6 How reliable are current estimates of fossil catarrhine phylogeny? An assessment using extant great apes and Old World monkeys

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Introduction

Cladistic analysis has been used for more than 20 years to reconstruct the phylogenetic relationships of fossil catarrhine species and genera (e.g. Delson & Andrews, 1975; Eldredge & Tattersall, 1975; Delson, 1977; Delson *et al.*, 1977; Tattersall & Eldredge, 1977; Andrews, 1978, 1992; Corruccini & McHenry, 1980; Harrison, 1982; Skelton & McHenry, 1986; Wood & Chamberlain, 1986, 1987; Andrews & Martin, 1987; Chamberlain & Wood, 1987; Strasser & Delson, 1987; Stringer, 1987; Wood, 1988, 1991, 1992; Skelton & McHenry, 1992; Lieberman *et al.*, 1996; Begun *et al.*, 1997; Cameron, 1997; Rae, 1997; Strait *et al.*, 1997). However, it is now apparent that, in contrast to the situation with higher-level primate taxa (Harrison, 1993), few of the relationships supported by these analyses can be considered to be reliable. This is demonstrated by the small increases in length required to alter the topologies of the most parsimonious cladograms. For example, the addition of only one step converts the *Homo* monophyly seen in Wood's (1991) most parsimonious cladogram into *Homo* paraphyly, as well as altering the relationships of *A. africanus* (Wood, 1992). Likewise, the addition of two steps to the cladogram preferred by Strait *et al.* (1997) results in *Homo* paraphyly (Wood & Collard, 1999). These examples are taken from the hominin palaeontological literature, but they could easily have been taken from studies of Miocene hominoids, Eurasian pliopithecids, or fossil Old World monkeys (e.g. Harrison, 1993; Rae, 1997). The unreliability of the most parsimonious cladograms is also illustrated by the results of Corruccini's (1994) bootstrap re-analysis of hominin data from Wood & Chamberlain (1986), Skelton *et al.* (1986), Chamberlain & Wood (1987) and Skelton & McHenry (1992). He found the relationships of most of the species and genera to be ambiguous. The only statistically significant result he obtained was that *Paranthropus robustus* and *P. boisei* are more closely related to each other than they are to any other species.

Our inability to reliably reconstruct the phylogenetic relationships of fossil catarrhine species and genera has frequently been attributed to faulty alpha taxonomy, the choice of characters examined or to the way in which the cladistic methodology has been implemented (Chamberlain & Wood, 1987; Skelton & McHenry, 1992; Strait *et al.*, 1997; Skelton & McHenry, 1998;

Strait & Grine, 1998). Recently, however, it has been suggested that the
problem may lie with the data on which we normally rely (Hartman, 1988;
Lieberman, 1995, 1997, 1999; Lieberman *et al.*, 1996). Unlike the investiga-
tion of the relationships between living taxa, in which any available evi-
dence, be it anatomical, biochemical, genetic or behavioural, can be used to
establish relationships, studies involving fossil taxa are limited to those
parts of the phenotype that are commonly preserved in the fossil record. As
far as the fossil catarrhines are concerned, this means that cladistic studies
are mostly based on evidence that can be gleaned from the various hard
tissues that make up the bones and teeth. Thus, most studies have been
based upon dental, cranial, mandibular and, to a lesser extent, postcranial
characters. This is certainly so for the fossil hominins (e.g. Eldredge &
Tattersall, 1975; Tattersall & Eldredge, 1977; Delson *et al.*, 1977; Corruccini &
McHenry, 1980; Skelton *et al.*, 1986; Wood & Chamberlain, 1986, 1987;
Chamberlain & Wood, 1987; Arsuaga *et al.*, 1991; Wood, 1991, 1992; Skelton
& McHenry, 1992; Lieberman *et al.*, 1996; Strait *et al.*, 1997), and perusal of
published cladograms suggest that this is also the case for investigations of
the evolutionary relationships of other fossil catarrhines (e.g. Harrison,
1982, 1989; Andrews & Martin, 1987; Strasser & Delson, 1987; Andrews, 1992;
Rose *et al.*, 1992; Benefit, 1993; Moyà-Solà & Köhler, 1993, 1995; Kelley *et al.*,
1995; Begun *et al.*, 1997; Cameron, 1997; McCrossin & Benefit, 1997; Rae,
1997).

How can we assess the reliability of catarrhine craniodental evidence for
reconstructing the phylogenetic relationships of species and genera? One
approach is to analyse comparable evidence from closely-related extant
taxa whose relationships have been established using molecular techniques
and judge the resulting morphology-based hypotheses against the molecu-
lar phylogeny (Hartman, 1988). Congruence between the morphological
and molecular phylogenies for the extant taxa indicates that the fossil
evidence can be reasonably assumed to be reliable for phylogenetic recon-
struction, whereas incongruence suggests the converse.

This approach, which assumes that molecular data are superior to mor-
phological data for phylogenetic reconstruction, is rejected by some
cladists, who deny that some classes of data are more reliable than others for
the purposes of phylogenetic reconstruction, and argue that cladistic ana-
lyses should be based on all the available evidence (e.g. Smith, 1994; Kluge,
1998). We understand why these workers take this view, but believe they are
mistaken. There are several reasons why, when a conflict occurs between
molecular and hard tissue-based phylogenies, the former should be fa-
voured, at least at the low taxonomic levels being considered here. First,
phylogenetic relationships are genetic relationships. It is genes that are
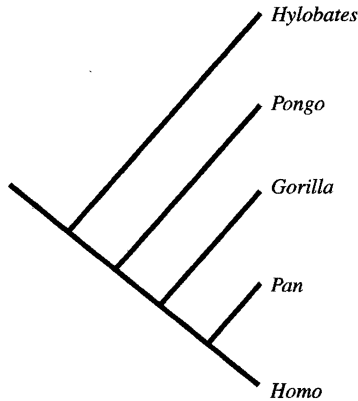
[Figure 6.1]
Hominoid molecular relationships.

passed between generations, not morphological characters. Thus, in phylogenetics, morphology can never be more than a proxy for molecular data. Secondly, it is well documented that many reproductively-defined species are genetically distinct, but dentally and osteologically indistinguishable. Since speciation events create phylogenetic relationships, there is thus an a priori expectation that characters of the teeth and skeleton will be less useful for phylogeny estimation than genetical characters. Thirdly, because many osseous and other morphological characters are clearly influenced by epigenetic effects, such as the forces generated by chewing (Lieberman *et al.*, 1996; Lieberman & Wood, 1999), they can be expected to mislead us more frequently than molecular evidence. Lastly, some of the techniques of molecular phylogenetics have been successfully tested on laboratory taxa of known phylogeny (Fitch & Atchley, 1987; Atchley & Fitch, 1991; Hillis *et al.*, 1992), whereas comparable analyses of morphological data have not been successful (Fitch & Atchley, 1987).

Within the primates, there are several examples of cladograms that are supported by multiple, independent, lines of biomolecular and karyological evidence. By any criteria, the molecular-based phylogeny for the living hominoids is well-established (Ruvolo, 1994, 1995, 1997), and we elected to use this as one test of the likely phylogenetic utility of fossil catarrhine craniodental data (Figure 6.1). Another group for which there is molecular data, albeit on a less comprehensive scale as those for the living hominids, is the papionins (Disotell, 1994, 1996; Disotell *et al.*, 1992; Harris & Disotell, 1998), and we used this as the other test group (Figure 6.2).
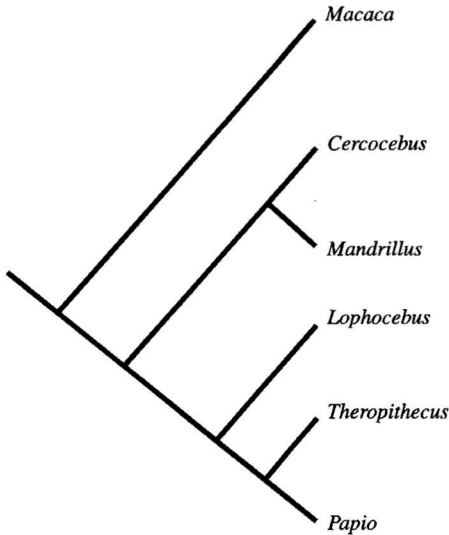
[Figure 6.2]
Papionin molecular relationships.

Materials

Morphology can be translated into character states for cladistic analysis in two main ways. The first breaks the phenotype up into anatomical components and expresses the variation within each component in terms of qualitative categories, or 'states'. Thus, an osseous prominence is 'strong', 'reduced' or 'absent', a bony contour is described as 'arched' or 'less-arched', and a feature is categorised as 'not developed' or 'developed'. To date, the majority of cladistic analyses of the catarrhines have used this approach (e.g. Delson & Andrews, 1975; Eldredge & Tattersall, 1975; Delson *et al.*, 1977; Skelton *et al.*, 1986; Skelton & McHenry, 1992; Lieberman *et al.*, 1996; Begun *et al.*, 1997; Strait *et al.*, 1997). However, we are not persuaded that it is a desirable way to express morphological variation, since it is clear that the assessment of discrete character states is often a highly subjective exercise. This is demonstrated by a recent debate concerning the Miocene hominoid *Afropithecus turkanensis*, in which some researchers scored its inferior mandibular torus as 'weakly-developed', while others considered the torus to be 'well-developed' (Leakey & Leakey, 1986; Andrews & Martin, 1987; Conroy, 1994). It is also demonstrated by the difficulty encountered by Strait *et al.* (1997) and Ahern (1998) in reproducing the scores used in previous analyses of the early hominins. Another reason for rejecting

122 qualitative character assessment is that it is difficult to counter the confounding effects of body size differences between taxa (Kappelman, 1996). This point is exemplified by the assessment of Wood *et al.* (1998) of the likelihood of association between OH 8 and OH 35, the *Homo habilis* left talus and distal left tibia from Olduvai Gorge, Tanzania. When Wood and co-workers did not correct for body size, they obtained the same result as had been obtained in earlier discrete character assessments: the talus and the tibia appeared to have belonged to the same individual. However, when they controlled for differences in body size, they found that it was questionable whether the two bones had come from animals belonging to the same species, let alone the same individual.

The second way of expressing character state variation is to collect interlandmark distances, and then use one of a number of coding methods to break up the continuous distribution into discontinuous states. Opponents of this approach complain that measurements are unsuitable for cladistic analysis, that the coding methods break the spectrum of measurements into 'artificial' character states, and/or that cladistic analyses based on measurement data are no more than 'thinly-disguised' phenetic analyses (e.g. Pimentel & Riggins, 1987; Crisp & Weston, 1987; Cranston & Humphries, 1988; Crowe, 1994; Disotell, 1994; Moore, 1994). We contend, however, that none of these objections is valid. As Maddison *et al.* (1984), Felsenstein (1988), Swofford & Olsen (1990), Lieberman (1995) and, most especially, Rae (1998) have pointed out, there is no intrinsic difference between discrete and continuous characters as far as the cladistic methodology is concerned. The only criterion a character must fulfil for use in a cladistic analysis is that its states are homologous, and measurement-based characters can meet this criterion as well as discrete characters (Rae, 1998). This is supported by the character conflict indices obtained in cladistic analyses of the early hominins. If the metrical method of capturing information for phylogenetic analysis really is unsuitable for cladistic analysis, one would expect there to be more character conflict in studies that used measurement-based characters than in those that employed non-metrical characters. Yet, the character conflict indices obtained by Chamberlain & Wood (1987) and Wood (1991, 1992) from quantitative data are comparable with those obtained by Lieberman *et al.* (1996) and Strait *et al.* (1997) from qualitative data. The 'artificiality' argument is also easy to refute, for coding is no more 'artificial' than is the decision to break up into discontinuous states what is, with very few exceptions, such as tooth cusp and root number, continuously-distributed morphology. Moreover, a number of the methods that have been developed to convert continuously distributed characters into discrete character states are based on statistical tests, and are therefore, by convention, non-arbitrary

(e.g. Thorpe, 1984; Strait *et al.*, 1996). Lastly, it is difficult to understand the argument that cladistic analyses based on measurement data are just phenetic analyses in disguise, because unlike phenetic analysis, metrical cladistics does not group taxa on the basis of overall similarity. In metrical cladistics, as in non-metrical cladistics, only those parts of the phenotype that are inferred to be shared-derived are used to group taxa into clades.

We accept that some measurements may be unsuitable because their termini span structures that have different embryonic origins, and perhaps therefore different phylogenetic histories. However, we contend that in many cases a combination of measurements can provide just as focused, but more objective, information about a structure than can an equivalent non-metrical description. It is noteworthy that few opponents complain about three other aspects of the metrical approach. First, it is quantitative, which is a desirable attribute in science. Secondly, given appropriate techni-cal rigour, anyone can repeat the procedure and verify the observations. Thirdly, levels of intra- and interobserver error for most hominin, and presumably also other catarrhines, craniodental metrical data are low (Wood, 1991). It is for these reasons that we opted to rely principally on metrical data for our tests. In particular, we regard the requirement that the observations are replicable as paramount.

We used measurements of the cranium, mandible and dentition that have been used in hominin cladistic analyses to compile two quantitative data sets, one for the ape and human superfamily, Hominoidea, and one for the extant baboon, macaque and mangabey tribe, Papionini. The hominoid data set comprised values for 129 measurements recorded on mixed sex samples of *Gorilla, Homo, Pan, Pongo* and an outgroup. The measurements are listed in Table 6.1. Seventy-seven of the measurements were recorded on 37 *Gorilla gorilla* (20 males, 17 females), 75 *Homo sapiens* (40 males, 35 females), 35 *Pan troglodytes* (13 males, 22 females), 41 *Pongo pygmaeus* (20 males, 21 females) and 24 *Colobus guereza* (12 males, 12 females). These data were taken from Wood *et al.* (1991). The other 52 measurements were recorded on 20 *G. gorilla* (10 males, 10 females), 20 *H. sapiens* (10 males, 10 females), 20 *Pan troglodytes* (10 males, 10 females), 20 *Pongo pygmaeus* (10 males, 10 females) and 20 *C. guereza* (10 males, 10 females). These data were taken from Chamberlain (1987).

The papionin data set consisted of values for 62 measurements recorded on mixed sex samples of *Cercocebus, Lophocebus, Macaca, Mandrillus, Pa-pio, Theropithecus* and several outgroups. The measurements are given in Table 6.2. The 62 measurements were recorded on 26 *Cercocebus galeritus/torquatus* (13 males, 13 females), 40 *Lophocebus albigena/atterimus* (20 males, 20 females), 40 *Macaca fascicularis/mulatta* (20 males, 20 females),

Table 6.1. *Hominoid metric variables*

Variable	Definition	Variable	Definition
P1	I^1 labiolingual diameter	M16	M_3 buccolingual diameter
P2	I^1 mesiodistal diameter	M17	M_3 mesiodistal diameter
P3	I^2 labiolingual diameter	M18	Maximum cusp height
P4	I^2 mesiodistal diameter	M19	Condylar height
P5	C^1 mesiodistal diameter	M20	Bicondylar breadth
P6	C^1 labiolingual diameter	M21	Coronoid height
P7	C^1 labial height	M22	Bicoronoid breadth
P8	P^3 Buccolingual diameter	M23	Right condylar head width
P9	P^3 mesiodistal diameter	M24	Right condylar head
P10	P^4 Buccolingual diameter		anterior-posterior breadth
P11	P^4 mesiodistal diameter	M25	Ramal breadth
P12	M^1 Buccolingual diameter	M26	Bigonial width
P13	M^1 mesiodistal diameter	M27	Height of mandibular body at M_1
P14	M^2 Buccolingual diameter	M28	Thickness of mandibular body of M_1
P15	M^2 mesiodistal diameter	M29	Symphyseal height
P16	M^3 Buccolingual diameter	M30	Symphyseal thickness
P17	M^3 mesiodistal diameter	M31	Inner alveolar breadth at M_3
P18	Outer alveolar breadth at M^3	M32	Maximum mandibular length
P19	Inter upper canine breadth	M33	Inter lower canine distance
P20	Palate length	M34	Mandibular corpus height at M_3
P21	Inner alveolar breadth at M^3	M35	Height of foramen spinosum
P22	Palate depth at M^1	M36	Height of mental foramen
P23	Prosthion to plane of M^3	M37	Breadth between lower second
P24	Maxillo-Alveolar breadth (M^2B-M^2 B)		molars
P25	Breadth between upper second	M38	Lower incisor alveolar length
	molars (M^2L-M^2L)	M39	Lower premolar alveolar length
P26	Palate depth at incisive fossa	M40	Lower molar alveolar length
P27	Palate depth at upper second	F1	Right orbital breadth
	molars	F2	Right orbital height
P28	Maxillary alveolar subtense	F3	Interorbital breadth
P29	Upper incisor alveolar length	F4	Biorbital breadth
P30	Upper premolar alveolar length	F5	Nasion-Rhinion
P31	Upper molar alveolar length	F6	Nasion-nasospinale
M1	I_1 labiolingual diameter	F7	Maximum nasal width
M2	I_1 mesiodistal diameter	F8	Nasospinale-Prosthion
M3	I_2 labiolingual diameter	F9	Bijugal breadth
M4	I_2 mesiodistal diameter	F10	Bizygomatic breadth
M5	C_1 labiolingual diameter	F11	Upper facial breadth
M6	C_1 mesiodistal diameter	F12	Lower facial breadth
M7	C_1 labial height	F13	Breadth between infraorbital
M8	P_3 buccolingual diameter		foramina
M9	P_3 mesiodistal diameter	F14	Lower nasal bone breadth
M10	P_4 buccolingual diameter	F15	Facial height
M11	P_4 mesiodistal diameter	F16	Height of infraorbital foramen
M12	M_1 buccolingual diameter	F17	Height of orbital margin
M13	M_1 mesiodistal diameter	F18	Upper malar height
M14	M_2 buccolingual diameter	F19	Lower malar height
M15	M_2 mesiodistal diameter	F20	Upper facial prognathism

Table 6.1. *(cont.)*

Variable	Definition	Variable	Definition
F21	Lower facial prognathism	C16	Breadth of mandibular fossa
F22	Malar prognathism	C17	Length of tympanic plate
F23	Naso-frontal subtense	C18	Length of petrous temporal
F24	Maxillary subtense	C19	Position of foramen ovale
C1	Glabella-Opisthocranion	C20	Position of infratemporal crest
C2	Minimum post-orbital breadth	C21	Length of foramen magnum
C3	Basion-Bregma	C22	Breadth of foramen magnum
C4	Maximum bi-parietal breadth	C23	Length of infratemporal fossa
C5	Biporionic width	C24	Breadth of infratemporal fossa
C6	Mastoid length	C25	Opisthion-infratemporal subtense
C7	Coronale-Coronale	C26	Basiooccipital length
C8	Opisthion-Inion	C27	Parietal thickness at Lambda
C9	Bimastoid width	C28	Frontal sagittal chord
C10	Posterior skull length	C29	Parietal sagittal chord
C11	Breadth across tympanic plates	C30	Parietal coronal chord
C12	Breadth between carotid canals	C31	Occipital sagittal chord
C13	Breadth between petrous apices	C32	Frontal sagittal arc
C14	Breadth between foramen ovale	C33	Occipital sagittal arc
C15	Breadth between infratemporal crests	C34	Auricular height

62 *Mandrillus leucopheus/sphinx* (42 males, 20 females), 39 *Papio anubis/ cynocephalus* (20 males, 19 females), 44 *Theropithecus gelada* (22 males, 22 females), 10 *Cercopithecus aethiops* (five males, five females), 7 *Colobus badius* (three males, four females), 10 *Erythrocebus patas* (five males, five females) and 17 *Pan troglodytes* (10 males, seven females). These data were taken from Collard (1998). Fifty-five of the measurements were recorded on a further 14 *Cercocebus torquatus* (seven males, seven females), 14 *Colobus badius* (seven males, seven females) and 12 *P. troglodytes* (five males, seven females). These data were taken from Chamberlain *et al.* (unpublished data). No consistent differences were found between the data from Collard (1998) and Chamberlain *et al.* (unpublished data) using Student's two-tailed t-test.

To relate our study to as many published cladistic analyses of the fossil catarrhines as possible, we also generated a hominoid qualitative data matrix from published data. This consisted of the states of 96 cranial and dental characters recorded on specimens of *Gorilla, Homo, Hylobates, Pan, Pongo* and an outgroup. The characters were obtained from several sources. Sixty-two were characters used by Shoshani *et al.* (1996) that are wholly craniodental and which vary among the hominoids. Two characters were

Table 6.2. *Papionin metric variables*

Variable	Definition	Variable	Definition
P1	Maxillo-alveolar length	F2	Alveolar height
P2	Maxillo-alveolar breadth	F3	Superior facial breadth
P3	Incisive canal-palatomaxillary	F4	Bizygomatic breadth
	suture	F5	Bimaxillary breadth
P4	Upper incisor alveolar length	F6	Anterior interorbital breadth
P5	Palatal height at M^1	F7	Orbital height
P6	Upper premolar alveolar length	F8	Minimum malar height
P7	Upper molar length	F9	Maximum nasal aperture width
P8	Canine interalveolar distance	F10	Nasal height
P9	Last premolar interalveolar	F11	Sagittal length of nasal bones
	distance	F12	Superior breadth of nasal bones
P10	Second molar interalveolar	F13	Inferior breadth of nasal bones
	distance	F14	Zygomaxillare – Porion
P11	I^1 mesiodistal crown diameter	F15	Upper facial prognathism
P12	I^1 labiolingual crown diameter	F16	Lower facial prognathism
P13	C^1 Mesiodistal crown diameter	C1	Glabella – opisthocranion
P14	C^1 labiolingual crown diameter	C2	Bregma – basion
P15	M^3 interalveolar distance	C3	Minimum frontal breadth
P16	Palate depth at incisive fossa	C4	Biporionic breadth
M1	Symphyseal height	C5	Glabella-Bregma
M2	Maximum symphyseal depth	C6	Postglabellar sulcus-bregma
M3	Corpus height at M_1	C7	Parietal sagittal chord
M4	Corpus width at M_1	C8	Parietal lambdoid chord
M5	Corpus height at M_3	C9	Lambda – inion
M6	Corpus width at M_3	C10	Occipital sagittal length
M7	Lower premolar alveolar length	C11	Foramen magnum maximum
M8	Lower molar alveolar length		width
M9	P_4 mesiodistal crown diameter	C12	Occipital condyle maximum
M10	P_4 Buccolingual crown diameter		length
M11	M_1 mesiodistal crown diameter	C13	Lambda thickness of parietal
M12	M_1 Buccolingual crown diameter	C14	Breadth between carotid canals
M13	M_2 mesiodistal crown diameter	C15	Breadth between petrous apices
M14	M_2 Buccolingual crown diameter	C16	Length of tympanic plate
F1	Superior facial height		

taken from Braga (1995), six from Andrews (1987), four from Schwartz (1984) and two from Delson & Andrews (1975). The other 20 characters were the craniodental characters in Groves (1986) that were neglected, without explanation, by Shoshani *et al.* (1996). The characters and states are listed in Appendix 6.1.

Methods

A character state data matrix was derived from each metric data set. The confounding effects of the body-size differences between the taxa were minimised by dividing each value by the geometric mean of all the values for the appropriate specimen (Jungers *et al.*, 1995). Allometry-based size-adjustment methods were not employed as recent phylogenetic analyses have indicated that isometric and allometric methods give similar results when applied to primate craniodental data (Creel, 1986; M. Singleton, 1996, unpublished data). The size-adjusted data were then converted into discrete character states using divergence coding (Thorpe, 1984). In divergence coding, the mean values for the taxa are calculated, and the differences between them tested for statistical significance. The means are then ranked in ascending order, and a taxon-by-taxon matrix compiled. Each cell in the top row of the matrix is filled with a taxon name such that the rank of the taxa decreases from left to right. The cells of the first column of the matrix are also filled with the names of the taxa on the basis of their rank, with the highest ranked taxon being placed in the top cell and the lowest ranked taxon in the bottom cell. Thereafter, each column of the matrix is filled with − 1s, + 1s and 0s. A cell is filled with a − 1 if the mean of the taxon in the column is greater than the mean of the taxon in the row and the difference between the means is significant. A cell is filled with a + 1 if the mean of the column taxon is significantly lower than the mean of the row taxon. If the difference between the means of the column and row taxa is not significant, the cell is filled with 0. Once the matrix is completely filled, the total of 0s, − 1s and + 1s for each column is calculated. Lastly, an integer (in this case 10) is added to each taxon total to make them positive figures, and therefore suitable for use in computer-based phylogenetics programmes. It should be noted that divergence coding is just one of several coding methods that have been described in recent years. It should also be noted that, at the moment, there is no consensus regarding the relative effectiveness of these methods. We elected to use divergence coding because it appears to be one of the most robust of the methods that are appropriate for analysing fossil taxa. The quantitative matrices are reproduced in Appendices 6.2 and 6.3.

The quantitative and qualitative matrices were used to perform two tests of the hypothesis that conventional craniodental characters are reliable for reconstructing the phylogenetic relationships of fossil catarrhine species and genera. The first was based on parsimony analysis, which identifies the cladogram that requires the smallest number of *ad hoc* hypotheses of homoplasy to account for the observed distribution of character states. Each matrix was subjected to parsimony analysis using the branch-and-bound

search routine of PAUP 3.0s (Swofford, 1991). Because the states of the metrical characters can be assumed to have evolved serially, the characters were treated as freely-reversing, linearly-ordered variables (Chamberlain & Wood, 1987; Wood, 1991, 1992; Slowinski, 1993; Rae, 1997). Some of the qualitative characters were also considered to be ordered characters, but the majority were treated as unordered variables (see Appendix 6.3 for details). Lastly, the most parsimonious cladogram or – if several equally parsimonious cladograms were favoured – the strict consensus cladogram was compared to the appropriate consensus molecular cladogram (Figures. 6.1 and 6.2). The hypothesis was considered to be supported if an analysis favoured a fully-resolved cladogram matching the molecular cladogram, or a partially-resolved cladogram comprising only molecular clades. The hypothesis was also considered supported if a strict consensus of several equally-parsimonious cladograms comprised only clades that were compatible with the molecular cladogram. These criteria were stipulated because in parsimony analysis it is not legitimate to accept some clades of a cladogram and reject others.

The second test employed the phylogenetic bootstrap, which is a resampling procedure that assigns a confidence interval to the clades that comprise the most parsimonious cladogram (Felsenstein, 1985). Using PAUP, 10 000 matrices were derived from each quantitative matrix by sampling with replacement. The bootstrap matrices were subjected to parsimony analysis, and a consensus of the most parsimonious cladograms was computed using a confidence region of 70% (Hillis & Bull, 1993). Thereafter, the clades of the consensus cladogram were compared with the appropriate molecular cladogram. The hypothesis was judged to be supported if all the clades of the consensus cladogram were compatible with the molecular cladogram.

Results

The hypothesis that catarrhine craniodental data are reliable for reconstructing the phylogenetic relationships of species and genera was not supported by the parsimony analyses. None of the matrices yielded a cladogram that was completely compatible with the group's molecular cladogram. The hominoid metric cladogram (informative characters = 118, length = 1093, consistency index [CI] = 0.77) suggested that *Homo* was the sister taxon of a (*Gorilla, Pan, Pongo*) clade, and that *Pan* was the sister taxon of a (*Gorilla, Pongo*) clade. The papionin metric cladogram (informative characters = 61, length = 923, CI = 0.69) suggested that *Lophocebus* is the sister of the other papionins; that *Cercocebus* is the sister of the baboons and

macaques; that *Macaca* is the sister of the baboons; and that *Theropithecus* is the sister of *Mandrillus* and *Papio*. Two equally parsimonious cladograms were derived from the hominoid qualitative matrix (informative characters = 64, length = 135, CI = 0.66). The first agreed with the hominoid molecular cladogram in locating *Hylobates* as the basal hominoid. However, it differed from the molecular cladogram in positing a sister group relationship between *Pan* and *Gorilla*, and another between *Homo* and *Pongo*. The second cladogram was wholly incompatible with the molecular cladogram. It suggested that *Homo* is the sister of a clade comprising *Gorilla, Hylobates, Pan* and *Pongo*; that *Pongo* is the sister of *Gorilla, Hylobates* and *Pan*; and that *Hylobates* is the sister of *Gorilla* and *Pan*.

The bootstrap analyses also failed to uphold the hypothesis. None of the clades supported by 70% or more of the bootstrap samples was compatible with the consensus molecular cladograms. The hominoid quantitative analysis supported a (*Gorilla, Pan, Pongo*) clade at 95%, and a (*Gorilla, Pongo*) clade at 73%. The papionin quantitative analysis supported a (*Cercocebus, Macaca,* baboon) clade at 98%; a (*Macaca,* baboon) clade at 78%; a baboon clade at 97%; and a (*Mandrillus, Papio*) clade at 73%. The analysis of the hominoid qualitative data yielded one clade, which incorrectly linked *Gorilla* and *Pan* to the exclusion of the other taxa (92%).

Discussion

The results of the parsimony and bootstrap tests suggest that cladistic analyses based on catarrhine craniodental morphology cannot be relied on to recover phylogenetic relationships. Indeed, the outcomes of the tests show that the methods can generate results that are positively misleading. For example, in a number of the parsimony analyses of the quantitative data, the 'true' cladograms were less parsimonious than a substantial number of 'false' cladograms. Likewise, the bootstrap-based tests indicate that craniodental data can return impressive levels of statistical support for patterns of phylogenetic relationship that are most likely incorrect. For instance, in the hominoid analyses, the 'false' (*Gorilla, Pan, Pongo*) clade was identified in more than 70% of the bootstrap cladograms. Likewise, the 'false' (*Mandrillus, Papio*) clade was supported by more than 70% of the bootstrap cladograms in several of the papionin analyses. In other words, cladistic analyses of catarrhine gross craniodental morphology may yield not only 'false-positive' results, but 'false-positive' results that, by a substantial margin, pass the statistical test favoured by many researchers. These results are in line with those of Hartman (1988) and Harrison (1993). The

former found that hominoid molar morphology was uninformative for cladistic analysis, while the latter concluded that his attempts to use cladistics to resolve the inferred relationships *among* closely related fossil primates, such as the early Miocene catarrhines from East Africa or the Eurasian pliopithecids, had been 'largely unsuccessful'. Our results are also in line with Pilbeam's (1996) conclusion that we currently know little about the phylogenetic relationships of the Miocene hominoids.

The implication of our results, and those described by Hartman (1988), Harrison (1993) and Pilbeam (1996), is that phylogenetic hypotheses for fossil hominins and other fossil catarrhines that are based solely on craniodental evidence may not be reliable. Most likely, these hypotheses reflect a mixture of the 'true' phylogeny and the phylogenetically-misleading effects of convergence, parallelism, reversal and/or behaviourally-induced morphogenesis. If anything, the results of the present study are likely to have over-estimated the reliability of fossil phylogenetic hypotheses, since our study did not account for two other factors that routinely complicate analyses of the hominin and hominid fossil records, namely contentious alpha taxonomy and intraspecific morphological change through time. In addition, as part of another study we have applied the same logic to two other groups of living primates, the platyrrhines and strepsirhines (Collard & Wood, unpublished data). These groups have less well supported molecular phylogenies than is the case for the hominoids and papionins, but the conclusions are similar. Primate craniodental data perform poorly in attempts to use them to recover the relevant phylogenetic history generated from molecular evidence.

How can the reliability of fossil catarrhine phylogenetic hypotheses be improved? One strategy is to devise techniques for characterising catarrhine craniodental morphology that are more sensitive to any phylogenetic signal than the methods presently in use (Rae, 1999). Recent studies suggest that such techniques may include the construction of metavariables using discriminant function analysis and principal component analysis (Aiello *et al.*, 1999; Collard, unpublished data). Since exogenetic stimuli can be expected to confound phylogenetic reconstruction (Lieberman, 1995, 1997, 1999), another approach is to focus on characters that are known to be minimally affected by such stimuli, for example, dental enamel and the structures of the middle and inner ear (Masali, 1968; Rak & Clarke, 1979a,b; Beynon *et al.*, 1998; Spoor & Zonneveld, 1998; Collard & Moggi-Cecchi, unpublished data). A third strategy is to develop rigorous comparative methods for discriminating between phylogenetically-informative and phylogenetically-misleading craniodental similarities. For example, the pursuit of detailed information about the ontogeny of characters may help identify convergences, parallel-

isms and reversals (Wood, 1988; Bromage, 1989; Lieberman *et al.*, 1996), while functional analyses may enable researchers to predict where resemblances resulting from behaviourally-induced morphogenesis are likely to occur in the hominid cranium (Lieberman, 1995, 1997, 1999; Lieberman *et al.*, 1996). A fourth approach is to develop techniques for assigning postcranial specimens to taxa in the absence of associated skeletons, thereby overcoming the taphonomy-imposed focus on craniodental morphology and enabling hominin cladistic analyses to be based on a wider sample of the phenotype (e.g. Aiello & Wood, 1994; Wood *et al.*, 1998). We also suggest that more attention should be paid to non-morphological lines of evidence that may have a bearing on the phylogenetic relationships of fossil catarrhines, such as biogeography, stratigraphy and behavioural indicators (e.g. Turner & Wood, 1993; Augustí *et al.*, 1996; Collard *et al.*, 1999). Lastly, it is worth noting that, even if craniodental data prove to be inadequate by themselves for phylogenetic reconstruction, this does not mean that they cannot be used to recover information about evolutionary history. To adapt a phrase used in connection with the punctuated equilibrium model of evolution, homoplasies are data. The presence of homoplasies suggests that different clades responded in similar ways to biotic influences, and, providing we can eventually obtain a reliable phylogeny for the fossil catarrhines, craniodental homoplasies promise to be a rich source of information about the history of catarrhine adaptations.

Acknowledgements

Appendix 6.1. Characters for hominoid qualitative analysis

Unless otherwise indicated, the character state descriptions in the following are taken verbatim from the references for the characters.

1. Depth of subarcuate fossa

Ref.:	Shoshani *et al.* (1996) #12.
States:	(0) deep; (1) moderately deep to shallow; (2) very shallow to non-existent.
Dist.:	*Homo* 2; *Pan* 2; *Gorilla* 2; *Pongo* 2; *Hylobates* 1; *Colobus* 0.
Notes:	States as per Shoshani *et al.* (1996). Treated as ordered character in analysis – *contra* Soshani *et al.* (1996) – because states are clearly additive.

2. Morphology of the mandibular symphysis

Ref.:	Shoshani *et al.* (1996) #29.
States:	(1) elongated and spout-like with an angle of 150°–145°; (2) symphysis with an angle of 137°–115°; (3) angle of mandibular symphysis (excluding the simian shelf) to horizontal ramus is narrow, approaching vertical when observed dorsally and laterally, with a mandibular symphysis angle of about 100°–90° or less.
Dist.:	*Homo* 3; *Pan* 2; *Gorilla* 1; *Pongo* 2; *Hylobates* 2; *Colobus* 1.
Notes:	Treated as unordered because it was not clear that the states formed a straight-forward additive sequence.

3. Distinctiveness of angular process of mandible

Ref.:	Shoshani *et al.* (1996) #33.
States:	(0) distinct, with posterior projection; (1) not distinct.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* 1.

4. Direction of incisive (anterior palatine) foramen

Ref.:	Shoshani *et al.* (1996) #36.
States:	(0) opening is directed dorsoventrally as in most mammals and the observer can see through the foramen; (1) foramen is directed diagonally, from anterior-ventral to posterior-dorsal, leads to a tube-like structure, and one cannot see through the foramina.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* 0.

5. Carotid canal morphology when viewed from ventral side of cranium

Ref.:	Shoshani *et al.* (1996) #40.
States:	(0) canal perforates bulla away from basicranium and is clearly within it, opening of canal is directed medially, ventrally or ventro-medially, but the imaginary lines (one from each side) which emerge from these openings do not cross at the foramen magnum, or cross at its anterior border at the level of the occipital condyles; (1) canal perforates bulla away from basicranium and is clearly within it, opening is directed postero-medially and the imaginary lines which emerge from these openings cross the foramen magnum posterior to the occipital condyles, or caudal to the foramen magnum itself.

Dist.:   *Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 0; *Hylobates* 1; *Colobus* 0.

Notes: According to Shoshani *et al.*, to view states (1) and (2) place straight wires inside the carotid canals and note the point of intersection of the imaginary lines in continuation of these wires. In state (0), the lines cross at anterior end of the foramen magnum or in front of it, whereas in state (1) these imaginary lines cross posterior to the occipital condyles or caudal to the foramen magnum itself.

6. Size of upper first incisor relative to upper second incisor

Ref.:   Shoshani *et al.* (1996) #47.

States: (0) about the same size; (1) enlarged; (2) much enlarged.

Dist.:   *Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 2; *Hylobates* 0; *Colobus* 0.

Notes: Treated as an ordered variable.

7. Honing in males (back of upper canine sharpens against third lower premolar).

Ref.:   Shoshani *et al.* (1996) #48.

States: (1) present, i.e. P3 bilaterally compressed (sectorial) and modified for honing on C1, P3 is larger than P4 especially mesiodistally, also may involve honing C1 on C1; (2) honing reduced, P3 slightly buccolingually compressed, P3 is larger than P4 especially mesiodistally; (3) honing further reduced, P3 about the same size as P4 in length in occlusal view.

Dist.:   *Homo* 2; *Pan* 2; *Gorilla* 1; *Pongo* 1; *Hylobates* 1; *Colobus* 0.

Notes: Treated as ordered character.

8. Interorbital pillar width.

Ref.:   Shoshani *et al.* (1996) #101.

States: (0) wide; (1) narrow.

Dist.:   *Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* 0.

9. Depth of middle ear

Ref.:   Shoshani *et al.* (1996) #102.

States: (0) shallow; (1) deepened, more than 8.5mm.

Dist.:   *Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 0; *Hylobates* 0; *Colobus* ?.

10. Axis of ear bones

Ref.:   Shoshani *et al.* (1996) #103.

States: (0) acute angle; (1) right angle or more.

Dist.:   *Homo* 0; *Pan* 0; *Gorilla* 1; *Pongo* 1; *Hylobates* 1; *Colobus* ?.

11. Area of inner ear

Ref.:   Shoshani *et al.* (1996) #104.

States: (0) low, $< 50mm^2$; (1) increased, $> 50mm^2$.

Dist.:   *Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 0; *Hylobates* 0; *Colobus* ?.

12. Klinorhynchy (a deep foreshortened facial skeleton which bends downward with respect to the cranial base)

Ref.:	Shoshani *et al.* (1996) #106.
States:	(0) airorynch or straight; (1) more klinorhynch; (2) strongly klinorhynch.
Dist.:	*Homo* 2; *Pan* 2; *Gorilla* 2; *Pongo* 0; *Hylobates* 1; *Colobus* 0.
Notes:	Treated as ordered character.

13. Frontozygomatic suture

Ref.:	Shoshani *et al.* (1996) #107.
States:	(0) vertical; (1) medially directed.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* 0.

14. Relative height of upper face

Ref.:	Shoshani *et al.* (1996) #108.
States:	(0) high, index about 70; (1) reduced.
Dist.:	*Homo* 1; *Pan* 0; *Gorilla* 0; *Pongo* 0; *Hylobates* 1; *Colobus* 0.

15. Facial index (upper face height as a percentage of facial breadth)

Ref.:	Shoshani *et al.* (1996) #109.
States:	(0) low, index about 50; (1) increased.
Dist.:	*Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* 0.

16. Height of mandibular symphysis relative to length of the lower toothrow

Ref.:	Shoshani *et al.* (1996) #110.
States:	(0) low, its height about 60% of toothrow length; (1) deepened, at least 75% of tooth row length.
Dist.:	*Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* 1.

17. Presence/absence of frontal sinus

Ref.:	Shoshani *et al.* (1996) #111.
States:	(0) absent; (1) present.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 0; *Hylobates* 0; *Colobus* 0.

18. Pyriform aperture

Ref.:	Shoshani *et al.* (1996) #112.
States:	(0) narrow; (1) widened; (2) very wide.
Dist.:	*Homo* 2; *Pan* 2; *Gorilla* 2; *Pongo* 1; *Hylobates* 2; *Colobus* 0.
Notes:	Treated as ordered.

19. Position of infraorbital foramina relative to zygomaxillary suture

Ref.:	Shoshani *et al.* (1996) #113.
States:	(0) close to suture; (1) further from suture.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* 1.

20. Orientation of zygomatic bone

Ref.:	Shoshani *et al.* (1996) #114.
States:	(0) more frontally; (1) more superolaterally; (2) still further superolaterally.
Dist.:	*Homo* 2; *Pan* 2; *Gorilla* 2; *Pongo* 1; *Hylobates* 0; *Colobus* 1.
Notes:	Treated as ordered character in analysis.

21. Frontal bone

Ref.:	Shoshani *et al.* (1996) #115
States:	(0) flat; (1) more convex; (2) strongly convex.
Dist.:	*Homo* 2; *Pan* 0; *Gorilla* 0; *Pongo* 2; *Hylobates* 1; *Colobus* 2.
Notes:	Treated as ordered character in analysis.

22. Glabella prominence

Ref.:	Shoshani *et al.* (1996) #116
States:	(0) strong; (1) reduced; (2) absent.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 2; *Colobus* 0.
Notes:	Treated as ordered character in analysis.

23. Number of incisive foramina

Ref.:	Shoshani *et al.* (1996) #117
States:	(0) double, i.e. one on each side of the midline; (1) single, confluency of two foramina, at least close to the surface.
Dist.:	*Homo* 1; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* 0.

24. Maxillary sinus

Ref.:	Shoshani *et al.* (1996) #118
States:	(0) small; (1) expanded.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* 0.

25. Supraorbital development

Ref.:	Shoshani *et al.* (1996) #119
States:	(0) weak; (1) more-marked; (2) torus-like.
Dist.:	*Homo* 2; *Pan* 2; *Gorilla* 2; *Pongo* 0; *Hylobates* 1; *Colobus* 1.
Notes:	Treated as ordered character in analysis.

26. Supraorbital contour

Ref.:	Shoshani *et al.* (1996) #120
States:	(0) arched; (1) less arched.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 1; *Pongo* 0; *Hylobates* 0; *Colobus* 1.

27. Orbits

Ref.:	Shoshani *et al.* (1996) #121.
States:	(0) as wide as high; (1) high-oval.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* 0.

28. Supraorbital trigon
Ref.:	Shoshani *et al.* (1996) #122.
States:	(0) not developed; (1) developed.
Dist.:	*Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* 1.
Notes:	Supraorbital trigon is the triangular area enclosed by the torus and the backwardly converging temporal lines.

29. Nasal width
Ref.:	Shoshani *et al.* (1996) #123.
States:	(0) broad; (1) reduced.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* 0.

30. Length of nasals
Ref.:	Shoshani *et al.* (1996) #124.
States:	(0) long; (1) shortened.
Dist.:	*Homo* 1; *Pan* 0; *Gorilla* 0; *Pongo* 0; *Hylobates* 1; *Colobus* 1.

31. Size of zygomatic foramina
Ref.:	Shoshani *et al.* (1996) #126.
States:	(0) very small; (1) enlarged.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* 0.

32. Position of zygomatic foramina
Ref.:	Shoshani *et al.* (1996) #127.
States:	(0) at or below plane of orbital rim; (1) above plane of orbital rim.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* 1.

33. Size of incisive foramina
Ref.:	Shoshani *et al.* (1996) #128.
States:	(0) large; (1) reduced in size; (2) tiny.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 2; *Hylobates* 0; *Colobus* 0.
Notes:	Treated as ordered character in analysis.

34. Size and shape of palatine foramina
Ref.:	Shoshani *et al.* (1996) #129.
States:	(0) large and wide; (1) small and narrow.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* 0.

35. Premaxillary suture in adult
Ref.:	Shoshani *et al.* (1996) #130.
States:	(0) patent; (1) obliterated.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 0; *Pongo* 0; *Hylobates* 0; *Colobus* 0.

36. Foramen lacerum medium
Ref.:	Shoshani *et al.* (1996) #131.
States:	(0) absent; (1) present.
Dist.:	*Homo* 1; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* 1.
Notes:	This is a small space, bilateral to the anterior edge of the basioccipital, just behind the suture with the basisphenoid; bordered laterally by the anterior end of the petrosal. In humans it is covered over with cartilage but pierced by the ascending pharyngeal artery. It is large in *Homo*, small in *Pongo*, and absent in *Pan* in which the medial side of the anterior petrosal fills up the gap.

37. Posterior convergence of temporal lines
Ref.:	Shoshani *et al.* (1996) #132.
States:	(0) converge posteriorly; (1) do not converge.
Dist.:	*Homo* 1; *Pan* 0; *Gorilla* 0; *Pongo* 0; *Hylobates* 1; *Colobus* 1.
Notes:	This character is apparently not redundant with #28 (supraorbital trigon) as the distribution of states is different.

38. Mesial groove on male canine
Ref.:	Shoshani *et al.* (1996) #159.
States:	(0) extends onto root; (1) present; (2) absent.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 2; *Hylobates* 1; *Colobus* 0.
Notes:	Shoshani *et al.*'s states (0 = present; 1 = extends onto root; 2 = absent) changed so that character can be treated as an ordered character.

39. Relative height of male canine
Ref.:	Shoshani *et al.* (1996) #160.
States:	(0) high relative to mesiodistal length; (1) lower relative to mesiodistal length.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* 1.

40. Upper I2 occlusal edge
Ref.:	Shoshani *et al.* (1996) #161.
States:	(0) slopes distally; (1) does not slope distally.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 0; *Pongo* 0; *Hylobates* 0; *Colobus* 0.

41. Robusticity of canines
Ref.:	Shoshani *et al.* (1996) #162.
States:	(0) slender; (1) more robust.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* 0.

42. Basal keel of lower canines
Ref.:	Shoshani *et al.* (1996) #163.
States:	(0) present; (1) absent.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 0; *Pongo* 0; *Hylobates* 0; *Colobus* 0.

43. Basal area of paracone of upper premolars

Ref.:	Shoshani *et al.* (1996) #164.
States:	(0) subequal to protocone; (1) smaller than protocone.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 1; *Colobus* 1.

44. Molar cingulum

Ref.:	Shoshani *et al.* (1996) #165.
States:	(0) prominent, shelf-like; (1) reduced, incomplete, (2) fragmented or absent.
Dist.:	*Homo* 2; *Pan* 2; *Gorilla* 1; *Pongo* 2; *Hylobates* 1; *Colobus* 1.
Notes:	Treated as ordered character in analysis.

45. Protoconid apex on lower dP3

Ref.:	Shoshani *et al.* (1996) #166.
States:	(0) more lingual from the median axis; (1) truncated buccally from the median axis.
Dist.:	*Homo* 1; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

46. Metaconid of lower dP3

Ref.:	Shoshani *et al.* (1996) #167.
States:	(0) present; (1) absent.
Dist.:	*Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 0; *Hylobates* 0; *Colobus* ?.

47. Protocristid of lower dP3

Ref.:	Shoshani *et al.* (1996) #168.
States:	(0) aligned with tooth mesiodistal axis; (1) angled.
Dist.:	*Homo* 1; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

48. Talonid basin of lower dP3

Ref.:	Shoshani *et al.* (1996) #169.
States:	(0) open distally; (1) closed.
Dist.:	*Homo* 1; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

49. Metaconid of lower dP4

Ref.:	Shoshani *et al.* (1996) #170.
States:	(0) subequal to protoconid; (1) increased relative to protoconid on lower dP4.
Dist.:	*Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 0; *Hylobates* 0; *Colobus* ?.

50. Crista obliqua on lower dP4

Ref.:	Shoshani *et al.* (1996) #171.
States:	(0) does not reach protoconid apex; (1) reaches protoconid apex.
Dist.:	*Homo* 1; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 1; *Colobus* ?.

51. Talonid basin on lower dP4

Ref.:	Shoshani *et al.* (1996) #172.
States:	(0) open distally; (1) closed.
Dist.:	*Homo* 1; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 1; *Colobus* ?.

52. Protocone of upper dP3, in crown view

Ref.: Shoshani *et al.* (1996) #173.
States: (0) larger than paracone; (1) smaller than paracone.
Dist.: *Homo* 1; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

53. Preprotocrista of upper dP4

Ref.: Shoshani *et al.* (1996) #174.
States: (0) weak; (1) more developed.
Dist.: *Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

54. Postprotocrista of upper dP4

Ref.: Shoshani *et al.* (1996) #175.
States: (0) poor; (1) more developed; (2) still more developed.
Dist.: *Homo* 2; *Pan* 2; *Gorilla* 2; *Pongo* 1; *Hylobates* 1; *Colobus* 0.
Notes: Treated as ordered character in analysis.

55. Protocristid grooves of molars

Ref.: Shoshani *et al.* (1996) #176.
States: (0) prominent; (1) barely visible.
Dist.: *Homo* 0; *Pan* 1; *Gorilla* 0; *Pongo* 1; *Hylobates* 1; *Colobus* 0.

56. Lingual marginal ridges of molars

Ref.: Shoshani *et al.* (1996) #177.
States: (0) hardly appreciable; (1) more prominent; (2) very prominent.
Dist.: *Homo* 1; *Pan* 1; *Gorilla* 2; *Pongo* 1; *Hylobates* 1; *Colobus* 0.
Notes: Treated as ordered character in analysis.

57. Thickness of molar enamel

Ref.: Shoshani *et al.* (1996) #178.
States: (0) thin; (1) increased thickness; (2) very thick.
Dist.: *Homo* 2; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* ?.
Notes: Treated as ordered character in analysis.

58. Proportion of Pattern 3 enamel

Ref.: Shoshani *et al.* (1996) #179.
States: (0) high; (1) reduced; (2) very reduced.
Dist.: *Homo* 0; *Pan* 2; *Gorilla* 2; *Pongo* 1; *Hylobates* 0; *Colobus* ?.
Notes: Treated as ordered character in analysis.

59. Insertion of genioglossus

Ref.: Shoshani *et al.* (1996) #185.
States: (0) above inferior transverse torus of internal (or posterior) of mandibular symphysis; (1) shifted to inferior transverse torus.
Dist.: *Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* 0.

60. Insertion of geniohyoideus
Ref.:	Shoshani *et al.* (1996) #186.
States:	(0) basally on inferior transverse torus; (1) higher on inferior transverse torus; (2) above inferior transverse torus.
Dist.:	*Homo* 2; *Pan* 2; *Gorilla* 1; *Pongo* 0; *Hylobates* 1; *Colobus* 0.
Notes:	Treated as ordered character in analysis.

61. Insertion of digastric
Ref.:	Shoshani *et al.* (1996) #187.
States:	(0) posterior to inferior transverse torus; (1) inferior transverse torus; (2) not on symphysis.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 0; *Pongo* 2; *Hylobates* 0; *Colobus* 0.
Notes:	Treated as unordered character in analysis.

62. Encephalization
Ref.:	Shoshani *et al.* (1996) #220.
States:	(0) low, <1.2; (1) increased, >1.2–1.9; (2) high >1.9.
Dist.:	*Homo* 2; *Pan* 1; *Gorilla* 0; *Pongo* 1; *Hylobates* 2; *Colobus* 0.
Notes:	Shoshani *et al.*'s (1996) character states (0 = low, <10; 1 = increased, 10–11; 2 = high >11) and distributions (*Homo* 2; *Pan* 2; *Gorilla* 0; *Pongo* 0; *Hylobates* 1; *Colobus* ?) updated using Kappelman's (1996) data. Treated as ordered character in analysis.

63. Retroarticular canal
Ref.:	Braga (1995).
States:	(0) absent; (1) present.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* ?; *Colobus* ?.

64. Condylar canal
Ref.:	Braga (1995).
States:	(0) absent; (1) present.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 0; *Hylobates* ?; *Colobus* ?.

65. Incisive fossa
Ref.:	Andrews (1987)
States:	(0) absent; (1) deep; (2) extends through palate.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 0; *Hylobates* 2; *Colobus* ?.
Notes:	Treated as an ordered character in analysis.

66. Molar dentine horns
Ref.:	Andrews (1987)
States:	(0) high; (1) low.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

67. Molar enamel wrinkling
Ref.:	Andrews (1987)
States:	(0) smooth or slight wrinkling; (1) deep secondary wrinkling.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

68. Postorbital sulcus
Ref.:   Andrews (1987)
States: (0) absent; (1) present.
Dist.:   *Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 0; *Hylobates* 0; *Colobus* ?.

69. Ethmoid-lacrymal contact
Ref.:   Andrews (1987)
States: (0) long, 100%; (1) short, 40–90%.
Dist.:   *Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 0; *Hylobates* 0; *Colobus* ?.

70. Fronto-maxillary contact in orbits
Ref.:   Andrews (1987)
States: (0) no contact; (1) contact, 30–50%.
Dist.:   *Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 0; *Hylobates* 0; *Colobus* ?.

71. Nasal floor morphology
Ref.:   Andrews (1987).
States: (0) nasal floor stepped; (1) nasal floor unstepped.
Dist.:   *Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

72. Palatine fenestrae reduced in size
Ref.:   Schwartz (1984)
States: (0) no; (1) yes.
Dist.:   *Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

73. Cheek tooth height
Ref.:   Schwartz (1984).
States: (0) low; (1) medium; (2) medium-high; (3) high.
Dist.:   *Homo* 0; *Pan* 2; *Gorilla* 3; *Pongo* 0; *Hylobates* 1; *Colobus* ?.
Notes: This may be a corollary of thick enamel (Andrews, 1987). Treated as an ordered character.

74. Lower M3 smaller than lower M2
Ref.:   Schwartz (1984); Andrews (1987).
States: (0) no; (1) yes.
Dist.:   *Homo* 1; *Pan* 1; *Gorilla* 0; *Pongo* 1; *Hylobates* 1; *Colobus* ?.
Notes: States for *Pan* and *Hylobates* are from Andrews (1987). Others from Schwartz (1984).

75. Number of zygomatic foramina
Ref.:   Schwartz (1984).
States: (0) 1–2; (1) 1–2 +.
Dist.:   *Homo* 0; *Pan* 0; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* ?.
Notes: States and distribution from Schwartz (1984).

76. Post talonid basin

Ref.:	Groves (1986) #201.
States:	(0) absent; (1) small; (2) narrow.
Dist.:	*Homo* 1; *Pan* 2; *Gorilla* 2; *Pongo* 3; *Hylobates* 0; *Colobus* ?.
Notes:	Treated as unordered character because it was not clear that states form a linear transformation series.

77. Relative depth of mandible

Ref.:	Delson & Andrews (1975) Table 2 #1.
States:	(0) deep/moderate; (1) moderate; (2) shallow.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 2; *Colobus* 0.
Notes:	Treated as an ordered character in analysis.

78. Mandibular shape

Ref.:	Delson & Andrews (1975) Table 2 #2.
States:	(0) shallows mesially/constant; (1) constant; (2) deepens.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 2; *Colobus* 0.
Notes:	Treated as an ordered character in analysis.

79. Ethmo-sphenoid contact

Ref.:	Groves (1986) #24.
States:	(0) none/very short, 0–39%; (1) short, 40–90%; (2) long, 91–100%.
Dist.:	*Homo* 2; *Pan* 1; *Gorilla* 1; *Pongo* 2; *Hylobates* 0; *Colobus* ?.
Notes:	Data from Groves (1986). States adapted from Andrews (1987) states for Ethmoid-lacrymal contact (#69 in this list). Treated as an ordered character in analysis.

80. Zygomatic bone

Ref.:	Groves (1986) #31.
States:	(0) curved; (1) flattened.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

81. Relative face height

Ref.:	Groves (1986) #31.
States:	(0) 19–24; (1) 27–30.
Dist.:	*Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

82. Canine length as percentage of upper M1 (male)

Ref.:	Groves (1986) #177.
States:	(0) short, 61–81%; (1) longer, 101–182%.
Dist.:	*Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 1; *Colobus* ?.

83. Canine length as percentage of upper M1 (female)

Ref.:	Groves (1986) #178.
States:	(0) short, 61–81%; (1) longer, 92–144%.
Dist.:	*Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 1; *Colobus* ?.

84. Canine length as percentage of upper P4 (male)

Ref.:	Groves (1986) #179.
States:	(0) short, 116–160%; (1) longer, 215–543%.
Dist.:	*Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 1; *Colobus* ?.

85. Canine length as percentage of upper P4 (female)

Ref.:	Groves (1986) #179.
States:	(0) short, 116–178%; (1) longer, 187–273%; (2) still longer, 307–543%.
Dist.:	*Homo* 0; *Pan* 1; *Gorilla* 0; *Pongo* ?; *Hylobates* 2; *Colobus* ?.
Notes:	Treated as an ordered character in analysis.

86. Angle between tooth rows

Ref.:	Groves (1986) #182.
States:	(0) low, -5–$16°+$; (1) high, 20–$40°$.
Dist.:	*Homo* 1; *Pan* 0; *Gorilla* 0; *Pongo* 0; *Hylobates* 0; *Colobus* ?.

87. Eruption after upper I2

Ref.:	Groves (1986) #183.
States:	(0) PCPM; (1) MPPC.
Dist.:	*Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 1; *Colobus* ?.

88. Eruption after lower I2

Ref.:	Groves (1986) #184.
States:	(0) CPPM; (1) MPPC.
Dist.:	*Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 1; *Colobus* ?.

89. Upper I1 lingual crenulations

Ref.:	Groves (1986) #187.
States:	(0) absent; (1) marginal; (2) whole surface.
Dist.:	*Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 2; *Hylobates* 1; *Colobus* ?.
Notes:	Treated as an ordered character in analysis.

90. Upper I1 cingulum tubercle

Ref.:	Groves (1986) #188.
States:	(0) present; (1) absent.
Dist.:	*Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 0; *Hylobates* 1; *Colobus* ?.
Notes:	Groves' (1986) three states recognises three states: (1) usually present; (2) incipient; and (3) absent. As 'incipient' is clearly encompassed by usually present, the two states were collapsed into one.

91. Number of upper I1 ridges

Ref.:	Groves (1986) #189.
States:	(0) one; (1) one or more than one; (2) always more than one.
Dist.:	*Homo* 1; *Pan* 0; *Gorilla* 2; *Pongo* 1; *Hylobates* 0; *Colobus* ?.
Notes:	Treated as an ordered character in analysis.

92. Canine sexual dimorphism

Ref.:	Groves (1986) #191.
States:	(0) monomorphic; (1) dimorphic.
Dist.:	*Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

93. Canine elongation

Ref.:	Groves (1986) #193.
States:	(0) buccolingual; (1) none; (2) mesiodistal.
Dist.:	*Homo* 0; *Pan* 2; *Gorilla* 2; *Pongo* 2; *Hylobates* 1; *Colobus* ?.
Notes:	Treated as an ordered character.

94. Lower P3 metaconid

Ref.:	Groves (1986) #197.
States:	(0) absent; (1) tiny; (2) small
Dist.:	*Homo* 2; *Pan* 0/1; *Gorilla* 1; *Pongo* 2; *Hylobates* 0; *Colobus* ?.
Notes:	Treated as an ordered character in analysis.

95. Trigonid basin

Ref.:	Groves (1986) #199.
States:	(0) narrow slit; (1) fair; (2) wider.
Dist.:	*Homo* 1; *Pan* 2; *Gorilla* 2; *Pongo* 1; *Hylobates* 0; *Colobus* ?.
Notes:	Groves' states are: *Homo* fair; *Pan* fairly wide; *Gorilla* rather wide; *Pongo* fair; *Hylobates* narrow slit; Outgroup (monkeys) varies. Treated as an ordered character in analysis.

96. Sulcus obliqus

Ref.:	Groves (1986) #200.
States:	(0) weak to moderate definition; (1) strong to very strong definition.
Dist.:	*Homo* 0; *Pan* 0; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* ?.
Notes:	Groves' (1986) identifies five states: poor; present; fair; strong; very strong.

Appendix 6.2. Quantitative character state data matrix used in hominoid analyses

Characters   P1 P2 P3 P4 P5 P6 P7 P8 P9 P10 P11 P12 P13 P14 P15 P16 P17 P18 P19 P20 P21 P22 P23 P24 P25 P26 P27 P28 P29 P30 P31 M1 M2 M3 M4 M5 M6 M7 M8 M9 M10 M11 M12 M13 M14 M15 M16 M17 M18 M19 M20 M21 M22 M23 M24 M25 M26 M27 M28 M29 M30 M31 M32 M33 M34 M35 M36 M37 M38 M39 M40 F1 F2 F3 F4 F5 F6 F7 F8 F9 F10 F11 F12 F13 F14 F15 F16 F17 F18 F19 F20 F21 F22 F23 F24 C1 C2 C3 C4 C5 C6 C7 C8 C9 C10 C11 C12 C13 C14 C15 C16 C17 C18 C19 C20 C21 C22 C23 C24 C25 C26 C27 C28 C29 C30 C31 C32 C33 C34

Colobus E E B C B 8 6 E 8 8 6 D 6 A 6 8 6 A B 7 9 A 6 8 A B D C C 7 6 A C B E 8 C 6 E ? E 6
E 8 C 7 B 6 6 A 9 A 8 D B 8 E 6 C B 7 C 6 E 7 8 B B B 6 6 6 7 C 8 D 9 E E 8 8 8 B B
9 C D E C C 6 9 7 6 7 8 8 C A B E 9 D D E C A D 7 8 C C 7 8 8 E 7 6 9 E 8 E 8 9 B
E 9 E A

Gorilla B A B B 8 8 8 6 8 8 9 A A A 8 B 8 E B 7 E 8 8 E E B 8 9 A 9 8 C C B A 9 8 A 6 7 7 9
9 9 7 7 7 8 A 7 E 7 C 7 9 A B D 6 8 7 E B A A 9 7 E B A 8 D E 9 C 6 6 9 A B D B 8 B
6 6 8 6 6 6 A 9 9 B 7 B E E E E C E 6 D A 8 D C D E 7 8 A 8 8 B C A 7 A C B D D E
A C A E

Homo B C C 7 E E E B D C D 6 8 6 A 6 D 6 E E 6 B E A 6 B D E E E E E C E C E E E B D
A D 6 7 7 B 7 B 8 E 6 E 6 D E E 7 A B E E 6 E C E 9 E 6 E E E 8 7 6 6 D E 6 C 6 7 A
D 7 9 E D C C E A E E 8 E 6 6 6 6 7 6 6 8 6 6 E 6 6 7 6 E E E E E 6 7 E D A E 6 6 6
6 6 6 6 6

Pan 8 7 6 6 A C B B D E D C D E D E C A 6 B A C C 9 A B 8 8 7 C C 7 7 7 6 A 7 A B B
C D C D E E E E D C C D C A A B B D A B B A 9 6 C E B 8 7 C C A B 9 A 9 A 9 7
B D 7 C 7 C 9 8 9 A 9 A 9 A B 9 B A 9 8 B 9 9 B 9 C 8 B B A B A 8 A 8 8 9 C A D 7
8 B A 9 9 A 9 A A

Pongo 6 7 A D 7 8 B 8 8 8 9 9 D A D B B A 8 B B 9 A 9 A 6 8 7 7 8 A 7 7 7 8 9 8 A 8 9 7 9
9 D A B B B D 7 9 7 C 7 6 7 7 8 B 6 B 8 9 8 7 A 7 B 7 8 A D B E E 9 B C 7 E 9 E 6 E
E 9 8 9 8 9 E 9 A E 9 E C 9 C 7 9 C C 9 8 8 A 8 D B 7 8 9 C C A C A 8 9 8 8 D D A
A E A A

Appendix 6.3. Quantitative character state data matrix used in papionin analyses

Characters P1 P2 P3 P4 P5 P6 P7 P8 P9 P10 P11 P12 P13 P14 P15 P16 M1
M2 M3 M4 M5 M6 M7 M8 M9 M10 M11 M12 M13 M14 F1 F2
F3 F4 F5 F6 F7 F8 F9 F10 F11 F12 F13 F14 F15 F16 C1 C2 C3
C4 C5 C6 C7 C8 C9 C10 C11 C12 C13 C14 C15 C16

Cercocebus C 6 F 9 C 6 B B A 9 9 6 C 9 C A C B 9 6 8 8 A C 8 5 B 6 C 6 B A 9 A 7
B 8 D D B B D 7 9 A B B A 9 9 9 7 C 7 6 5 8 B 8 8 A B

Lophocebus C 8 9 4 B C E 6 6 7 5 6 D G 5 B C C 6 C 5 F C E D E E D E F F G 7 8
4 A 8 8 C E E 9 D 9 6 D 4 6 4 7 6 4 6 4 6 7 4 5 C 4 5 C

Macaca C 5 F C 5 B 8 B A A A 6 B 9 8 5 B C E C C 6 B 8 8 A 6 B 8 9 B B 8 7
B G 4 9 D A A G 7 9 6 A 7 6 6 A 7 A 6 C D D 8 B B 8 A C

Mandrillus 6 E 4 A B 4 9 B E F D D 5 8 G 9 5 5 A A C 9 4 8 5 C C G 8 B 6 B D F
F E D D D 5 4 8 E 9 G 6 G G E F G E G F A D F B C G F 8

Pan G 9 9 9 C D G 4 4 4 5 E A 7 6 F D G G 7 G 8 G G G 5 C 6 G D F 4 4
8 C 4 8 G 4 G G 4 E 9 D G 7 6 9 4 D E 6 7 8 6 8 G 4 8 5 B

Papio 6 E 9 A 5 C 8 B A A C B B B A A C 9 B G C F 8 8 8 E B C 8 9 5 B D F
E A D 7 7 5 6 7 8 G D 8 E E C F D E C C B D F B C D A C

Theropithecus 6 E 9 G E C 4 G G F G G 8 A D A 5 5 4 7 5 9 9 4 8 A 4 6 4 7 7 6 G 7 7
6 G 4 8 9 9 D 7 9 6 6 B C G A 6 7 C D G D C 5 B D F 4

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