlargement and cusp heteromorphy as a functional adaptation to hard object feeding will be assessed relative to both living and fossil taxa examined in the present study. This section also highlights the significance of the results of the present study with respect to the alternative phylogenetic hypotheses regarding the phyletic position of *Proconsul* relative to the extant apes, as advanced by Andrews (1985, 1992; Andrews and Martin, 1987a) and Harrison (1987; Harrison and Rook, 1977).

##### RELATIVE UPPER PREMOLAR ENLARGEMENT

The results of character state analyses using only extant anthropoid taxa show

that relative upper premolar enlargement does not diagnose living great apes as a clade. Only one of the five characters tested pertaining to relative upper premolar enlargement was shown to have a synapomorphous condition within the Hominidae. While Character 3 was in fact shown to support the monophyly of an extant great ape clade, the relative enlargement of the third premolar in relation to the second molar cannot be interpreted as a definite hominid synapomorphy due to ambiguity at the outgroup node as well as all subsequent nodes below it (see Figure 4.9). As such, it is not possible to conclude that this character state is 'derived' relative to the condition found in the hypothetical anthropoid and hominoid ancestors since the direction of character change is not known.

Of the remaining characters tested, only Character 7 also reconstructs the ancestral hominid morphotype (see Figure 4.11). The moderate enlargement of P<sup>4</sup> relative to the first molar characterizing the last common ancestor of the extant hominids, however, is a retention of the ancestral catarrhine condition that is also retained at the base of the Hominoidea. This is interesting only inasmuch as the presence of this character state in *Gorilla gorilla* may simply represent retention of the primitive condition in the absence of negative selection.

Furthermore, the results of character evolution analysis using only extant taxa clearly show that relative upper premolar enlargement is an extremely homoplasious character (see Figures 4.8 – 4.11). The evidence for this is clearly reflected in the low consistency indices for all five character distribution trees, which range from 0.31 to 0.55 (see Table 4.4). As such, this indicates that relative upper premolar enlargement is rather useless in providing evidence of common ancestry relationships, since it can be seen to have evolved independently in several different lineages. For example, the results presented in Figure 4.8 show

that *Pongo pygmaeus* evolved a relatively greatly enlarged P<sup>3</sup> convergently with *Cebus apella*, and Figures 4.10 – 4.11 show that *Gorilla gorilla* and *Alouatta seniculus* convergently share a relatively moderately enlarged P<sup>4</sup>.

The character distribution tree corresponding to Character 5 displays the highest amount of homoplasy of all five trees, and Figure 4.10 shows that almost every taxon examined exhibits a slightly different degree of upper fourth premolar enlargement relative to the first molar. The character distribution tree corresponding to Character 7, in which the same character was measured using a different index, yields the second lowest CI but exhibits slightly more convergences than Character 5.

The high amount of variation in relative upper premolar enlargement across all anthropoid taxa examined, and the failure of this character to diagnose extant ape clades, indicates that the strength of the phylogenetic signal contained within this character is comparatively weak. So the question then becomes, what is driving the selection for an adaptation of relatively greatly enlarged premolars among extant taxa such as *Pongo pygmaeus*, *Cebus apella*, *Cebus olivaceus*, and *Ateles paniscus*? The results show that not only are these taxa consistently characterized by the greatest relative upper premolar enlargement of all the extant species analyzed, this enlargement is greatest for the anterior upper premolar (see Figures 4.2 and 4.3).

It is possible that the underlying function of the upper premolars is the same for all four extant taxa and, therefore, there is strong selective pressure for an adaptation towards relative upper premolar enlargement. The one commonality linking *Pongo pygmaeus*, *Cebus apella*, *Cebus olivaceus*, and *Ateles paniscus* together is their diet; all species are frugivorous and incorporate a high proportion

of hard fruit and seeds in their dietary regime. For example, the fruit diet of *Cebus apella* contains 41.6% husked fruits and this species has been observed using its premolars or molars for processing larger fruits that are covered with a thick skin or husk (Janson and Boinski, 1992). Furthermore, this species exploits very hard palm seeds and tough vegetable tissues during periods in which fruit is scarce (Janson and Boinski, 1992). Janson and Boinski (1992) reasoned that specialization for processing extreme food types in *Cebus apella* is directly reflected in dental traits that include the presence of very thick dental enamel and a robustly built mandible. Indeed, a strong functional association between dental enamel thickness and dietary adaptation has been demonstrated by Dumont (1995). Thus, just as the presence of thick enamel would be an advantageous adaptation to hard fruit eaters in that it delays the onset of dentine penetrance, it is also possible that a widely spread crown on the anterior upper premolar functions to distribute high forces from the cusps of the tooth across an enlarged crown base (Leakey and Walker, 1997). The specialization of relatively great enlargement of P<sup>3</sup> may have evolved convergently in *Cebus apella*, *Cebus olivaceus*, *Ateles paniscus*, and *Pongo pygmaeus*, due to the fact that this character functions to dissipate the high forces that are ultimately generated by processing the hard fruit items and seeds that are known to be a major component of these species's diets.

The presence of relatively great upper premolar enlargement in fossil taxa such as *Afropithecus*, *Heliopithecus*, *Morotopithecus*, and *Equatorius* hint at a similar adaptation for hard fruit eating. Leakey and Walker (1997:234) have argued that "*Afropithecus* was almost certainly a committed sclerocarp feeder" since its robustly built jaw, large-rooted and low-crowned laterally splayed canines, procumbent incisors, and thick dental enamel mimic the specializations seen in the

pitheciines who are known dedicated seed predators. Of course the exact pitheciine morphology is not necessarily duplicated in *Afropithecus*, but some amount of difference is expected given its geologic age and differences in geographical distribution and body size (Leakey and Walker, 1997). Nevertheless, *Afropithecus* possesses the majority of craniodental features characterizing the pitheciines, of which its canine morphology perhaps provides the most convincing evidence pointing to an adaptation of sclerocarp feeding.

The combination of a reduction in crown length and the robust, stout roots characterizing the canines of *Afropithecus*, coupled with a lack of sexual dental dimorphism, suggest that this fossil taxon used its canines more for food preparation rather than aggressive display (Leakey and Walker, 1997). Indeed, this character combination is present in the pitheciine *Chiropotes*, which uses its canines to puncture and open hard fruit items (Leakey and Walker, 1997). The fossil hominoid *Morotopithecus* displays a similar upper canine morphology, as well as other sclerocarp adaptations including procumbent upper incisors, and buccal and lingual basal flare of the upper premolars. Though *Equatorius* is also characterized by the latter features, its canines not only show pronounced sexual dimorphism, they have longer crowns relative to the roots, which led Leakey and Walker (1997:235) to conclude that the sclerocarp adaptations of *Equatorius* were “much less developed than in *Afropithecus*”. Unfortunately, BM(NH) M.35145 does not preserve the canine or the lateral incisor; the alveoli, however, suggest that *Heliopithecus* possessed a large, robust canine and it is possible that the lateral incisor root may have been procumbent (Leakey and Walker, 1997). Apart from this speculation, it is certain that *Heliopithecus* shares the same degree of relative upper premolar enlargement characterizing *Afropithecus*, *Morotopithecus*,

and *Equatorius* (see Figures 4.13 and 4.14).

It is hypothesized, therefore, that the buccal and lingual basal flare characterizing the upper premolars of the fossil hominoids *Afropithecus*, *Heliopithecus*, *Morotopithecus*, and *Equatorius* functions to diffuse the forces that are generated by puncturing and breaking open hard fruit items with the canines. Confirmation of this obviously requires further fossil discoveries so that hypothesis testing regarding this character is based on comparative anatomy rather than speculative morphological traits. Furthermore, it would be interesting to test whether relative upper premolar enlargement among extant anthropoid taxa is correlated with percentage of hard objects in the diet; such a database, however, does not yet exist.

Based on the findings of the present character state analysis, therefore, it is hypothesized that the resemblances in upper premolar morphology between *Afropithecus*, *Heliopithecus*, *Morotopithecus*, and *Equatorius* and the extant Asian great apes (as well as the living platyrrhines *Cebus apella*, *Cebus olivaceus*, and *Ateles paniscus*), are convergent. As such, relative upper premolar enlargement is related to a similar adaptation to hard object feeding in these living and fossil taxa, and does not indicate a close phylogenetic relationship amongst them.

Despite the failure of relative upper premolar enlargement to diagnose the extant great apes as a clade, some interesting comparisons can be made between these taxa, and parallels may be drawn with *Proconsul* spp. The results of character state analyses performed in the present study found that not only are the dental proportions of *Pan troglodytes* generally smaller than those of *Pongo pygmaeus* and *Gorilla gorilla*, but *Pan troglodytes* consistently displays less of a differential between the premolar to first molar ratio and the premolar to second

molar ratio than *Gorilla gorilla*. This is due to the fact that *Pan troglodytes* exhibits first and second molars that are virtually identical to one another in terms of occlusal area (mean occlusal area of M<sup>1</sup> is 115.14, and mean occlusal area of M<sup>2</sup> is 116.79). In fact, eight of the twenty specimens of *Pan troglodytes* analyzed, displayed an M<sup>1</sup> that was larger in occlusal area than M<sup>2</sup>. Interestingly, these eight specimens were equally represented by both females and males. Furthermore, *Pongo pygmaeus* displays a similar lack in disparity between both premolar and molar ratios since three of the nine specimens examined possessed slightly larger M<sup>1</sup>'s than M<sup>2</sup>'s, of which all three specimens were represented by females. In stark contrast, all specimens of *Gorilla gorilla* display a considerably larger occlusal area of M<sup>2</sup> compared to that of M<sup>1</sup> (mean occlusal area of M<sup>1</sup> is 224.19, and mean occlusal area of M<sup>2</sup> is 251.61); hence, *Gorilla gorilla* consistently yielded a slightly lower premolar to second molar ratio than premolar to first molar ratio. All three extant taxa, however, are similar in that they possess larger upper third premolars than fourth premolars and thus, all exhibit a larger P<sup>3</sup>/molar ratio than P<sup>4</sup>/molar ratio.

The interesting parallel to be drawn here is that similar to *Gorilla gorilla*, *Proconsul* spp. displays a pronounced disparity between the premolar to first molar ratio and the premolar to second molar ratio, such that the former is consistently much higher than the latter. This has the effect of categorizing *Proconsul* spp. as having smaller premolars in relation to M<sup>2</sup> (Characters 3 and 6), but enlarged premolars in relation to M<sup>1</sup> (Characters 2, 5, and 7). The fact that they possess considerably larger upper second molars than first molars, however, appears to be artificially deflating the premolar/M<sup>2</sup> ratio. This is especially true for *P. nyanzae* and *P. major*, both of whom exhibit much larger M<sup>2</sup>'s than M<sup>1</sup>'s, even in

comparison to *Gorilla gorilla*: mean occlusal area of M<sup>1</sup> for *P. nyanzae* is 95.67, and 141.61 for M<sup>2</sup>; and occlusal area of M<sup>1</sup> for *P. major* is 105.09, and 163.35 for M<sup>2</sup>. Therefore, in Figure 4.13 both *P. major* and *P. nyanzae* are given a code of 7 for Character 2, which is identical to that of *Pongo pygmaeus*, but in Figure 4.14 both *Proconsul* species are coded as 4 for Character 3, which is markedly lower than the code of 7 allocated to *Pongo pygmaeus*. Thus, studies in which premolar proportions are analyzed relative only to the upper second molar will be more successful at supporting an hypothesis of *Proconsul* spp. possessing relatively smaller premolars than the extant hominids.

#### UPPER PREMOLAR CUSP HETEROMORPHY

The results of character state analysis using only extant anthropoid taxa show that a reduction in upper premolar cusp heteromorphy does not diagnose living great apes as a clade nor does it diagnose extant hominoids as a clade. Neither of the two characters tested pertaining to upper premolar cusp heteromorphy can be interpreted as having a synapomorphous condition within the Hominidae or the Hominoidea, due to retention of the ancestral anthropoid condition at the base of both of these nodes. In fact, the results of character state optimization for cusp heteromorphy on the upper third premolar (Character 1) show that both *Pongo pygmaeus* and *Gorilla gorilla* are characterized by the ancestral anthropoid condition in which the paracone is slightly higher than the protocone, while *Pan troglodytes* and *Symphalangus syndactylus* convergently share further reduction in cusp heteromorphy with four cercopithecoid species (see Figure 4.8). In contrast, the results of character state optimization for cusp heteromorphy on the upper fourth premolar (Character 4) show that virtually all extant anthropoid taxa

examined retain the ancestral anthropoid condition, in which both the paracone and protocone are of more or less equal height (see Figure 4.9). Interestingly, the atelines are autapomorphic in possessing P<sup>4</sup>s that are relatively quite cusp heteromorphic.

The character distribution tree corresponding to Character 4 shows the least amount of homoplasy of both the characters tested (CI is 0.60; see Table 4.4). This is in stark contrast to the character distribution tree derived for Character 1 in which the tree length (23 steps) in relation to the number of possible character state changes (8 changes) indicates that this tree has a greater number of statements of homoplasy, and fewer statements of homology for the data used, than the tree derived for Character 4. Indeed, the results presented in Figure 4.8 show that two of the character states are convergent among the hominoids and several cercopithecoids, which indicates that cusp heteromorphy on the upper third premolar is a rather useless indicator of common ancestry relationships, since these particular character states evolved independently in the taxa that are characterized by them. Similarly, cusp heteromorphy on the upper fourth premolar is phylogenetically uninformative, but for a different reason. Although the character distribution tree corresponding to Character 4 contains more statements about homology than homoplasy, the results presented in Figure 4.9 show that the character state diagnosing virtually all members of the ingroup represents a symplesiomorphy. As such, the character state in which the cusps of P<sup>4</sup> are of more or less equal height does not indicate common ancestry relationships within the Anthropeida, due to the fact this character state originated earlier than any members included within this study group (Brooks and McLennan, 1991). Therefore, in order for cusp heteromorphy on P<sup>4</sup> to become

phylogenetically useful, the temporal scale of the present study needs to be increased (Brooks and McLennan, 1991).

The failure of a reduction in cusp heteromorphy on P<sup>3</sup> to diagnose either an extant great ape clade or a living hominoid clade, coupled with the high amount of variation in P<sup>3</sup> cusp heteromorphy across all extant anthropoid taxa examined, indicates that the strength of the phylogenetic signal contained within this character is comparatively weak. What remains unclear, however, is what then is driving selection for greater cusp heteromorphy on the anterior upper premolar than on the fourth upper premolar. The results of T-tests for equality of means of males and females for Character 1 failed to show significant differences ( $p < 0.05$ ) in cusp heteromorphy on P<sup>3</sup> between the sexes, even for species that are characterized by extreme sexual dimorphism in canine length (see Table 4.2). Thus, an hypothesis of the males of species characterized by sexual dental dimorphism displaying greater cusp heteromorphy on P<sup>3</sup> than the females of the species cannot be supported.

If cusp heteromorphy on P<sup>3</sup> is related neither to phylogeny nor to sexual dental dimorphism, then perhaps the anterior upper premolar is assuming a caniniform form in some anthropoid species because its function is similar to that of the upper canine. As mentioned above, hard object feeders tend to use the canine and/or premolars to puncture and break open tough-skinned fruit items; the results presented in Figure 4.8, however, indicate that both cebid species exhibit the lowest degree of cusp heteromorphy on P<sup>3</sup> than any other extant anthropoid taxa examined. Furthermore, *Pongo pygmaeus* is characterized by P<sup>3</sup>s in which the paracone is only slightly more elevated than the protocone. Interestingly, the purported fossil sclerocarp feeder *Heliopithecus* shares with the extant folivore

*Colobus guereza* the highest degree of P<sup>3</sup> cusp heteromorphy of all extant and extinct taxa analyzed. Unfortunately, due to weathering and preservation, data of relative cusp height on P<sup>3</sup> is not available for *Afropithecus* or *Morotopithecus*, but Figure 4.12 shows that *Equatorius* is not characterized by any substantial degree of cusp heteromorphy on the anterior upper premolar.

Thus, the results of the present analysis are inconclusive with regards to the functional significance of cusp heteromorphy on the anterior upper premolar, since the results show that no one dietary adaptation appears to be correlated with either extreme cusp heteromorphy or a reduction in the disparity in height between the paracone and protocone on P<sup>3</sup>.

#### **PROCONSUL IN A COMPARATIVE CONTEXT**

Previous phylogenetic analyses that have attempted to place the fossil taxon *Proconsul* relative to living hominoids have argued that, although *Proconsul* does not share the derived condition of relative upper premolar enlargement with the extant hominids, it is linked to the Hominoidea through a reduction in upper premolar cusp heteromorphy (Andrews, 1985, 1992; Andrews and Martin, 1987a, b). Conversely, *Proconsul* has been excluded from the Hominoidea partly on the basis that it lacks the derived hominid conditions of relative upper premolar enlargement and a reduction in upper premolar cusp heteromorphy (Harrison, 1987; Harrison and Rook, 1997). In light of these statements, the results of the present study are significant for two very important reasons. Firstly, the analyses of Andrews (1985, 1992; Andrews and Martin, 1987a) and Harrison (1987; Harrison and Rook, 1997) were based on the *a posteriori* determination of character states of both the living and fossil taxa included in these studies. The

results of character state analyses using only extant anthropoid taxa in the present study, however, show that not only are both dental characters extremely homoplasious, they do not ultimately diagnose the groups of living taxa for which they were proposed. Thus, any phylogenetic analysis that uses these characters in an attempt to place *Proconsul* relative to the living hominoids will be fundamentally flawed, since these characters do not even provide evidence of common ancestry relationships among extant anthropoid taxa.

These findings underscore the importance of testing characters *a priori* to determine their reliability as phylogenetic indicators. A character is only useful for phylogenetic inference if it can first be shown to be congruent among extant primate taxa. If a character *can* be shown to resolve relationships among living taxa, only then can it be applied to the fossil record in the hope of deriving some meaningful inferences about the complex evolutionary history of the order Primates.

Secondly, by virtue of the fact that *Proconsul* is characterized by considerably larger upper second molars than first molars, premolar proportions determined relative to the first molar will consistently be higher than proportions determined relative to the second molar. Furthermore, *Proconsul* possesses larger anterior upper premolars than fourth premolars. Therefore, the results of character state analyses performed in the present study characterize *Proconsul* by relatively great enlargement of P<sup>3</sup> in relation to M<sup>1</sup> (which it is seen to share with two extant hominid taxa), but only moderate enlargement of P<sup>3</sup> relative to M<sup>2</sup> (see Figures 4.13 and 4.14). Moreover, *Proconsul* is defined by relatively small P<sup>4</sup>s in relation to M<sup>2</sup>, but by moderate enlargement of P<sup>4</sup> relative to M<sup>1</sup> (which *P. nyanzae* is seen to share with one extant hominid species) (see Figures 4.17 and 4.16).

Thus, analyses in which premolar proportions are considered relative only to the first molar will tend to group some or all *Proconsul* species with the extant hominids, whereas analyses that consider premolar proportions relative only to the second molar will tend *not* to group *Proconsul* with the extant hominids. Hence, data derived from premolar to second molar ratios will tend to support Harrison and Rook's (1997) hypothesis in which *Proconsul* is purported to be distinguished from the extant hominids by exhibiting relatively much smaller upper premolars.

## CONCLUSIONS

The results of the present study indicate that there is only a very weak phylogenetic signal contained within relative upper premolar enlargement and a reduction in upper premolar cusp heteromorphy, as both dental characters have failed to diagnose extant apes and/or great apes as a clade. The results indicate that relative upper premolar enlargement appears to be a dietary adaptation to hard object feeding, however, the functional significance of upper premolar cusp heteromorphy or the lack thereof, presently remains unclear.

Rather than clarifying the directionality of character evolution for both dental characters, the inclusion of fossil taxa has had the effect of causing more ambiguity at the hypothetical ancestral nodes in the majority of topologies examined. This highlights the fact that both characters provide more statements about homoplasy than they do about shared homology. Thus, phylogenetic analyses that include relative upper premolar enlargement and/or upper premolar cusp heteromorphy in an attempt to place fossil taxa relative to extant species, and to one another, will be fundamentally flawed, since neither character provides convincing evidence of common ancestry relationships.

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