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Homoplasy and the early hominid masticatory system: inferences from analyses of extant hominoids and papionins

Early hominid masticatory characters are widely considered to be more prone to homoplasy than characters from other regions of the early hominid skull and therefore less reliable for phylogenetic reconstruction. This hypothesis has important implications for current reconstructions of early hominid phylogeny, but it has never been tested. In this paper we evaluate the likely veracity of the hypothesis using craniometric data from extant primate groups for which reliable consensus molecular phylogenies are available.

Datasets representing the extant large-bodied hominoid genera and the extant papionin genera were compiled from standard measurements. The data were adjusted to minimise the confounding effects of body size, and then converted into discrete character states using divergence coding. Each dataset was divided into four regional character groups: (1) palate and upper dentition, (2) mandible and lower dentition, (3) face and (4) cranial vault and base. Thereafter, the regional character groups were analysed using cladistic methods and the resulting phylogenetic hypotheses judged against the consensus molecular phylogenies for the hominoids and papionins.

The analyses indicated that the regions dominated by masticatory characters—the palate and upper dentition, and the mandible and lower dentition—are no less reliable for phylogenetic reconstruction than the other regions of the skull. The four regions were equally affected by homoplasy and were, therefore, equally unreliable for phylogenetic reconstruction. This finding challenges the recent suggestion that *Paranthropus* is polyphyletic, which is based on the assumption that masticatory characters are especially prone to homoplasy. Our finding also suggests that, contrary to current practice, there is no *a priori* reason to de-emphasise the phylogenetic significance of the masticatory similarities between *Homo rudolfensis* and the australopiths. The corollary of this is that *H. rudolfensis* is unlikely to be a member of the *Homo* clade and should therefore be allocated to another genus.

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Introduction

A homoplasy is a resemblance between taxa that can be ascribed to processes other than descent from a common ancestor and which implies phylogenetic relationships that conflict with the best estimate of phylogeny for the taxa (Willey, 1911; Simpson, 1961; Cain, 1982; Patterson, 1982; Sober, 1988; Sanderson & Hufford, 1996; Lockwood & Fleagle, 1999). There are believed to be several forms of homoplasy. Analogous and convergent homoplasies are caused by adaptation to similar environments (Simpson, 1953). Analogies and convergences differ in that natural selection operates on different developmental processes in the former, but on the same developmental processes in the

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latter (Lieberman *et al.*, 1996). Parallel homoplasies, or parallelisms, result from aspects of ontogeny that limit phenotypic diversity, but which have no necessary connection with the demands of the environment (Wake, 1991). Parallelisms, in other words, are by-products of development, not adaptations (cf Gould & Lewontin, 1979). A fourth type of homoplasy is reversal, in which, for example, encephalisation increases and then decreases, or molar crowns enlarge and then reduce in size (Simpson, 1953). Most cases of reversal are probably due to natural selection, but the authors of a recent assessment of silenced gene reactivation have suggested that reversals may also be neutral with regard to adaptation (Marshall *et al.*, 1994). The last form of homoplasy is epigenetic similarity or homoiology. Homoiologies result from phenotypic similarities in the way that different genotypes interact with the environment (Lieberman *et al.*, 1996). That is, they are phylogenetically misleading morphological similarities that can be attributed primarily to non-genetic factors.

Homoplasies are problematic for those attempting to reconstruct the phylogenetic relationships of the early hominids because they can be mistaken for shared derived similarities, or synapomorphies, which are the principal evidence for phylogeny. When a character state data matrix contains a small number of homoplasies in relation to the number of synapomorphies, it is possible to obtain an unambiguous estimate of phylogeny using parsimony analysis. This form of analysis favours the hypothesis of relationship that requires the least number of character state changes to account for the distribution of character states among a group of taxa (Quicke, 1993; Kitching *et al.*, 1998; Schuh, 1999). However, in phylogenetic studies of the hominids the ratio of inferred homoplasies to putative synapomorphies has generally been high (e.g., Skelton *et al.*, 1986; Wood & Chamberlain, 1986; Chamberlain & Wood, 1987; Wood & Chamberlain, 1987; Wood, 1991; Skelton & McHenry, 1992; Lieberman *et al.*, 1996; Strait *et al.*, 1997). In these circumstances parsimony analysis is incapable of unambiguously resolving the relationships of the taxa. Instead, it yields several competing hypotheses of relationship that can be considered equally parsimonious (Lieberman *et al.*, 1996).

The confounding effect of homoplasy can be observed by comparing the support for the most parsimonious cladograms, obtained in published cladistic analyses of the early hominids, with the support for the next most parsimonious cladograms recovered in these analyses. For example, Skelton *et al.*'s (1986) most parsimonious cladogram, which places *Homo habilis* in a sister group with *Paranthropus*, is supported by only one more character than their next most parsimonious cladogram, which places *Australopithecus africanus* in a sister group with *Paranthropus* to the exclusion of *H. habilis*. Likewise, the cladograms favoured by Wood (1991) and Strait *et al.* (1997), both of which suggest that *Homo* is monophyletic, are only one or two steps shorter than cladograms in which *Homo* is paraphyletic (Wood & Collard, 1999). In these and other studies, the presence of numerous homoplasies among the character state data means that taxonomically significant alterations in cladogram topology require relatively few extra character state changes. Consequently, because of these high levels of homoplasy, it is impossible to place much, if any, confidence in the most parsimonious cladograms recovered in recent phylogenetic analyses of the early hominids (Corruccini, 1994; Wood & Collard, 1999).

It is widely assumed that homoplasies are not randomly distributed across the early hominid cranium. Characters from the masticatory apparatus are especially prone to homoplasy, according to a number of authors. The early, pioneering, decade of

hominid cladistic studies between 1975 and 1985 paid little attention to the extent to which attempts to recover phylogenetic history might be compromised by homoplasy. Wood & Chamberlain (1986) appear to have been the first to draw attention to empirical evidence of high levels of what they termed inferred homoplasies, or broken synapomorphies. However, they made no specific suggestions about the likelihood that homoplasies were located in a particular morphological region or functional system.

The notion that characters drawn from the early hominid masticatory system are especially prone to homoplasy appears to have had its origin in the conclusions arrived at in Skelton *et al.* (1986). Their preferred cladogram suggested that *A. afarensis* is the sister species of a clade comprising *A. africanus*, *H. habilis* and *Paranthropus*, and that *A. africanus* is the sister species of a (*H. habilis*, *Paranthropus*) clade. This implied that the craniodental similarities between *A. afarensis* and *H. habilis*, namely their relative dental and facial reduction, must have resulted from a reversal in the lineage leading to *H. habilis*. In a follow-up to their 1986 study, Skelton & McHenry (1992) were explicit in suggesting that ''homoplasy appears especially prevalent in traits relating to heavy chewing'' (p. 342) and they concluded that ''traits related to heavy chewing are not reliable for reconstructing hominid phylogeny'' (p. 345). Other authors who have suggested that the early hominid masticatory system is especially prone to homoplasy include Wood (e.g., 1988; Turner & Wood, 1993), McHenry (1994, 1996), Lieberman *et al.* (1996) and Asfaw *et al.* (1999). It is also worth noting that Begun (1994) has argued in relation to the Miocene apes that the mandible is particularly susceptible to homoplastic change and is therefore a poor source of characters for phylogeny estimation.

The assumption that early hominid masticatory characters are more prone to homoplasy, and therefore less reliable for phylogenetic reconstruction, than other regions of the cranium has been justified in a number of ways. Some authors have supported the hypothesis because masticatory characters have apparently been found to be homoplastic in other mammalian groups (e.g., Wood, 1988; Turner & Wood, 1993). Others have argued that masticatory characters are especially susceptible to homoplasy because they are part of a feeding adaptation and ''traits related to this type of adaptation have long been recognised as being unreliable'' (Skelton & McHenry, 1992: 343), but the precise source of this hypothesis is not provided. Recently, Lieberman *et al.* (1996) have argued that bony characters of the early hominid masticatory system are likely to be especially homoplastic because they derive from intramembranous bone whose development is particularly sensitive to non-genetic factors, especially mechanical force. Lieberman and colleagues contrast these characters with basicranial characters, which develop from cartilaginous percursors whose initial growth appears to be less influenced by non-genetic factors.

Although several justifications have been offered for the ''masticatory homoplasy hypothesis'', it has never been tested formally. We suggest that one way in which the hypothesis can be evaluated is to determine whether the masticatory characters of extant primates are more prone to homoplasy than characters from other regions of the skull. Accurate assessments of homoplasy are dependent on an accurate phylogeny, and developments in molecular systematics enable us to be reasonably confident about the phylogenetic relationships of at least two groups of primates, the hominoids (Ruvolo, 1997) and papionins (Harris & Disotell, 1998; Harris, 2000). The approach we adopt in this study is comparable to those employed recently to investigate the phylogenetic utility of hominoid molar morphology (Hartman, 1988), higher primate

craniodental morphology (Collard & Wood, 2000) and hominoid soft-tissue features (Gibbs *et al.*, 2000). We gathered craniodental data from closely related extant primate taxa whose relationships have been established using molecular techniques, and compared phylogenetic hypotheses derived from the different cranial regions with the molecular phylogeny. Congruence between the regional morphological and molecular phylogenies for the extant taxa was taken to indicate that the corresponding hominid fossil evidence can be reasonably assumed to be reliable for phylogenetic reconstruction, whereas incongruence was assumed to indicate the reverse.

Recently a number of researchers have expressed concern about the validity of hominid cladistic analyses that employ large numbers of cranial and dental characters (e.g., Asfaw *et al.*, 1999; McCollum, 1999; Lovejoy *et al.*, 1999; McCollum & Sharpe, 2001). Such analyses, according to these researchers, are unlikely to be reliable because many craniodental characters are correlated either developmentally or functionally, and character correlation violates the primary tenet of cladistics, which is that characters should be independent. The solution to the problem of character correlation, offered by at least some of the researchers in question, is to abandon the cladistic methodology in favour of a return to the traditional practice of outlining phylogenetic relationships without reference to a formal analysis (e.g., Asfaw *et al.*, 1999).

Whilst we acknowledge that character interdependence may be a problem in cladistic analyses of hominid craniodental morphology, we believe the problem is considerably more complex than has been presented. First, morphogenetic studies published in the last few years have shown that features which are tightly integrated in terms of their function, such as upper and lower molars, need not be closely linked developmentally (Thomas *et al.*, 1997; Ferguson *et al.*, 1998; Hlusko & Mahaney, 2000). Second, a recent assessment of hypotheses of functional and structural integration in the hominid cranial base found considerably lower degrees of integration than predicted by the hypotheses (Strait, 2001). Third, recently discovered hominid specimens display combinations of character states that undermine hitherto widespread assumptions about dental and craniofacial character correlation (Leakey *et al.*, 2001). Last, there is evidence from the dentition that characters that might be expected to be redundant are not in fact correlated in such a way that they should be treated as a single character in phylogenetic analyses. For example, Butler (1999) has shown in relation to modern human deciduous and permanent molars that ''partition of the tooth between trigonid and talonid is independent of tooth size'' (p. 26). Likewise, studies have shown that fossil hominid mandibular and maxillary teeth may yield different taxonomic hypotheses (Wood & Engelman, 1988; Suwa *et al.*, 1994), and that the buccolingual and mesiodistal diameters of extant hominoid teeth can produce different hypotheses of relationship (Collard, 1998). In light of these observations, we contend that too little is known about the issue of character correlation at the moment to use it as a justification for abandoning the use of multiple craniodental characters in cladistic analyses of hominids and other primates.

A number of researchers have also expressed doubts about the usefulness of higher primate cranial and dental data for phylogenetic analysis (as opposed to questioning the validity of analysing such data cladistically) (e.g., Hartman, 1988; Harrison, 1993; Pilbeam, 1996; Jablonski, 1999). We are also sceptical about the phylogenetic utility of standard higher primate craniodental data, at least at the species and genus level (Collard & Wood, 2000). However, the design of the current

study is such that it focuses on the relative reliability of different cranial regions for phylogenetic reconstruction, which is a different issue from whether or not craniodental data can be relied on for phylogeny estimation.

Materials and methods

Morphology can be translated into character states for cladistic analysis in two main ways. The first breaks up the phenotype into anatomical components, and expresses 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 hominids have used this approach (e.g., Eldredge & Tattersall, 1975; Delson *et al.*, 1977; Skelton *et al.*, 1986; Skelton & McHenry, 1992; Lieberman *et al.*, 1996; 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 highly subjective. 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 have described the torus as ''well-developed'' (Leakey & Leakey, 1986; Andrews & Martin, 1987; Conroy, 1994). The subjectivity of qualitative morphological characters 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 hominids. Another reason for questioning the utility of qualitative character assessment is that it is difficult to counter the confounding effects of body size differences between taxa. This point is exemplified by Wood and colleagues' (1998) examination of the likelihood of association between OH 8 and OH 35, the *H. habilis* left talus and distal left tibia from Olduvai Gorge, Tanzania. When Wood *et al.* (1998) did not correct for body size, they obtained the same result as had been obtained in earlier discrete character assessments, i.e., the talus and the tibia appeared to belong 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 the continuous distribution up into discontinuous states. Opponents of this approach (e.g., Crisp & Weston, 1987; Pimentel & Riggins, 1987; Cranston & Humphries, 1988; Crowe, 1994; Disotell, 1994; Moore, 1994) argue that measurements are unsuitable for cladistic analysis, and that cladistic analyses based on measurement data are no more than ''thinly-disguised'' phenetic analyses. They also argue that the aforementioned coding methods break the spectrum of measurements into ''artificial'' character states. We contend that these objections are not valid. As Maddison *et al.* (1984), Felsenstein (1988), Swofford & Olsen (1990), Thiele (1993), Lieberman (1995) and, most recently, 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 goodness-of-fit indices obtained in cladistic analyses of the early hominids. 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 goodness-of-fit indices obtained by Chamberlain & Wood (1987) and Wood (1991, 1992*b*) from quantitative data are comparable with those obtained by Lieberman *et al.* (1996) and Strait *et al.* (1997) from qualitative data. The ''artificiality'' argument can also be refuted, for coding is no more ''artificial'' than is the decision to break up into discontinuous states what is, with 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 cladistic does not group taxa on the basis of overall similarity. In cladistic analyses of metric data, as in cladistic analyses of conventional data, 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 termini span structures have different embryonic origins (McCollum & Sharpe, 2001), 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. Second, given appropriate technical rigour, anyone can repeat the procedure and verify the observations. Third, levels of intra- and inter-observer error for most higher primate craniodental metrical data are low (e.g. Wood, 1991). It is for these reasons that we opted to rely on metrical data for our tests.

We compiled two datasets using measurements of the cranium, mandible and dentition comparable to those that have been used in the few cladometric analyses of the hominids that have been carried out (Corruccini & McHenry, 1980; Wood & Chamberlain, 1986, 1987; Chamberlain & Wood, 1987; Stringer, 1987; Wood, 1991). The first dataset was for the ape and human superfamily, Hominoidea, the second for the extant baboon, macaque and mangabey tribe, Papionini. The hominoid dataset comprised values for 129 measurements recorded on mixed sex samples of *Gorilla*, *Homo*, *Pan*, *Pongo* and an outgroup, *Colobus*. Seventy-seven of the measurements were recorded on 37 *G. gorilla* (20 males, 17 females), 75 *H. sapiens* (40 males, 35 females), 35 *P. troglodytes* (13 males, 22 females), 41 *P. pygmaeus* (20 males, 21 females) and 24 *C. guereza* (12 males, 12 females). The other 52 measurements were recorded on 20 *G. gorilla* (ten males, ten females), 20 *H. sapiens* (ten males, ten females), 20 *P. troglodytes* (ten males, ten females), 20 *P. pygmaeus* (ten males, ten females) and 20 *C. guereza* (ten males, ten females). The data were taken from Collard & Wood (2000). The measurements are listed in Table 1. The palate and upper dentition are represented by 31 measurements, the mandible and lower dentition by 40, the face by 24 measurements and the cranial vault and base by 34 measurements. The cranial and mandibular measurements were rounded up to the nearest 1 mm, and the dental measurements to the nearest 0·1 mm.

The papionin data set consisted of values for 62 measurements recorded on mixed sex samples of *Cercocebus*, *Lophocebus*, *Macaca*,

Table 1 Measurements used to compile the hominoid dataset

Character	Definition	Source
P1	I^1 labiolingual diameter	Wood (1975) #1
P2	I^1 mesiodistal diameter	Wood (1975) #2
P3	I^2 labiolingual diameter	Wood (1975) #3
P4	I^2 mesiodistal diameter	Wood (1975) #4
P5	C^1 mesiodistal diameter	Wood (1975) #5
P6	C^1 labiolingual diameter	Wood (1975) #6
P7	C^1 labial height	Wood (1975) #7
P8	P^3 labiolingual diameter	Wood (1975) #8
P9	P^3 mesiodistal diameter	Wood (1975) #9
P10	P^4 labiolingual diameter	Wood (1975) #10
P11	P^4 mesiodistal diameter	Wood (1975) #11
P12	M^1 labiolingual diameter	Wood (1975) #12
P13	M^1 mesiodistal diameter	Wood (1975) #13
P14	M^2 labiolingual diameter	Wood (1975) #14
P15	M^2 mesiodistal diameter	Wood (1975) #15
P16	M^3 labiolingual diameter	Wood (1975) #16
P17	M^3 mesiodistal diameter	Wood (1975) #17
P18	Outer alveolar breadth at M^3	Wood (1975) #61
P19	Inter upper canine breadth	Wood (1975) #63
P20	Palate length	Wood (1975) #64
P21	Inner alveolar breadth at M^3	Wood (1975) #65
P22	Palate depth at M^1	Wood (1975) #66
P23	Prosthion to plane of M^3	Wood (1975) #68
P24	Maxillo–Alveolar breadth (M^2B–M^2B)	Chamberlain (1987) #P2
P25	Breath between upper second molars (M^2L–M^2L)	Chamberlain (1987) #P4
P26	Palate depth at incisive fossa	Chamberlain (1987) #P5
P27	Palate depth at upper second molars	Chamberlain (1987) #P6
P28	Maxillary alveolar subtense	Chamberlain (1987) #P7
P29	Upper incisor alveolar length	Chamberlain (1987) #P8
P30	Upper premolar alveolar length	Chamberlain (1987) #P9
P31	Upper molar alveolar length	Chamberlain (1987) #P10
M1	I_1 labiolingual diameter	Wood (1975) #18
M2	I_1 mesiodistal diameter	Wood (1975) #19
M3	I_2 labiolingual diameter	Wood (1975) #20
M4	I_2 mesiodistal diameter	Wood (1975) #21
M5	C_1 labiolingual diameter	Wood (1975) #22
M6	C_1 mesiodistal diameter	Wood (1975) #23
M7	C_1 labial height	Wood (1975) #24
M8	P_3 buccolingual diameter	Wood (1975) #25
M9	P_3 mesiodistal diameter	Wood (1975) #26
M10	P_4 buccolingual diameter	Wood (1975) #27
M11	P_4 mesiodistal diameter	Wood (1975) #28
M12	M_1 buccolingual diameter	Wood (1975) #29
M13	M_1 mesiodistal diameter	Wood (1975) #30
M14	M_2 buccolingual diameter	Wood (1975) #31
M15	M_2 mesiodistal diameter	Wood (1975) #32
M16	M_3 buccolingual diameter	Wood (1975) #33
M17	M_3 mesiodistal diameter	Wood (1975) #34
M18	Maximum cusp height	Wood (1975) #35
M19	Condylar height	Wood (1975) #36
M20	Bicondylar breadth	Wood (1975) #37
M21	Coronoid height	Wood (1975) #38
M22	Bicoronoid breadth	Wood (1975) #39
M23	Right condylar head width	Wood (1975) #40
M24	Right condylar head anterior-posterior breath	Wood (1975) #41

Table 1 *Continued*

Character	Definition	Source
M25	Ramal breadth	Wood (1975) #42
M26	Bigonial width	Wood (1975) #44
M27	Height of mandibular body at M_1	Wood (1975) #45
M28	Thickness of mandibular body of M_1	Wood (1975) #46
M29	Symphyseal height	Wood (1975) #47
M30	Symphyseal thickness	Wood (1975) #48
M31	Inner alveolar breadth at M_3	Wood (1975) #49
M32	Maximum mandibular length	Wood (1975) #50
M33	Inter lower canine distance	Wood (1975) #51
M34	Mandibular corpus height at M_3	Chamberlain (1987) #M3
M35	Height of foramen spinosum	Chamberlain (1987) #M4
M36	Height of mental foramen	Chamberlain (1987) #M5
M37	Breadth between lower second molars	Chamberlain (1987) #M9
M38	Lower incisor alveolar length	Chamberlain (1987) #M10
M39	Lower premolar alveolar length	Chamberlain (1987) #M11
M40	Lower molar alveolar length	Chamberlain (1987) #M12
F1	Right orbital breadth	Wood (1975) #52
F2	Right orbital height	Wood (1975) #53
F3	Interorbital breadth	Wood (1975) #54
F4	Biorbital breadth	Wood (1975) #55
F5	Nasion–rhinion	Wood (1975) #56
F6	Nasion–nasospinale	Wood (1975) #57
F7	Maximum nasal width	Wood (1975) #58
F8	Nasospinale–prosthion	Wood (1975) #59
F9	Bijugal breadth	Wood (1975) #60
F10	Bizygomatic breadth	Wood (1975) #62
F11	Upper facial breadth	Chamberlain (1987) #F1
F12	Lower facial breadth	Chamberlain (1987) #F3
F13	Breadth between infraorbital foramina	Chamberlain (1987) #F8
F15	Facial height	Chamberlain (1987) #F10
F16	Height of infraorbital foramen	Chamberlain (1987) #F11
F17	Height of orbital margin	Chamberlain (1987) #F12
F18	Upper malar height	Chamberlain (1987) #F13
F19	Lower malar height	Chamberlain (1987) #F14
F20	Upper facial prognathism	Chamberlain (1987) #F15
F21	Lower facial prognathism	Chamberlain (1987) #F16
F22	Malar prognathism	Chamberlain (1987) #F17
F23	Naso-frontal subtense	Chamberlain (1987) #F18
F24	Maxillary subtense	Chamberlain (1987) #F19
C1	Glabella–opisthocranion	Wood (1975) #69
C2	Minimum post-orbital breadth	Wood (1975) #70
C3	Basion–bregma	Wood (1975) #71
C4	Maximum bi-parietal breadth	Wood (1975) #72
C5	Biporionic width	Wood (1975) #73
C6	Mastoid length	Wood (1975) #74
C7	Coronale–coronale	Wood (1975) #75
C8	Opisthion–inion	Wood (1975) #76
C9	Bimastoid width	Wood (1975) #77
C10	Posterior skull length	Wood (1975) #78
C11	Breadth across tympanic plates	Chamberlain (1987) #B1
C12	Breadth between carotid canals	Chamberlain (1987) #B2
C13	Breadth between petrous apices	Chamberlain (1987) #B3
C14	Breadth between foramen ovale	Chamberlain (1987) #B4
C15	Breadth between infratemporal crests	Chamberlain (1987) #B5
C16	Breadth of mandibular fossa	Chamberlain (1987) #B6

Table 1 ***Continued***

Character	Definition	Source
C17	Length of tympanic plate	Chamberlain (1987) #B7
C18	Length of petrous temporal	Chamberlain (1987) #B8
C19	Position of foramen ovale	Chamberlain (1987) #B9
C20	Position of infratemporal crest	Chamberlain (1987) #B10
C21	Length of foramen magnum	Chamberlain (1987) #B11
C22	Breadth of foramen magnum	Chamberlain (1987) #B12
C23	Length of infratemporal fossa	Chamberlain (1987) #B13
C24	Breadth of infratemporal fossa	Wood (1975) #B67
C25	Opisthion–infratemporal subtense	Chamberlain (1987) #B15
C26	Basiooccipital length	Chamberlain (1987) #B16
C27	Parietal thickness at Lambda	Chamberlain (1987) #V1
C28	Frontal sagittal chord	Chamberlain (1987) #V6
C29	Parietal sagittal chord	Chamberlain (1987) #V7
C30	Parietal coronal chord	Chamberlain (1987) #V8
C31	Occipital sagittal chord	Chamberlain (1987) #V9
C32	Frontal sagittal arc	Chamberlain (1987) #V10
C33	Occipital sagittal arc	Chamberlain (1987) #V11
C34	Auricular height	Chamberlain (1987) #V12

Mandrillus, *Papio*, *Theropithecus* and an outgroup, *Pan*. The 62 measurements were recorded on 26 *C. galeritus*/*torquatus* (13 males, 13 females), 40 *L. albigena*/*aterrimus* (20 males, 20 females), 40 *M. fascicularis*/*mulatta* (20 males, 20 females), 62 *M. leucopheus*/*sphinx* (42 males, 20 females), 39 *P. anubis*/*cynocephalus* (20 males, 19 females), 44 *T. gelada* (22 males, 22 females) and 17 *P. troglodytes* (ten males, seven females). Fifty-five of the measurements were recorded on a further 14 *C. torquatus* (seven males, seven females) and 12 *P. troglodytes* (five males, seven females). The data were taken once again from Collard & Wood (2000). As before, the measurements were divided into regional groups. Sixteen measurements were assigned to the palate and upper dentition group, 14 to the mandible and lower dentition, 16 to the face and 16 to the cranial vault and base. The measurements are listed in Table 2. Again, the cranial and mandibular measurements were rounded up to the nearest 1 mm, and the dental measurements to the nearest 0·1 mm.

Before morphometric data are analysed cladistically they must be adjusted to minimise the confounding effects of any body size differences between the taxa and then converted into discrete character states (e.g., Chamberlain & Wood, 1987; Wood, 1991, 1992*a*,*b*; Rae, 1997). In the present study, size adjustment was accomplished by dividing each specimen value by the geometric mean of all the specimen's values (Jungers *et al.*, 1995). This method, which is one of the Mosimann family of shape ratios, equalises the volumes of the specimens while maintaining their original shapes.

The size-adjusted data were converted into discrete character states using divergence coding (Thorpe, 1984). This method proceeds by calculating the mean values for the taxa and testing the differences among them 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

Table 2 **Measurements used to compile the papionin dataset**

Character	Definition	Source
P1	Maxillo–alveolar length	Wood (1991) #87
P2	Maxillo–alveolar breadth	Wood (1991) #88
P3	Incisive canal–palatomaxillary suture	Wood (1991) #92
P4	Upper incisor alveolar length	Wood (1991) #94
P5	Palatal height at M^1	Wood (1991) #103
P6	Upper premolar alveolar length	Wood (1991) #96
P7	Upper molar length	Wood (1991) #97
P8	Canine interalveolar distance	Wood (1991) #98
P9	Last premolar interalveolar distance	Wood (1991) #100
P10	Second molar interalveolar distance	Wood (1991) #101
P11	I^1 mesiodistal crown diameter	Wood (1991) #186
P12	I^1 labiolingual crown diameter	Wood (1991) #187
P13	C^1 mesiodistal crown diameter	Wood (1991) #190
P14	C^1 labiolingual crown diameter	Wood (1991) #191
P15	M^3 interalveolar distance	Wood (1991) #93
P16	Palate depth at incisive fossa	Chamberlain (1987) #P5
M1	Symphyseal height	Wood (1991) #141
M2	Maximum symphyseal depth	Wood (1991) #142
M3	Corpus height at M_1	Wood (1991) #150
M4	Corpus width at M_1	Wood (1991) #151
M5	Corpus height at M_3	Wood (1991) #157
M6	Corpus width at M_3	Wood (1991) #158
M7	Lower premolar alveolar length	Wood (1991) #167
M8	Lower molar alveolar length	Wood (1991) #168
M9	P_4 mesiodistal crown diameter	Wood (1991) #271
M10	P_4 labiolingual crown diameter	Wood (1991) #272
M11	M_1 mesiodistal crown diameter	Wood (1991) #285
M12	M_1 labiolingual crown diameter	Wood (1991) #286
M13	M_2 mesiodistal crown diameter	Wood (1991) #313
M14	M_2 labiolingual crown diameter	Wood (1991) #314
F1	Superior facial height	Wood (1991) #43
F2	Alveolar height	Wood (1991) #45
F3	Superior facial breadth	Wood (1991) #49
F4	Bizygomatic breadth	Wood (1991) #52
F5	Bimaxillary breadth	Wood (1991) #53
F6	Anterior interorbital breadth	Wood (1991) #55
F7	Orbital height	Wood (1991) #57
F8	Minimum malar height	Wood (1991) #59
F9	Maximum nasal aperture width	Wood (1991) #68
F10	Nasal height	Wood (1991) #69
F11	Sagittal length of nasal bones	Wood (1991) #71
F12	Superior breadth of nasal bones	Wood (1991) #73
F13	Inferior breadth of nasal bones	Wood (1991) #74
F14	Zygomaxillare–Porion	Wood (1991) #127
F15	Upper facial prognathism	Chamberlain (1987) #F15
F16	Lower facial prognathism	Chamberlain (1987) #F16
C1	Glabella–opisthocranion	Wood (1991) #1
C2	Bregma–basion	Wood (1991) #4
C3	Minimum frontal breadth	Wood (1991) #8
C4	Biporionic breadth	Wood (1991) #11
C5	Glabella–bregma	Wood (1991) #17
C6	Postglabellar sulcus–bregma	Wood (1991) #19
C7	Parietal sagittal chord	Wood (1991) #25
C8	Parietal lambdoid chord	Wood (1991) #31
C9	Lambda–inion	Wood (1991) #35

Table 2 **Measurements used to compile the papionin dataset**

Character	Definition	Source
C10	Occipital sagittal length	Wood (1991) #39
C11	Foramen magnum maximum width	Wood (1991) #77
C12	Occipital condyle maximum length	Wood (1991) #78
C13	Lambda thickness of parietal	Wood (1991) #107
C14	Breadth between carotid canals	Chamberlain (1987) #B2
C15	Breadth between petrous apices	Chamberlain (1987) #B3
C16	Length of tympanic plate	Chamberlain (1987) #B7

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 cell in the column of the matrix is filled with -1, $+1$ or 0. A cell is scored as -1 if the mean of the taxon in the column is greater than the mean of the taxon in the row, and if the difference between the means is significant. A cell is scored as $+1$ 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 $+1$s for each column is calculated. Lastly, an integer is added to each taxon total. In converting both datasets, Student's *t*-test (two-tailed) was used to test for statistical significance ($P \leq 0{\cdot}05$) and 10 was added to each taxon total.

Testing the assumption that early hominid masticatory characters are especially susceptible to homoplastic change is complicated by the fact that assigning characters to functional systems is difficult and subjective, with many characters being involved in more than one functional system (e.g., Skelton & McHenry, 1998; Strait & Grine, 1998). For this study, we divided the cranium into four regions: (1) the palate and upper dentition, (2) the mandible and lower dentition, (3) the face and (4) the cranial vault and base. These regions were selected on the basis that they are relatively straightforward to delimit morphometrically. We assumed that if the masticatory homoplasy hypothesis is correct the regions of the skull most closely linked to mastication—the palate and upper dentition, and the mandible and lower dentition—should be less reliable for reconstructing phylogeny than the characters from the face and the cranial vault and base. We acknowledge that other selective pressures may influence the form of the teeth and jaws (e.g., aggression among males favouring canine enlargement), and that there are very probably links between mastication and some characters from the face and the cranial vault and base. But we contend that for the purposes of this study the assumption that mastication affects characters of the teeth and jaws more strongly than it affects characters from the face and cranial vault and base is a reasonable one.

The hominoid and papionin datasets were used to perform three tests of the hypothesis that masticatory characters are more prone to homoplasy and therefore less reliable for phylogenetic reconstruction than characters from other regions of the skull. In the first, each regional character group was subjected to parsimony analysis using Swofford's (1998) phylogeny reconstruction program PAUP* 4.0, and the resulting minimum length cladograms compared with the appropriate consensus molecular cladogram (Figures 1 and 2).

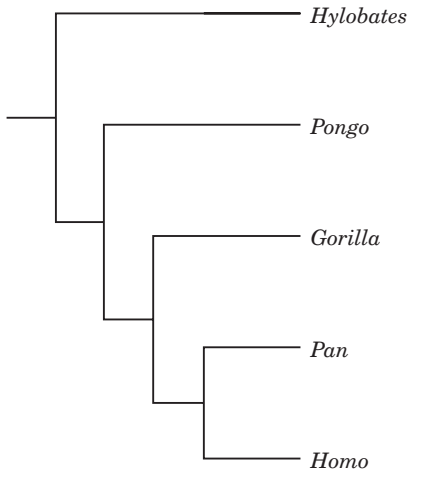

Figure 1. Hominoid molecular relationships.

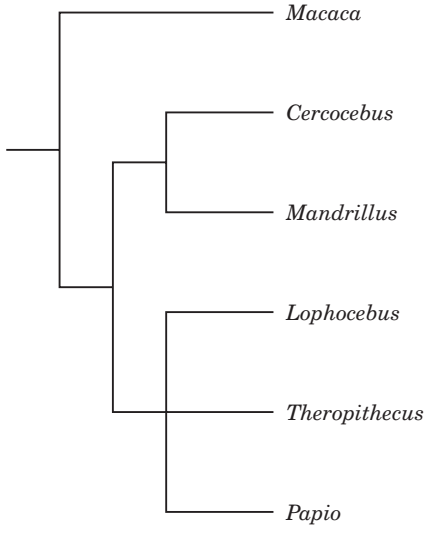

Figure 2. Papionin molecular relationships.

Characters were treated as linearly ordered and freely reversing (Chamberlain & Wood, 1987; Slowinski, 1993; Rae, 1997), and minimum length cladograms were identified using the branch-and-bound algorithm. The hypothesis was considered supported if the cranial vault, or face, characters favoured a cladogram that was identical to, or compatible with, the molecular cladogram, but the palate, mandible and dental characters did not favour such a cladogram. A compatible cladogram could be a partially resolved cladogram that comprised only molecular clades, or the strict consensus of several equally parsimonious cladograms that comprised only molecular clades.

The second test of the hypothesis was based on the phylogenetic bootstrap, which is a method for assessing the confidence interval associated with a given clade (Felsenstein, 1985; Sanderson, 1995). Using PAUP* 4.0, 10,000 artificial matrices were derived from each regional matrix by sampling with replacement. The artificial 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 cladograms were compared to the appropriate molecular cladogram. The hypothesis was judged to be supported if all the clades of the cladogram obtained from the face characters were compatible with the molecular cladogram, but those of the cladograms obtained from the palate and upper dentition and the mandible and lower dentition characters were not. The hypothesis was also judged to be supported if all the clades of the cladograms obtained from the cranial vault and base characters were compatible with the molecular cladogram, but those of the cladograms obtained from the palate and upper dentition and the mandible and lower dentition characters were not.

The third test of the hypothesis was based on the consistency index (CI), which is a measure of the amount of homoplasy implied by a given cladogram. The CI for a single character is calculated by dividing the minimum number of character state changes required by any conceivable cladogram (m) by the number of changes required by the focal cladogram (s) (Swofford, 1991). The CI for two or more characters is computed as M/S, where M and S are the sums of the

m and *s* values for the individual characters (Swofford, 1991). A CI of 1 indicates that a cladogram requires no homoplastic changes to be hypothesised, and the level of homoplasy increases as CI decreases. Each regional matrix was imported into the phylogeny exploration program MacClade 3 (Maddison & Maddison, 1992). A cladogram with the same ingroup branching pattern as the group's molecular cladogram was set up and rooted by placing the outgroup as the sister taxon of the other taxa. With the characters treated as linearly ordered and freely reversing, the uninformative characters were excluded from the data matrix and the CI recorded. Lastly, the rank order of the CIs of the regional cladograms was determined and a comparison made with the rank order obtained in the other analysis. The hypothesis was judged supported if, in both the hominoid and papionin data sets, the CIs of the face and cranial vault character groups were higher than those of the palate and upper dentition and mandible and lower dentition character groups. In the papionin analyses, the *Lophocebus*/*Papio*/*Theropithecus* trichotomy shown in the molecular cladogram (Figure 2) was resolved in favour of a sister group relationship between *Papio* and *Theropithecus*, since this fitted the morphological data better than the other arrangement suggested by the molecular evidence—a sister group relationship between *Lophocebus* and *Papio* (Harris, 2000).

Results

In the first test of the masticatory homoplasy hypothesis, regional groups of characters from the hominoids and papionins were subjected to parsimony analysis and the resulting cladograms compared to the consensus molecular cladograms for the groups. The hypothesis was considered to be supported if the characters from the cranial vault and base, or face, favoured a cladogram that was identical to, or compatible with, the molecular cladogram, whilst the palate, mandible and dental characters did not favour such a cladogram. This test did not support the hypothesis.

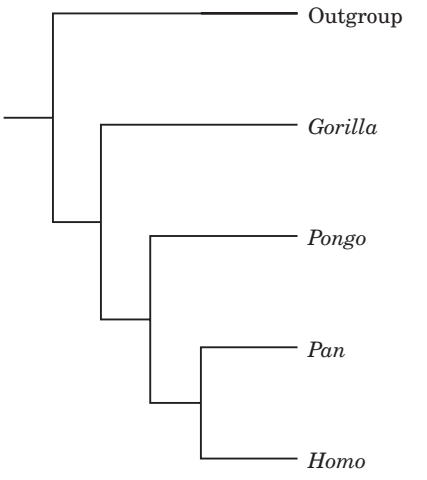

Figure 3. Cladogram yielded by hominoid palate and upper dentition characters.

None of the cladograms obtained from the hominoid regional character groups was compatible with the hominoid molecular cladogram (Figure 1). The cladogram obtained from the palate and upper dentition data set (Figure 3) suggested that *Gorilla* is the sister taxon of a clade comprising *Homo*, *Pan*, and *Pongo*, and that *Pongo* is the sister taxon of a (*Homo*, *Pan*) clade (the goodness-of-fit statistics associated with all the cladograms discussed in this section are given in Table 3). The cladogram derived from the mandible and lower dentition data set (Figure 4) indicated that *Homo* is the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and that *Gorilla* is the sister taxon of a clade comprising *Pan* and *Pongo*. The cladograms yielded by the face and cranial vault and base data sets (Figure 5) suggested that *Homo* is the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and that *Pan* is the sister taxon of a (*Gorilla*, *Pongo*) clade.

Table 3 **Goodness-of-fit statistics for most parsimonious cladograms**

Region	IC	CI	RI	CL
Hominoids				
Palate and upper dentition	27	0·78	0·47	238
Mandible and lower dentition	39	0·74	0·32	377
Face	22	0·85	0·63	188
Cranial vault and base	30	0·80	0·49	267
Papionins				
Palate and upper dentition	16	0·79	0·20	209
Mandible and lower dentition	14	0·67	0·08	219
Face	15	0·68	0·20	236
Cranial vault and base	16	0·72	0·18	229

IC=number of informative characters. CI=consistency index. RI=retention index. CL=cladogram length.

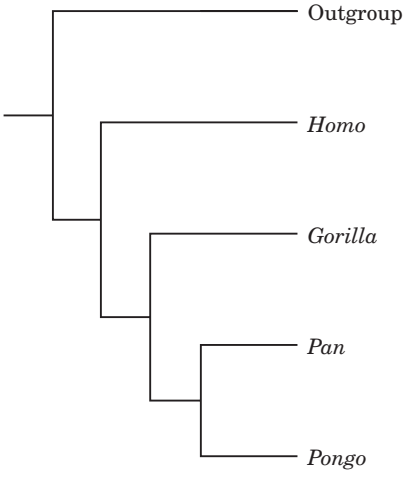

Figure 4. Cladogram yielded by the hominoid mandible and lower dentition data set.

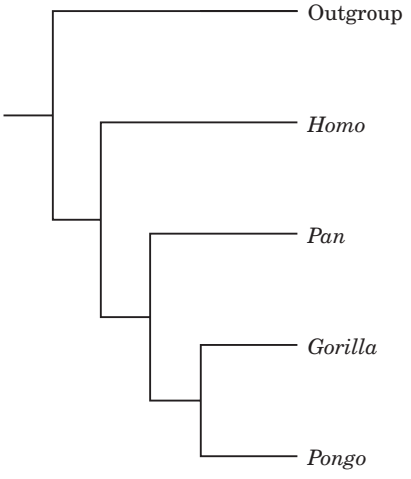

Figure 5. Cladogram yielded by the hominoid face and cranial vault and base data sets.

Similarly, none of the cladograms favoured by the papionin regional character groups was compatible with the papionin consensus molecular cladogram (Figure 2). The palate and upper dentition cladogram (Figure 6) separated *Lophocebus* from *Cercocebus*, *Macaca* and the baboons, and grouped *Cercocebus* and *Macaca* together in a clade that was the sister taxon of a clade comprising the three baboon genera. Within the latter clade, *Papio* was positioned as the sister taxon of a (*Mandrillus*, *Theropithecus*) clade. The cladogram favoured by the mandible and lower dentition characters (Figure 7) suggested that *Lophocebus* is the basal papionin, and that *Cercocebus* is the sister taxon of a clade consisting of *Macaca* and the baboons. It also suggested that *Theropithecus* is the sister taxon of a (*Macaca*, *Mandrillus*, *Papio*) clade, and that *Macaca* is the sister taxon of a clade comprising *Mandrillus* and *Papio*. The cladogram obtained from the face characters and from the cranial vault and base characters (Figure 8) was similar to the mandible and lower dentition cladogram. The only

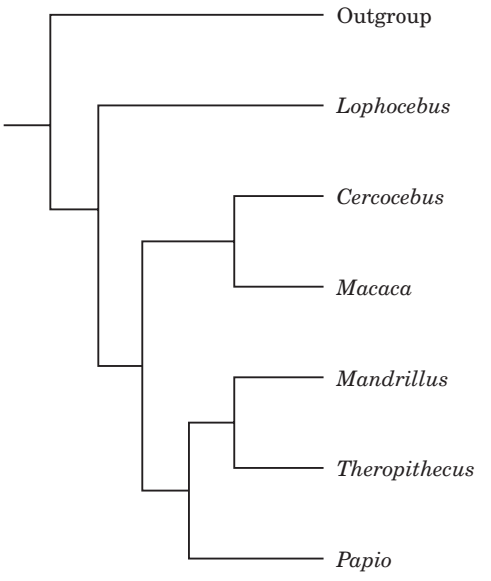

Figure 6. Cladogram yielded by the papionin palate and upper dentition data set.

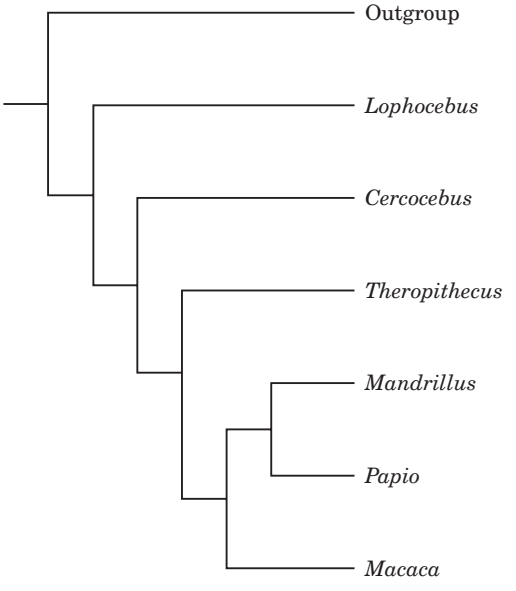

Figure 7. Cladogram yielded by the papionin mandible and lower dentition data set.

difference was that the former suggested that *Theropithecus* is the sister taxon of *Mandrillus* and *Papio* rather than *Macaca*, which was positioned as the sister taxon of the three baboon genera.

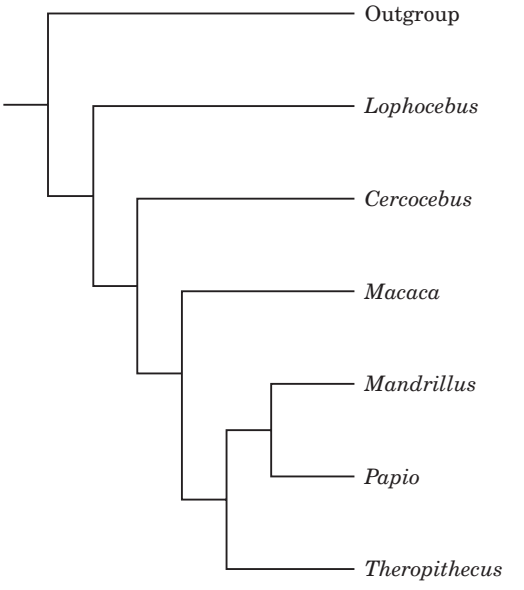

Figure 8. Cladogram yielded by the papionin face and cranial vault and base data sets.

In the second test of the hypothesis, hominoid and papionin regional character groups were bootstrapped using a confidence region of 70%, and the resulting clades were compared to the consensus molecular cladograms for the groups. The hypothesis was judged to be supported if all the clades obtained from the face characters were compatible with the molecular cladogram, but those obtained from the palate and upper dentition and the mandible and lower dentition characters were not. The hypothesis was also judged to be supported if all the clades obtained from the cranial vault and base characters were compatible with the molecular cladogram, but those obtained from the palate and upper dentition and the mandible and lower dentition characters were not. This test also did not support the hypothesis.

None of the hominoid regional character groups yielded clades that were compatible with the hominoid molecular cladogram

Table 4 Percentage support for clades recovered in the bootstrap analyses

Character group	Clade	Percentage
Hominoids		
Palate and upper dentition	No ≥70% clades recovered	
Mandible and lower dentition	No ≥70% clades recovered	
Face	(*Gorilla*, *Pongo*, *Pan*)	100
	(*Gorilla*, *Pongo*)	71
Cranial vault and base	(*Gorilla*, *Pongo*, *Pan*)	84
	(*Gorilla*, *Pongo*)	86
Papionins		
Palate and upper dentition	(*Cercocebus*, *Macaca*, *Mandrillus*, *Papio*, *Theropithecus*)	95
	(*Mandrillus*, *Papio*, *Theropithecus*)	89
	(*Mandrillus*, *Theropithecus*)	98
Mandible and lower dentition	No ≥70% clades recovered	
Face	(*Cercocebus*, *Macaca*, *Mandrillus*, *Papio*, *Theropithecus*)	73
	(*Mandrillus*, *Papio*)	91
Cranial vault and base	(*Mandrillus*, *Papio*, *Theropithecus*)	92
	(*Mandrillus*, *Papio*)	85

(Table 4). Neither the palate and upper dentition characters nor the mandible and lower dentition characters yielded clades that were supported by 70% or more bootstrap replicates. The face and cranial vault and base characters yielded well supported clades but these were not compatible with the hominoid molecular cladogram. One linked *Gorilla*, *Pan* and *Pongo* to the exclusion of *Homo*. The other grouped *Gorilla* and *Pongo* to the exclusion of *Homo* and *Pan*.

The papionin regional character groups also failed to yield clades that were compatible with the papionin molecular cladogram (Table 4). No clades were recovered from the mandible and lower dentition characters. Three clades were obtained from the palate and upper dentition character group, none of which was compatible with the papionin consensus molecular cladogram. The first comprised *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*, the second consisted of *Mandrillus*, *Papio* and *Theropithecus*, and the third comprised *Mandrillus* and *Papio*. Two non-molecular clades were retrieved from the papionin face character group. One was identical to the first clade recovered from the palate and upper dentition characters, the second contained *Mandrillus* and *Papio*. Two non-molecular clades were also recovered from the cranial vault and base characters. One comprised the three baboon genera, *Mandrillus*, *Papio* and *Theropithecus*, the other consisted of *Mandrillus* and *Papio*.

In the third test of the hypothesis, the hominoid and papionin molecular relationships were imposed on the appropriate regional character groups, the rank order of the CIs of the regional cladograms was determined, and a comparison made between the rank orders obtained in the two datasets. The hypothesis was judged supported if, in both the hominoid and papionin datasets, the CIs of the face and cranial vault character groups were higher than those of the palate and upper dentition and mandible and lower dentition character groups. Again, this test failed to support the hypothesis.

In the hominoid analysis, the palate measurements had the highet CI (0·74), the face and mandible and lower dentition character groups were tied second highest (0·71), and the cranial vault and base traits had the lowest CI (0·69). In the papionin

Table 5 **Goodness-of-fit statistics**

Region	CI	Rank	RI	Rank	PD	Rank
Hominoids						
Palate and upper dentition	0·74	1	0·33	1	6%	2
Mandible and lower dentition	0·71	2	0·21	2	4%	1
Face	0·71	2	0·15	3	19%	4
Cranial vault and base	0·69	4	0·09	4	15%	3
Papionins						
Palate and upper dentition	0·62	1	0·20	1	29%	3
Mandible and lower dentition	0·56	2	0·08	3	20%	1
Face	0·55	3	0·20	1	22%	2
Cranial vault and base	0·55	3	0·18	2	31%	4

Goodness-of-fit statistics obtained when molecular cladogram topology was imposed on the regional data sets, together with percentage difference in length between most parsimonious and molecular cladograms.

The latter was calculated by subtracting the length of the most parsimonious cladogram from the length of the molecular-topology cladogram, dividing the resulting figure by the length of the most parsimonious cladogram, and multiplying the product by 100. CI=consistency index. RI=retention index. PD=percentage difference in length between most parsimonious and molecular cladograms.

analysis, the palate and upper dentition characters had the highest CI (0·62), the mandible and lower dentition had the second highest CI (0·56), and the face and cranial vault and base character groups had the equal lowest CI (0·55). Thus, the hominoid and papionin datasets favoured different rank orders for the consistency indices of the different cranial regions, and the values for the two regions dominated by masticatory characters were not consistently the lowest. It is noteworthy that similar results were obtained when the retention index (Swofford, 1991) was used instead of the CI, and also when the percentage difference in length between the most parsimonious and molecular cladograms was calculated (Table 5).

Discussion

The hypothesis that early hominid masticatory characters are more homoplastic, and therefore less reliable for phylogeny reconstruction, than characters from other parts of the skull was not supported by the parsimony test. The criterion that the characters from the face and the cranial vault and base should favour cladograms that were identical to, or compatible with, the molecular cladogram, whilst the palatal and mandibular characters should favour cladograms that are incompatible with the molecular cladogram, was not fulfilled. None of the cladograms obtained from the hominoid regional character groups was compatible with the hominoid molecular cladogram. Likewise, none of the cladograms favoured by the papionin regional character groups was compatible with the papionin molecular cladogram.

The hypothesis also was not supported by the bootstrap test. The criterion that the clades obtained from the face and/or cranial vault and base characters should be compatible with the molecular cladogram, whilst those obtained from the palate and upper dentition and the mandible and lower dentition characters should be incompatible with the molecular cladogram, was not met. None of the hominoid regional character groups yielded clades that were compatible with the hominoid molecular cladogram, and none of the papionin regional

character groups yielded clades that were compatible with the papionin molecular cladogram.

Lastly, the hypothesis was not supported by the CI test. The criterion that in both the hominoids and papionins the mastication dominated regions—the palate and upper dentition, and the mandible and lower dentition—should have lower CIs than the face and the cranial vault and base was not fulfilled. When the branching pattern of the appropriate consensus molecular cladogram was imposed on the hominoid and papionin datasets, they yielded different rank orders for the CIs of the regional character groups, and the mastication dominated region CIs were not consistently lower than those for the other two regions.

The results of the three analyses indicate that the regions of the extant hominoid and papionin skull sampled in this study do not differ significantly in the amount of homoplasy they contain and therefore in their reliability for phylogenetic reconstruction. The regions with a strong functional emphasis on mastication—the palate and upper dentition, and the mandible and lower dentition—were not more prone to homoplasy than the other regions—the face, and the cranial vault and base. Rather, all four regions exhibited high levels of homoplasy. This indicates that mastication is no more significant as a cause of homoplasy in the extant higher primate skull than factors that affect regions of the skull not so directly linked with mastication.

Possible reasons for masticatory characters exhibiting homoplasy were reviewed earlier, but what factors might be responsible for homoplasy in regions of the skull not dominated by the functional demands of mastication? One factor likely to be significant in generating the homoplasy exhibited by the non-masticatory regions of the skull is sexual selection. It has been argued that the crania of male and female Old World monkeys differ principally in characters in the male cranium that relate to intermale competition for females (McCown, 1978). Given that the behaviours associated with intermale competition in Old World monkeys appear to be limited in number, and that the existence of limits on the number of options available to solve a given ecological problem can be expected to result in homoplastic change (Cain, 1982), it seems reasonable to suppose that characters involved in intermale competition may contribute considerable homoplasy to Old World monkey craniodental datasets. Since the crania of male and female great apes differ in similar ways to those of male and female Old World monkeys, it also seems reasonable to suppose that characters involved in intermale competition may contribute homoplasy to hominoid craniodental datasets as well. The most obvious intermale competition-related characters—long canines—are represented in the palate and upper dentition and mandible and lower dentition datasets, but it seems unlikely many other characters in those datasets are related to intermale competition. In contrast, the face and the cranial vault and base datasets seem likely to contain numerous characters that are in some way affected by intermale competition. For example, the elongated and inflated maxillae of male *Mandrillus* and *Papio* can plausibly be viewed as part of their sexual display apparatus, as can their bar-like supraorbital tori. Thus, we suspect that sexual selection may account for at least part of the homoplasy in the face and cranial vault and base datasets that offsets the homoplasy displayed by the palate and upper dentition and the mandible and lower dentition datasets (see also Harris, 2000). Admittedly this explanation is speculative. But the strong correlations between morphological characteristics (e.g., body size dimorphism, canine dimorphism, testes size) and the type and amount of intrasexual competition that have been documented in numerous primate studies

(e.g., Harvey *et al.*, 1978; Kay *et al.*, 1988; Plavcan & van Schaik, 1992, 1997; Sillén-Tullberg & Miller, 1993; Harcourt, 1995; Plavcan *et al.*, 1995) certainly suggest that morphology is highly responsive to sexual selection, which is what one would expect to see if sexual selection is an important cause of craniodental homoplasy among primates.

As noted earlier, we think there are reasons to be sceptical of the reliability of conventional craniodental characters for estimating primate phylogeny, at least at the species and genus level (Collard & Wood, 2000). Nevertheless, it is interesting to consider the implications of the present study for our understanding of early hominid phylogeny. The study is particularly relevant when considering the phylogenetic relationships of *P. aethiopicus*. As its generic name indicates, *P. aethiopicus* is widely considered to be more closely related to *P. boisei* and *P. robustus* than to any other early hominid species (e.g., Wood, 1992*a*,*b*; Lieberman *et al.*, 1996; Strait *et al.*, 1997; Strait & Grine, 1999). However, Skelton & McHenry (1992) argue that this hypothesis is incorrect because it is based mainly on characters of the masticatory system. Such characters, they aver, should not be relied on in phylogenetic analyses because they are especially prone to homoplasy. Skelton & McHenry (1992) suggest that, when the bias in favour of masticatory characters is corrected, *P. aethiopicus* is most parsimoniously interpreted as the sister species of a clade comprising *P. boisei*, *P. robustus*, *A. africanus* and the various species assigned to the genus *Homo*. The results of our analysis, which suggest there is no basis for the claim that masticatory characters are more prone to homoplasy than other cranial characters, weaken Skelton & McHenry's case. Instead, the findings of this study are consistent with the results of recent unweighted cladistic analyses of the early hominids, which suggest that *P. aethiopicus*, *P. boisei* and *P. robustus* form a clade to the exclusion of the other early hominid species (e.g., Wood, 1992*b*; Strait *et al.*, 1997; Strait & Grine, 1999).

The results of this study also have implications for our understanding of the phylogenetic relationships and classification of what is currently considered to be the earliest member of the human genus, *H. rudolfensis*. It has long been recognized that the specimens which comprise the hypodigm of this species combine neurocranial traits that are derived in the direction of later *Homo* (e.g., increased cranial capacity, inferred frontal lobe asymmetry in the region of Broca's speech, relatively coronally oriented petrous bones) with masticatory traits that are derived in the direction of *A. africanus* and *Paranthropus* (e.g., relatively great breadth of midface, P_3 root form, relative talonid size, thick dental enamel, marked relief where muscles attach to the lateral surface of the mandibular corpus) (e.g., Leakey, 1973). Yet with only a few exceptions (e.g., Walker, 1976), researchers have elected to assign the hypodigm to *Homo* rather than to *Australopithecus* or *Paranthropus*, thereby assuming the *Homo*-like characteristics to be homologous and the *A. africanus*/*Paranthropus*-like ones to be homoplastic (e.g., Leakey, 1973; Rak, 1983; Beynon & Wood, 1986; Bilsborough & Wood, 1988; Kimbel *et al.*, 1988; Groves, 1989; Wood, 1991, 1992*a*,*b*; Grine *et al.*, 1996; McHenry & Coffing, 2000; Wood & Richmond, 2000). This judgement is not based on the *Homo*-like traits outnumbering the *A. africanus*/*Paranthropus*-like traits, for analyses of the statistical confidence that can be attached to the clades recovered from early hominid craniodental data indicate that the relationships of *H. rudolfensis* are ambiguous (Corruccini, 1994; Wood & Collard, 1999). It has been claimed that *H. rudolfensis* shares a number of derived postcranial features with later *Homo* species (Wood, 1992*a*; McHenry & Coffing, 2000),

but the specimens that display these features cannot be linked reliably with the cranial bones that have been assigned to *H. rudolfensis* (Wood & Collard, 1999). Nor is the judgement based on the *Homo*-like traits being ''better'' than the *A. africanus*/*Paranthropus*-like traits. In a detailed review of the developmental bases of early hominid craniodental characters, Lieberman *et al.* (1996) found that *H. rudolfensis* shares more character states with *A. africanus* and the *Paranthropus* species that are probably developmentally homologous, and therefore ''better'', than it does with *H. ergaster*. Thus, the judgement that *H. rudolfensis* is more closely related to the other *Homo* species than it is to *A. africanus*/*Paranthropus* is based on the (usually unacknowledged) assumption that the neurocranial traits *H. rudolfensis* shares with the other *Homo* species are less to prone to homoplasy than the masticatory traits it shares with *A. africanus* and the *Paranthropus* species.

The results of this study support a reassessment of the relationships of *H. rudolfensis*, since they suggest that the neurocranial characteristics that align it with the other *Homo* species are no more reliable for phylogenetic reconstruction than the masticatory resemblances which align it with *A. africanus*/*Paranthropus*. Given that the number of ''good'' masticatory resemblances between *H. rudolfensis* and *A. africanus*/*Paranthropus* outnumber the ''good'' neurocranial resemblances between *H. rudolfensis* and the other *Homo* species (Lieberman *et al.*, 1996), the most parsimonious interpretation of the relationships of *H. rudolfensis* is that *A. africanus* and *Paranthropus*, and not the other *Homo* species, are the closest relatives to *H. rudolfensis*. As we have argued elsewhere (Wood & Collard, 1999), because genera should be both monophyletic and adaptively coherent, this means that *H. rudolfensis* should be removed from genus *Homo*. For the time being, we have advocated its inclusion in *Australopithecus* (Wood & Collard, 1999), but if initial assessments of the newly-discovered species *Kenyanthropus platyops* (Leakey *et al.*, 2001) are supported by subsequent research, then, as Lieberman (2001) suggests, *Australopithecus rudolfensis* should probably be renamed *Kenyanthropus rudolfensis*.

Conclusions

This study used data from the extant hominoids and papionins to evaluate the hypothesis that early hominid masticatory characters are more prone to homoplasy, and therefore less reliable for phylogenetic reconstruction, than characters from other regions of the skull. The analyses incorporated in the study suggest that the hypothesis is unlikely to be correct. Among the extant hominoids and papionins, the regions most closely associated with mastication—the palate and upper dentition and mandible and lower dentition—are no more unreliable as sources of phylogenetically informative characters than the face, or the cranial vault and base. Thus, it is unlikely that the regions of the early hominid skull differ in their susceptibility to homoplastic change, or in their reliability for phylogenetic reconstruction. This finding has important implications for our understanding of the early hominid species *P. aethiopicus*, since recent attempts to revise its relationships have been based on the assumption that masticatory characters are unreliable for phylogenetic reconstruction. The study also has important implications for our understanding of the relationships of *H. rudolfensis*. This species is considered to be a member of *Homo* largely because researchers downplay the phylogenetic utility of the masticatory characters it shares with *A. africanus* and *Paranthropus*. The findings of this study suggest that this is not a sound basis for retaining *H. rudolfensis* within the *Homo* genus.

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Appendix 1 Hominoid regional character state data matrices

Palate and upper dentition

	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18	P19	P20
Colobus	E	E	B	C	B	8	6	E	8	8	6	D	6	A	6	8	6	A	B	7
Gorilla	B	A	B	B	8	8	8	6	8	8	9	A	A	A	8	B	8	E	B	7
Homo	B	C	C	7	E	E	E	B	D	C	D	6	8	6	A	6	D	6	E	E
Pan	8	7	6	6	A	C	B	B	D	E	D	C	D	E	D	E	C	A	6	B
Pongo	6	7	A	D	7	8	B	8	8	8	9	9	D	A	D	B	B	A	8	B

	P21	P22	P23	P24	P25	P26	P27	P28	P29	P30	P31
Colobus	9	A	6	8	A	B	D	C	C	7	6
Gorilla	E	8	8	E	E	B	8	9	A	9	8
Homo	6	B	E	A	6	B	D	E	E	E	E
Pan	A	C	C	9	A	B	8	8	7	C	C
Pongo	B	9	A	9	A	6	8	7	7	8	A

Appendix 1 ***Continued***

Mandible and lower dentition

	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16	M17
Colobus	A	C	B	E	8	C	6	E	?	E	6	E	8	C	7	B	6
Gorilla	C	C	B	A	9	8	A	6	7	7	9	9	9	7	7	7	8
Homo	E	C	E	C	E	E	E	B	D	A	D	6	7	7	B	7	B
Pan	7	7	7	6	A	7	A	B	B	C	D	C	D	E	E	E	E
Pongo	7	7	7	8	9	8	A	8	9	7	9	9	D	A	B	B	B

	M18	M19	M20	M21	M22	M23	M34	M25	M26	M27	M28	M29	M30	M31	M32	M33	M34
Colobus	6	A	9	A	8	D	B	8	E	6	C	B	7	C	6	E	7
Gorilla	A	7	E	7	C	7	9	A	B	D	6	8	7	E	B	A	A
Homo	8	E	6	E	6	D	E	E	7	A	B	E	E	6	E	C	E
Pan	D	C	C	D	C	A	A	B	B	D	A	B	B	A	9	6	C
Pongo	D	7	9	7	C	7	6	7	7	8	B	6	B	8	9	8	7

	M35	M36	M37	M38	M39	M40
Colobus	8	B	B	B	6	6
Gorilla	9	7	E	B	A	8
Homo	9	E	6	E	E	E
Pan	E	B	8	7	C	C
Pongo	A	7	B	7	8	A

Face

	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	F13	F14	F15	F16	F17	F18
Colobus	6	7	C	8	D	9	E	E	8	8	8	B	B	9	C	D	E	C
Gorilla	D	E	9	C	6	6	9	A	B	D	B	8	B	6	6	8	6	6
Homo	8	7	6	6	D	E	6	C	6	7	A	D	7	9	E	D	C	C
Pan	A	B	9	A	9	A	9	7	B	D	7	C	7	C	9	8	9	A
Pongo	D	B	E	E	9	B	C	7	E	9	E	6	E	E	9	8	9	8

	F19	F20	F21	F22	F23	F24
Colobus	C	6	9	7	6	7
Gorilla	6	A	9	9	B	7
Homo	E	A	E	E	8	E
Pan	9	A	9	A	B	9
Pongo	9	E	9	A	E	9

Appendix 1 ***Continued***

Cranial vault and base	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15	C16	C17
Colobus	8	8	C	A	B	E	9	D	D	E	C	A	D	7	8	C	C
Gorilla	B	E	E	E	E	C	E	6	D	A	8	D	C	D	E	7	8
Homo	6	6	6	6	7	6	6	8	6	6	E	6	6	7	6	E	E
Pan	B	A	9	8	B	9	9	B	9	C	8	B	B	A	B	A	8
Pongo	E	C	9	C	7	9	C	C	9	8	8	A	8	D	B	7	8
	C18	C19	C20	C21	C22	C23	C24	C25	C26	C27	C28	C29	C30	C31	C32	C33	C34
Colobus	7	8	8	E	7	6	9	E	8	E	8	9	B	E	9	E	A
Gorilla	A	8	8	B	C	A	7	A	C	B	D	D	E	A	C	A	E
Homo	E	E	E	6	7	E	D	A	E	6	6	6	6	6	6	6	6
Pan	A	8	8	9	C	A	D	7	8	B	A	9	9	A	9	A	A
Pongo	9	C	C	A	C	A	8	9	8	8	D	D	A	A	E	A	A

Appendix 2 Papionin regional character state data matrices

Palate and upper dentition

	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16
Cercocebus	C	6	F	9	C	6	B	B	A	9	9	6	C	9	C	A
Lophocebus	C	8	9	4	B	C	E	6	6	7	5	6	D	G	5	B
Macaca	C	5	F	C	5	B	8	B	A	A	A	6	B	9	8	5
Mandrillus	6	E	4	A	B	4	9	B	E	F	D	D	5	8	G	9
Pan	G	9	9	9	C	D	G	4	4	4	5	E	A	7	6	F
Papio	6	E	9	A	5	C	8	B	A	A	C	B	B	B	A	A
Theropithecus	6	E	9	G	E	C	4	G	G	F	G	G	8	A	D	A

Mandible and lower dentition

	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Cercocebus	C	B	9	6	8	8	A	C	8	5	B	6	C	6
Lophocebus	C	C	6	C	5	F	C	E	D	E	E	D	E	F
Macaca	B	C	E	C	C	6	B	8	8	A	6	B	8	9
Mandrillus	5	5	A	A	C	9	4	8	5	C	C	G	8	B
Pan	D	G	G	7	G	8	G	G	G	5	C	6	G	D
Papio	C	9	B	G	C	F	8	8	8	E	B	C	8	9
Theropithecus	5	5	4	7	5	9	9	4	8	A	4	6	4	7

Face

	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	F13	F14	F15	F16
Cercocebus	B	A	9	A	7	B	8	D	D	B	B	D	7	9	A	B
Lophocebus	F	G	7	8	4	A	8	8	C	E	E	9	D	9	6	D
Macaca	B	B	8	7	B	G	4	9	D	A	A	G	7	9	6	A
Mandrillus	6	B	D	F	F	E	D	D	D	5	4	8	E	9	G	6
Pan	F	4	4	8	C	4	8	G	4	G	G	4	E	9	D	G
Papio	5	B	D	F	E	A	D	7	7	5	6	7	8	G	D	8
Theropithecus	7	6	G	7	7	6	G	4	8	9	9	D	7	9	6	6

Cranial vault and base

	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15	C16
Cercocebus	B	A	9	9	9	7	C	7	6	5	8	B	8	8	A	B
Lophocebus	4	6	4	7	6	4	6	4	6	7	4	5	C	4	5	C
Macaca	7	6	6	A	7	A	6	C	D	D	8	B	B	8	A	C
Mandrillus	G	G	E	F	G	E	G	F	A	D	F	B	C	G	F	8
Pan	7	6	9	4	D	E	6	7	8	6	8	G	4	8	5	B
Papio	E	E	C	F	D	E	C	C	B	D	F	B	C	D	A	C
Theropithecus	B	C	G	A	6	7	C	D	G	D	C	5	B	D	F	4