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Hominin homoiology: An assessment of the impact of phenotypic plasticity on phylogenetic analyses of humans and their fossil relatives☆

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Abstract

Homoiologies are phylogenetically misleading morphological similarities that are due to nongenetic factors. It has been claimed that homoiologies are common in the hominin skull, especially in regions affected by masticatory strain, and that their prevalence is one reason why reconstructing hominin phylogenetic relationships is difficult. To evaluate this ''homoiology hypothesis,'' we performed analyses on a group of extant primates for which a robust molecular phylogeny is available—the hominoids. We compiled a data set from measurements that developmental considerations and experimental evidence suggest differ in their likelihood of exhibiting masticatory-strain-induced phenotypic plasticity. We then used the coefficient of variation and *t*-tests to evaluate the phenotypic plasticity of the measurements. We predicted that, if the hypothesis is correct, the measurements of skeletal features that do not remodel and therefore are unaffected by phenotypic plasticity should be less variable than the measurements of skeletal features that remodel and are subject to low-to-moderate strains, and that the latter should be less variable than the measurements of skeletal features that remodel and are subject to moderate-to-high strains. Subsequently, we performed phylogenetic analyses on character state data derived from the measurements and compared the resulting phylogenetic hypotheses to the consensus molecular phylogeny for the hominoids. We predicted that, if the hypothesis is correct, agreement between the phylogenies should be best for the non-phenotypically-plastic characters, intermediate for the low-to-moderate-strain characters, and worst for the moderate-to-high-strain characters. The results of the coefficient of variation/*t*-test analyses were consistent with the predictions of the hypothesis to the extent that the moderate-to-high-strain measurements exhibited significantly more variability than the non-phenotypically-plastic and low-to-moderate-strain measurements. In contrast, the results of the phylogenetic analyses were not those predicted. The phylogeny derived from the moderate-to-high-strain characters matched the molecular phylogeny better than those obtained using the non-phenotypically-plastic and low-to-moderate-strain characters. Thus, our study supports the suggestion that mechanical loading results in phenotypic plasticity in the hominin skull, but it does not support the notion that homoiologies have a significant negative impact on hominin phylogenetics.

Keywords: Hominin; Phylogeny; Homoplasy; Homoiology; Hominoid; Variance

☆ Lycett and Collard (2005) was written as a follow-up to this paper, but it appeared first due to publication delays associated with the collection of papers presented in this special issue. To maintain consistency with the paper by Lycett and Collard (2005), only minor changes have been made to the present article during revision.

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Introduction

Knowledge of hominin phylogeny is necessary for the successful reconstruction of human evolutionary history. Without a reliable phylogeny, little confidence can be placed in hypotheses of ancestry or in hypotheses regarding the number and nature of adaptive changes in human evolution (Eldredge and Tattersall, 1975). A reliable phylogeny is also necessary to test evolutionary scenarios that link events in human evolution with changes in the environment and with wider patterns of faunal evolution (Eldredge and Tattersall, 1975). Unfortunately, the phylogenetic relationships of the species whose remains compose the hominin fossil record are currently far from certain. Despite a relatively rich, well-dated fossil record and many methodological improvements (e.g., Chamberlain and Wood, 1987; Skelton and McHenry, 1992; Lieberman et al., 1996; Strait et al., 1997; Strait and Grine, 1999), cladistic analyses have so far been unable to estimate the phylogenetic relationships of several fossil hominin species with a reasonable level of confidence (Corruccini, 1994; Lieberman et al., 1996; Wood and Collard, 1999; Strait and Grine, 2004).

Our inability to reliably reconstruct these relationships has frequently been attributed to taxonomic uncertainties, to the use of incorrect characters, and/or to the way in which the cladistic methodology has been implemented (e.g., Chamberlain and Wood, 1987; Skelton and McHenry, 1992; Lieberman, 1995, 1999; Strait et al., 1997; Skelton and McHenry, 1998; Strait and Grine, 1998; Lovejoy et al., 1999, 2000; McCollum, 1999; McCollum and Sharpe, 2001). In recent years, however, attention has focused on the confounding effects of homoplasies (e.g., Wood and Chamberlain, 1986; Skelton and McHenry, 1992; McHenry, 1994, 1996; Lieberman, 1997, 1999, 2000; Lieberman et al., 1996; Lockwood and Fleagle, 1999; Collard and Wood, 2000, 2001). Homoplasies are resemblances between taxa that result from processes other than descent from a common ancestor and which suggest relationships that are inconsistent with the best estimate of the phylogeny for the taxa (Willey, 1911; Simpson, 1961; Hennig, 1966; Cain, 1982; Patterson, 1982; Sober, 1988; Sanderson and Hufford, 1996; Lockwood and Fleagle, 1999).

Homoplasies are a problem for phylogenetic systematists because they can be mistaken for shared derived similarities (synapomorphies), which are the main 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, which favors the hypothesis of relationship requiring the least number of 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 hominins, the ratio of putative homoplasies to inferred synapomorphies has generally been around 1:2 (e.g., Skelton et al., 1986; Wood and Chamberlain, 1986; Chamberlain and Wood, 1987; Wood and Chamberlain, 1987; Wood, 1991; Skelton and McHenry, 1992; Lieberman et al., 1996; Strait et al., 1997). In these circumstances, parsimony analysis tends to yield several equally plausible phylogenies (Lieberman et al., 1996). For instance, Skelton et al.'s (1986) most parsimonious cladogram, in which *Homo habilis* and *Paranthropus* formed a clade to the exclusion of *Australopithecus africanus*, was supported by only one more character than the next most parsimonious cladogram, which linked *Paranthropus* with *A. africanus* to the exclusion of *H. habilis*. Similarly, although the cladograms favored by Wood (1991) and Strait et al. (1997) suggest that *Homo* is monophyletic, these cladograms are only slightly shorter than ones in which *Homo* is paraphyletic (Wood and Collard, 1999). The ambiguity that homoplasies introduce into hominin phylogenetic studies is further illustrated by the work of Strait and Grine (2004). Their bootstrap analyses returned insignificant levels of support for many fossil hominin phylogenetic relationships, and they failed to support the widely accepted relationships among the extant hominoids at the 70% level that is commonly used to classify clades as statistically significant in biological applications of the phylogenetic bootstrap (Hillis and Bull, 1993). The presence of numerous homoplasies among the character state data employed in these and other studies means that little confidence can be placed in published hominin phylogenies (Corruccini, 1994; Lieberman et al., 1996; Wood and Collard, 1999). Thus, developing a better understanding of the distribution and causes of homoplasy among humans and their closest fossil relatives represents a major challenge for hominin paleontology (Lieberman, 1995, 1997, 1999; Lockwood and Fleagle, 1999; Collard and Wood, 2000, 2001).

It is worth noting that hominin phylogenetic analyses are not unique in being confounded by extensive homoplasy. Several recent studies have shown that hard-tissue homoplasies occur in large numbers among many primate groups. For example, Hartman (1988) found that extant hominoid molar morphology was misleading regarding phylogenetic relationships due to diet-related convergence between humans and orangutans. Likewise, Harrison (1993) concluded that his attempts to resolve the relationships among closely related fossil primates, such as the early Miocene catarrhines of East Africa and the Eurasian pliopithecids, had been largely unsuccessful as a result of homoplasy. Most recently, Collard and Wood (2000) demonstrated that the crania of extant hominoids and papionins exhibit levels of homoplasy so high that phylogenetic analyses of qualitative and quantitative characters return strongly supported estimates of phylogeny that differ greatly from the groups' consensus molecular phylogenies, which are widely considered to be accurate. As such, there is a pressing need to understand not only hominin homoplasy, but also homoplasy among nonhuman primates (Lieberman, 1995, 1997, 1999; Lockwood and Fleagle, 1999; Collard and Wood, 2000, 2001).

It has been suggested that many hominin cranial homoplasies are likely to be homoiologies (Lieberman, 1995, 1997, 1999, 2000; Lieberman et al., 1996; Collard and Wood, 2000, 2001; Gibbs et al., 2000, 2002). Homoiologies are a phylogenetic consequence of phenotypic plasticity, the expression by a genotype of different phenotypes in response to different environmental conditions (Reidl, 1978;

Lieberman, 1995, 1997, 1999, 2000; Lieberman et al., 1996). That is, homoiologies are resemblances among a group of taxa that suggest relationships that conflict with the best estimate of phylogeny for the taxa, and which result primarily from epigenetic responses to internal and external stimuli. The "homoiology hypothesis" derives from studies on the effects of mechanical loading on bone, which suggest that a large, possibly predominant, proportion of variation in bone shape and size is a function of interactions between regions of the skeleton and their mechanical environments (Currey, 1984; Lanyon and Rubin, 1985; Frost, 1986, 1998; Herring, 1993; Lieberman, 1995, 1996, 1997, 1999, 2000; Lieberman and Crompton, 1998; Martin et al., 1998). Comparative studies and controlled experiments on vertebrate models, including modern humans, have shown that mechanical loading during growth substantially affects both cortical bone growth in diaphyses and trabecular bone growth in epiphyses (Currey, 1984; Lanyon and Rubin, 1985; Frost, 1986; Lieberman and Crompton, 1998; Martin et al., 1998). These effects may be systemic or local. For example, Lieberman (1996) found that pigs and armadillos exercised during growth had markedly thicker cortical bone than did individuals that were not exercised. This difference occurred not only in the limbs but also in the cranial vault, where strains are too low to induce osteogenic activity. In addition, studies of disuse (e.g., from denervation, bed-rest, and gravity-free environments) also indicate that bone resorbs—often at rapid rates—in many regions of the skeleton when subjected to lower than normal strain magnitudes or frequencies (Martin et al., 1998).

A typical example of these effects on a character that is used frequently in hominin paleontology is variation in the bicondylar angle of the femur. Mechanical loads from locomotion during growth influence this trait in many ways, as indicated by the absence of the angle in newborn infants, its increase with age until maturity, and by its absence in individuals immobilized during childhood (Tardieu, 1995). However, it should be noted that, while mechanical loading has been shown to influence many skeletal characters, the applicability of some rather extreme experimental studies (e.g., osteotomies) to natural variation is questionable (Bertram and Swartz, 1991), and for most characters it has been difficult to quantify the relative proportion of variation explained by genetic versus environmental effects.

Here we report a study in which the homoiology hypothesis was evaluated by determining whether or not predictions about the distribution and phylogenetic utility of phenotypically plastic traits were supported in analyses of extant primates. We focus on the phenotypic-plasticity-inducing effects of the strains associated with mastication, which experimental work suggests are sufficiently high in some regions of the skull to influence aspects of primate cranial and mandibular shape (Hylander, 1988). The first prediction tested was that skeletal features that do not remodel and therefore are unaffected by phenotypic plasticity should be less variable than skeletal features that remodel and are subject to low-to-moderate levels of strain, and that the latter should be less variable than skeletal features that remodel and are subject to moderate-to-high levels of strain (Wood and Lieberman, 2001). The second prediction tested in the study was that skeletal features that do not remodel and therefore are unaffected by phenotypic plasticity should be more reliable for phylogenetic reconstruction than skeletal features that remodel and are subject to low-to-moderate strain, and that the latter should be more reliable for phylogenetic reconstruction than skeletal features that remodel and are subject to moderate-to-high strain.

To test the first prediction, we employed the coefficient of variation and the *t*-test. To test the second, we adopted an approach that has been used to investigate the phylogenetic utility of hominoid molar morphology (Hartman, 1988), hominoid, papionin, and galagid cranial and dental morphology (Collard and Wood, 2000, 2001; Masters and Brothers, 2002; Strait and Grine, 2004), and hominoid soft-tissue features (Gibbs et al., 2000, 2002). We analyzed craniodental data for the hominoids using cladistic methods and compared the resulting phylogenetic hypotheses with the group's consensus molecular phylogeny (Fig. 1), which is widely considered to be reliable (Ruvolo, 1997; Gagneux and Varki, 2001; Page and Goodman, 2001). Incongruence between the morphological and molecular phylogenies was taken to indicate the presence of a relatively large number of homoplasies in the morphological data set, whereas congruence was assumed to indicate the presence of relatively few homoplasies. This analytical approach is controversial because it assumes that the molecular data are more reliable for phylogenetic reconstruction than the morphological data, and some researchers do not accept that certain data sets are more reliable than others for phylogenetic reconstruction (e.g., Kluge and Wolf, 1993; Kluge, 1998; O'Leary, 1999). However, we believe there are several reasons why it is reasonable to use the hominoid consensus molecular cladogram to evaluate the homoplasy content of different hominoid hard-tissue data sets. First, in phylogenetics, morphology can never be more than a proxy for genetic data because it is genes that are passed between generations, not morphological characters. Second, it is well documented that many "good," reproductively isolated species are genetically distinct, but dentally and osteologically

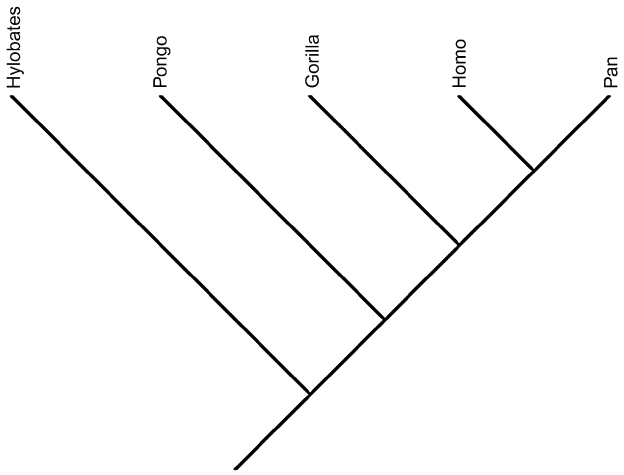

Fig. 1. Hominoid molecular relationships.

indistinguishable (Tattersall, 1986, 1992; Aiello et al., 2000). Since speciation events create phylogenetic relationships, there is thus an a priori expectation that skeletal characters will be less useful for phylogenetic reconstruction than genetic characters. Third, molecular phylogenetic techniques have been successfully tested on laboratory taxa of known phylogeny, whereas comparable analyses of morphological data have not been successful (Fitch and Atchley, 1987; Atchley and Fitch, 1991; Hillis et al., 1992). Lastly, and most importantly, multiple independent genes support the consensus molecular phylogeny for the hominoids (Ruvolo, 1997; Gagneux and Varki, 2001; Page and Goodman, 2001). Congruence among multiple independent lines of evidence is the best support possible for a phylogenetic hypothesis.

Materials and methods

Primate skeletal morphology is conventionally translated into character states for cladistic analysis in two main ways. The first breaks the phenotype up into character states qualitatively. Thus, a prominence is described as ''strong,'' ''reduced,'' or ''absent,'' a contour as ''arched'' or ''less-arched,'' and a feature as ''developed'' or ''not developed.'' This approach has been used in most hominin cladistic analyses (e.g., Eldredge and Tattersall, 1975; Delson et al., 1977; Skelton et al., 1986; Skelton and McHenry, 1992; Lieberman et al., 1996; Strait et al., 1997; Strait and Grine, 1999). However, such evaluations may not be the best way to express morphological variation. Despite claims to the contrary (Braga, 2001), there is ample evidence that the assessment of discrete character states can be highly subjective (e.g., Leakey and Leakey, 1986; Andrews and Martin, 1987; Conroy, 1994; Strait et al., 1997; Ahern, 1998). An additional 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 when assessing their states (e.g., Wood et al., 1998).

The second way of expressing character state variation is to collect metrical information about morphology, and then use a coding method to break the continuous distribution up into discontinuous states. Some researchers argue that measurements are unsuitable for cladistic analysis (e.g., Pimentel and Riggins, 1987; Crisp and Weston, 1987; Cranston and Humphries, 1988; Crowe, 1994; Disotell, 1994). They also argue that the aforementioned coding methods break the spectrum of measurements into ''artificial'' character states. However, these objections are overstated. Cladistically, there is no intrinsic difference between discrete and continuous characters (Maddison et al., 1984; Felsenstein, 1988; Swofford and Olsen, 1990; Thiele, 1993; Lieberman, 1995; Rae, 1998). The only criterion a character must fulfill 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). The suggestion that using metric data in a cladistic analysis is as valid as employing discrete data is supported by the goodness-of-fit indices obtained in cladistic analyses of the hominins. If metrical data were 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 nonmetrical characters. Yet, the goodness-of-fit indices obtained from hominin quantitative data (e.g., Chamberlain and Wood, 1987; Wood, 1991, 1992) are comparable with those yielded by hominin qualitative data (e.g., Lieberman et al., 1996; Strait et al., 1997). The ''artificiality'' argument can also be easily refuted, for coding is no more artificial than is the decision to break up into qualitative states what is, with few exceptions, 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 (e.g., Thorpe, 1984; Strait et al., 1996), which means that the character states employed in cladistic analyses of quantitative data can be reproduced more easily than those used in cladistic analyses of qualitative data.

We compiled a data set using measurements of the cranium, mandible, and dentition comparable to those that have been used in cladistic analyses of the hominins (e.g., Corruccini and McHenry, 1980; Wood and Chamberlain, 1986; Wood and Chamberlain, 1987; Chamberlain and Wood, 1987; Stringer, 1987; Wood, 1991). The data set consisted of values for 36 measurements 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). The latter were included as an outgroup. The measurements are listed in Table 1. The cranial and mandibular measurements were rounded up to the nearest 1 mm, and the dental measurements to the nearest 0.1 mm. The data were taken from Wood (1975). Previous studies that have used these data include Wood (1976) and Collard and Wood (2000, 2001).

The 36 measurements were selected on the basis of current knowledge of their likely propensity to exhibit phenotypic plasticity as a result of mastication-induced strain. Twelve were dental measurements. These were designated as non-phenotypically-plastic measurements, since dental enamel should not be affected by the forces generated by mastication and should therefore manifest, at most, only minor levels of phenotypic plasticity. Labiolingual and buccolingual crown dimensions were used in order to avoid the confounding effect of interstitial wear on mesiodistal dimensions. The other 24 measurements were cranial and mandibular measurements. Twelve of the cranial measurements were designated as likely to exhibit a low-to-moderate degree of phenotypic plasticity on the basis of the results of published in vivo strain-gauge studies (Hylander 1977, 1979, 1984, 1986, 1988; Hylander and Crompton, 1986; Hylander and Johnson, 1992, 1994; Hylander et al., 1991, 1992; Ross, 2001). These were orbital breadth, orbital height, interorbital breadth, biorbital breadth, nasion–rhinion, nasion–nasospinale, glabella–opisthocranion, basion–bregma, maximum biparietal breadth, biporionic breadth, coronale–coronale, and posterior skull length. Again, on the basis of experimental strain-gauge data, 12 measurements were designated as likely to exhibit a moderate-to-high degree of phenotypic plasticity. These were condylar

Table 1
Measurements employed in this study

Measurement	Code	
	Wood (1975)	Collard and Wood (2000, 2001)
I^1 labiolingual diameter	1	P1
I^2 labiolingual diameter	3	P3
C^1 labiolingual diameter	6	P6
M^1 labiolingual diameter	12	P12
M^2 labiolingual diameter	14	P14
M^3 labiolingual diameter	16	P16
I_1 labiolingual diameter	18	M1
I_2 labiolingual diameter	20	M3
C_1 labiolingual diameter	22	M5
M_1 buccolingual diameter	29	M12
M_2 buccolingual diameter	31	M14
M_3 buccolingual diameter	33	M16
Coronoid height	38	M21
Width of right condylar head	40	M23
Anteroposterior breadth of right condylar head	41	M24
Ramal breadth	42	M25
Bigonial width	44	M26
Height of mandibular body at M_1	45	M27
Thickness of mandibular body of M_1	46	M28
Symphyseal height	47	M29
Symphyseal thickness	48	M30
Inner alveolar breadth at M_3	49	M31
Distance between mandibular canines	51	M33
Right orbital breadth	52	F1
Right orbital height	53	F2
Interorbital breadth	54	F3
Biorbital breadth	55	F4
Nasion–rhinion	56	F5
Nasion–nasospinale	57	F6
Glabella–opisthocranion	69	C1
Basion–bregma	71	C3
Maximum biparietal breadth	72	C4
Biporionic width	73	C5
Coronale–coronale	75	C7
Posterior skull length	78	C10

height, coronoid height, width of the condylar head, anteroposterior breadth of the condylar head, ramal breadth, bigonial width, height of the mandibular corpus at M_1, thickness of the mandibular corpus at M_1, symphyseal height, symphyseal thickness, inner alveolar breadth at M_3, and the distance between the mandibular canines.

Two sets of analyses were carried out. The first sought to test the prediction from the homoiology hypothesis that the moderate-to-high-strain measurements are significantly more variable (i.e., more phenotypically plastic) than the low-to-moderate-strain measurements, and that the latter are significantly more variable than non-phenotypically-plastic measurements. In order to test this prediction, the coefficient of variation (CV) was computed for each measurement, and then the mean CVs for the three groups of measurements were compared. The significance of the difference between the average CV values for the three groups of measurements was assessed using a two-tailed *t*-test ($\alpha \leq 0.05$) following log transformation.

In the second analysis, we investigated whether the three groups of measurements differed in their ability to recover the phylogenetic relationships of the hominoids. To reduce the confounding effects of the body-size differences among the taxa, the data were size-adjusted prior to being converted into discrete character states (see Chamberlain and Wood, 1987; Wood, 1991, 1992; Rae, 1997). Size adjustment was accomplished by dividing each specimen value by the geometric mean of all of the specimen's values (Jungers et al., 1995). This method equalizes the volumes of the specimens while maintaining their original shapes (Jungers et al., 1995). Unfortunately, the method does not remove size-related shape differences among taxa (Jolly, 2001). However, we consider this to be a less serious drawback than those associated with the main alternative method, regression-based size adjustment (Jungers et al., 1995).

Thereafter, the size-adjusted data were converted into discrete character states using divergence coding (Thorpe, 1984). This technique proceeds by calculating the mean values for the taxa and testing the differences between them for statistical significance. The means are then ranked in ascending order, and a taxon-by-taxon matrix is 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 cell in the column of the matrix is scored 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 the difference between the means is significant. A cell 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 number of zeroes, negative ones, and positive ones in each column is calculated. Lastly, an integer is added to each taxon total. In converting the data set, Student's *t*-test (two-tailed) was used to test for statistical significance ($\alpha \leq 0.05$). Bonferroni correction was not employed because it heightens the risk of making type II errors (Perneger, 1998). An elevated type II error rate is especially problematic in divergence coding because fewer differences among the taxa will be recognized and therefore more false similarities will likely be incorporated into the character state data matrix. The integer added to each taxon total was five.

After coding, the data were subjected to parsimony analysis using the phylogenetic-reconstruction program PAUP* 4 (Swofford, 1998). Characters were treated as linearly ordered and freely reversing (Chamberlain and Wood, 1987; Slowinski, 1993; Rae, 1997), and the minimum-length cladogram was identified using the branch-and-bound algorithm. To assess the fit between the morphological cladogram and the group's consensus molecular phylogeny (Fig. 1), both topologies were imposed on the data set in MacClade 4 (Maddison and Maddison, 1998), with *Colobus* positioned as the outgroup, and the difference in length between them was calculated. In the context of the homoiology hypothesis, our expectation was that the non-phenotypically-plastic measurements would

exhibit the smallest increase in length between the most parsimonious cladogram and the molecular phylogeny, the low-to-moderate-strain measurements would exhibit an intermediate increase in length, and the moderate-to-high-strain measurements would exhibit the greatest increase in length.

Results

Two sets of analyses were carried out to evaluate the hypothesis that homoiology is a significant form of homoplasy among hominin taxa. In the first, the CV and *t*-tests were used to test the prediction that the moderate-to-high-strain measurements should be more variable than the low-to-moderate-strain measurements, and that the latter should be more variable than the non-phenotypically-plastic measurements. Table 2 summarizes the average CV for each group of measurements by taxon, along with the average CVs for all the taxa. Table 3 displays the results of the *t*-tests used to assess the significance of the differences between the average CVs for the three classes of measurements. As can be seen, the average CV for the moderate-to-high-strain measurements is higher than the average CV for non-phenotypically-plastic and low-to-moderate-strain measurements in all the taxa, and also when all of the taxa are pooled. The difference is significant at $p \leq 0.05$ according to the *t*-test. In contrast, the average CVs for the non-phenotypically-plastic and low-to-moderate-strain measurements are similar. In five of six taxa, the low-to-moderate-strain measurements yielded a higher average CV than the non-phenotypically-plastic measurements, but the difference is not significant according to the *t*-test ($p \leq 0.05$). Thus, the analyses were consistent with the prediction from the homoiology hypothesis with respect to the variation exhibited by the moderate-to-high-strain measurements versus the variation displayed by the non-phenotypically-plastic and low-to-moderate-strain measurements. However, the results did not accord with the prediction regarding the variation exhibited by the non-phenotypically-plastic and low-to-moderate-strain measurements since the latter were not significantly more variable than the former.

In the second set of analyses, parsimony analysis was used to test the prediction that the non-phenotypically-plastic characters should exhibit the smallest increase in length between the most parsimonious morphological cladogram for the hominoids and the group's molecular phylogeny, the low-to-moderate-strain characters should exhibit an intermediate increase in length, and the moderate-to-high-strain characters should exhibit the greatest increase in length. All three data sets returned a single most parsimonious cladogram, none of which agreed completely with the consensus molecular phylogeny for the extant hominoids (Fig. 1). The cladogram derived from the non-phenotypically-plastic characters suggested that *Gorilla*, *Pan*, and *Pongo* form a clade to the exclusion of *Homo*, and that *Pan* and *Pongo* form a clade to the exclusion of *Gorilla* (Fig. 2). The cladogram yielded by the low-to-moderate-strain characters also suggested that the three great apes form a clade to the exclusion of *Homo*, but unlike the non-phenotypically-plastic characters, the low-to-moderate-strain characters suggested that *Gorilla* and *Pongo* form a clade to the exclusion of *Pan* (Fig. 3). The cladogram obtained from the moderate-to-high-strain characters suggested that *Gorilla* and *Pongo* form a clade that is the sister taxon of a clade comprising *Homo* and *Pan* (Fig. 4). When the topology of the molecular phylogeny was imposed on the non-phenotypically-plastic characters, the length of the cladogram increased by 19%, from 81 to 96. When the topology of the molecular phylogeny was imposed on the low-to-moderate-strain characters, the cladogram length increased by 20%, from 101 to 121. When the topology of the molecular phylogeny was imposed

Table 2
Average CVs for the three classes of measurements used to test the variance prediction of the homoiology hypothesis

Taxon	NPP	LMS	MHS
Colobus	6.7	6.8	9.8
Gorilla	10.0	10.4	12.5
Homo	7.3	6.6	10.8
Pan	7.0	7.1	9.2
Pongo	10.1	10.9	15.3
All taxa	8.2	8.4	11.5

Abbreviations: NPP = non-phenotypically-plastic measurements; LMS = low-to-moderate strain measurements; MHS = moderate-to-high-strain measurements.

Table 3
P-values of the *t*-tests used to assess the significance of the differences between the average CVs for the three classes of measurements

Taxon	NPP vs. LMS	NPP vs. MHS	LMS vs. MHS
Colobus	0.80	0.01	0.01
Gorilla	0.93	0.07	0.09
Homo	0.19	0.00	0.00
Pan	0.89	0.02	0.02
Pongo	0.97	0.00	0.01
All taxa	0.74	0.00	0.00

Abbreviations: NPP = non-phenotypically-plastic measurements; LMS = low-to-moderate-strain measurements; MHS = moderate-to-high-strain measurements.

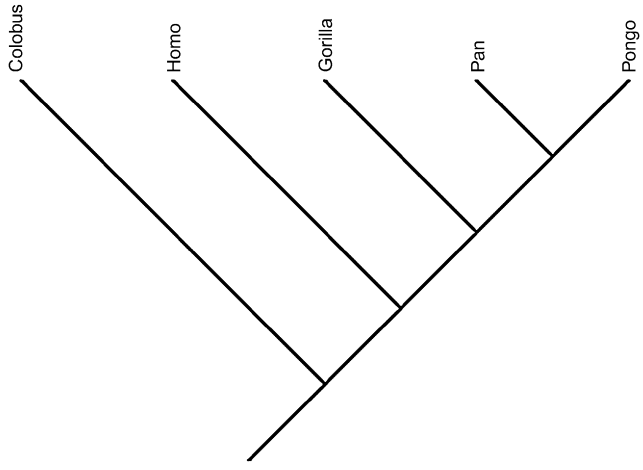

Fig. 2. Relationships suggested by the non-phenotypically-plastic measurements.

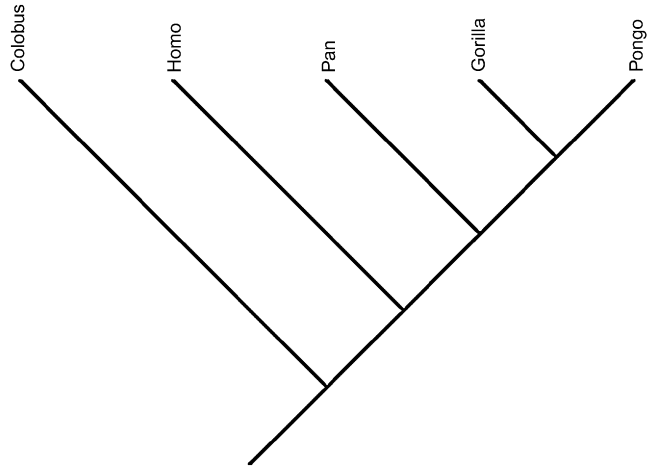

Fig. 3. Relationships suggested by the low-to-moderate-strain characters.

on the moderate-to-high-strain characters, the cladogram length increased by just 6%, from 112 to 119. Thus, the moderate-to-high-strain characters displayed a markedly better fit with the molecular phylogeny than either the low-to-moderate-strain or the non-phenotypically-plastic characters. This finding is not consistent with the predictions of the homoiology hypothesis.

Discussion

It has been suggested recently that homoiologies are a common form of homoplasy in the hominin skull, especially in those regions affected by mastication-related strain, and that their prevalence has contributed to our failure to date to obtain a reliable estimate of hominin phylogeny (Lieberman, 1995, 1997, 1999, 2000; Lieberman et al., 1996; Collard and Wood, 2000, 2001; Gibbs et al., 2000). In order to evaluate this hypothesis, we compiled a data set for the extant hominoid primates from measurements of skeletal features that developmental considerations and experimental evidence suggest differ in their likelihood of exhibiting masticatory-strain-induced phenotypic plasticity. We then subjected the data to analyses based on the CV and *t*-test in order to evaluate the prediction made by the homoiology hypothesis that, for each taxon, non-phenotypically-plastic measurements should be less variable than the low-to-moderate-strain measurements, and that the latter should be less variable than the moderate-to-high-strain measurements. Thereafter, we performed phylogenetic analyses using character state data derived from the three series of measurements and compared the resulting phylogenetic hypotheses to the hominoid consensus molecular phylogeny (Ruvolo, 1997; Gagneux and Varki, 2001; Page and Goodman, 2001). We reasoned that, if the homoiology hypothesis is correct, the agreement between the skeletal and molecular phylogenies would be best in the analyses of the non-phenotypically-plastic characters, intermediate in the analyses of the low-to-moderate-strain characters, and worst in the analyses of the moderate-to-high-strain characters.

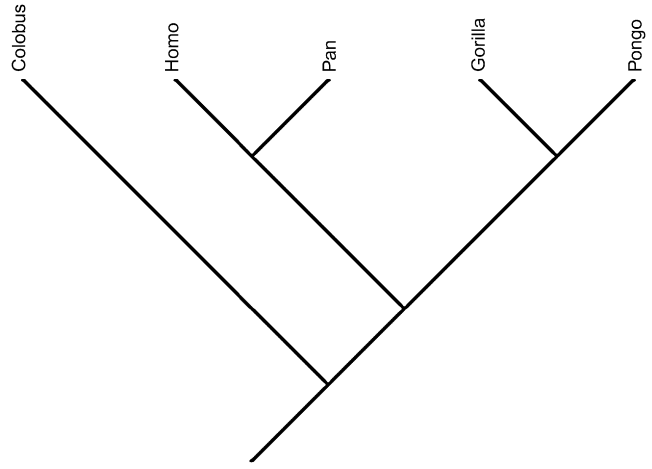

Fig. 4. Relationships suggested by the moderate-to-high-strain characters.

The results of the two analyses present an interesting paradox with regard to the utility of the different classes of skeletal features for testing phylogenetic hypotheses. The results of the CV/*t*-test analyses basically support the hypothesis that cranial measurements subjected skeletal features that are subject to moderate-to-high magnitudes of strain from mastication are more phenotypically plastic than skeletal features that are less subject to strain or constrained from changing in response to mechanical loading. The moderate-to-high-strain measurements exhibited significantly more variation than either the non-phenotypically-plastic measurements or the low-to-moderate-strain measurements. As noted by Wood and Lieberman (2001), such results suggest that skeletal traits that are subject to high levels of masticatory strain may be less reliable for taxonomic research than skeletal traits that are subject to low levels of masticatory strain. However, the results of the phylogenetic analysis did not support the hypothesis that skeletal features that are more phenotypically plastic are less useful for inferring phylogenetic relationships. Contrary to expectation, the fit between the phylogeny derived from the moderate-to-high-strain characters and the molecular phylogeny was considerably better than the fit between the phylogenies obtained from the non-phenotypically-plastic and low-to-moderate-strain characters and the molecular phylogeny. Also contrary to expectation, the non-phenotypically-plastic characters did not exhibit a better fit with the molecular phylogeny than the low-to-moderate-strain characters. Thus, the analyses support the suggestion that strain results in greater phenotypic plasticity in skeletal features, but they do not support the proposal that skeletal features that are more phenotypically plastic are more likely to be homoplastic.

What accounts for the latter unexpected result? Why might characters that are more phenotypically plastic be more reliable than the other types of characters in phylogenetic analyses? Without further study, it is not possible to be definitive, but we offer a few suggestions. One possibility is that we may be looking at chance effects whose underlying basis may not represent any genuine phylogenetic signal. For example, the hominoid moderate-to-high-strain characters may simply yield the correct phylogeny because the majority of cranial

characters used in the analysis are random with regard to the relationships they suggest and some of them necessarily must yield the correct relationships because there are so few ways in which the extant hominoid genera can be linked. Alternatively, the moderate-to-high-strain characters may constitute a complex of highly integrated, nonindependent characters whose phenotypic expression merely correlates well with the correct cladogram (Lieberman 1999; Lovejoy et al., 1999, 2000; McCollum, 1999; McCollum and Sharpe, 2001; Naylor and Adams, 2001; Strait 2001; see also Strait et al., 2007). Currently, there is little evidence to support either of these explanations. In particular, we have analyzed other sets of non-phenotypically-plastic, low-to-moderate-strain, and moderate-to-high-strain characters and obtained comparable results (unpublished data). These analyses suggest that the above-described results are unlikely to result from a ''lucky'' selection of characters. In addition, the goodness-of-fit indices associated with the most parsimonious cladograms (Table 4) indicate that not all of the moderate-to-high-strain characters support the same cladogram, which argues strongly against them forming a character complex.

A third possibility is that the measurements do not adequately reflect strain-related phenotypic plasticity in the primate skull, and that the differences in homoplasy levels among the three sets of measurements are therefore misleading (Callum Ross, personal communication). Given that the measurements were obtained from a data set generated to examine a different issue (Wood, 1975), this explanation is certainly plausible. However, it does not account for the finding that the dental measurements are more homoplastic than the bony measurements. Since dental enamel does not remodel in response to the forces generated by mastication, whereas bone does, if the homoiology hypothesis were correct, then the dental measurements would be expected to be less homoplastic than any set of bony measurements. Nevertheless, it would be worthwhile repeating this study with measurements that are linked more explicitly to mastication-related loading regimes.

A fourth possibility is that the congruence between the molecular phylogeny and the cladogram derived from the moderate-to-high-strain characters may reflect masticatory adaptations to dietary similarities between modern humans and chimps that are correlated with phylogeny. In theory, sister groups should have diets that are more similar to one another than either of them is to the diet of another taxon, providing they are not in direct competition for resources, in which case, character displacement would be expected. Chimps and modern humans tend to have more omnivorous, high-quality diets than the other great apes (Hladik, 1977; Hayden, 1981; Teleki, 1981; Goodall, 1986), and presumably they have lower bite-force equivalents relative to body mass in their postcanine dentition (Demes and Creel, 1988). Hence, we may be observing the morphological correlates of shared derived dietary behavior and/or a reaction norm to the strains elicited by the shared-derived diet (Schlichting and Pigliucci, 1998). However, the fact that the dental characters in our data set performed so poorly in the phylogenetic analyses, and that Hartman (1988) also found hominoid molar crown morphology to be phylogenetically misleading, indicates that phylogeny, diet, and masticatory morphology are not linked in a straightforward manner.

A fifth possible explanation for our findings is that homoiologous resemblances are primarily a problem in intraspecific phylogenetic analyses and do not affect interspecific analyses to any great extent. That is, phenotypic plasticity may be a major source of homoiology, but only in analyses of the relationships within species. In outlining the case for the importance of homoiology in hominin phylogenetics, Lieberman (1995) suggested that closely related individuals that behave in similar ways are likely to develop homoiologous osteological similarities. For example, individuals that have diets with similar levels of difficult-to-process items are likely to develop aspects of their masticatory system, such as enlarged alveolar processes, through similar responses to masticatory strain. However, when analyzing characters from different species, the situation is almost certainly more complicated because of morphological integration. As has been noted by a number of authors, few skeletal features are independent; instead, they are integrated at numerous hierarchical levels of development (Olsen and Miller, 1958; Cheverud, 1982; Lieberman, 1999; Lovejoy et al., 1999, 2000; McCollum, 1999; McCollum and Sharpe, 2001; Naylor and Adams, 2001; Strait, 2001; Lockwood, 2007; Strait et al., 2007). Thus, while the mechanisms by which bone tissue responds to strain may be conservative across species, the morphological effects of such responses may differ depending on a wide variety of other developmental and structural factors. Under such circumstances, it is perhaps unrealistic to expect a simple correspondence between the phenotypic plasticity of characters and their phylogenetic valence.

Support for the suggestion that homoiologies are unlikely to be a major form of homoplasy in interspecific studies comes from a recent study of ontogeny and homoplasy in the papionin face (Collard and O'Higgins, 2001). One of the analyses conducted in this study focused on early postnatal facial form and sought to determine if the facial homoplasies exhibited by adult papionins are to some degree present early in the postnatal period or if they develop only later in

Table 4
Lengths and goodness-of-fit indices associated with the most parsimonious cladograms derived from the three series of characters, along with the lengths and goodness-of-fit indices obtained when the topology of the consensus molecular phylogeny for the hominoids was imposed on the characters

	Most parsimonious				Molecular topology		
	IC	CL	CI	RI	CL	CI	RI
NPP	9	81	0.81	0.53	96	0.69	0.06
LMS	11	101	0.85	0.61	121	0.71	0.08
MHS	12	112	0.78	0.42	119	0.73	0.26
ALL	32	308	0.78	0.39	336	0.71	0.14

Abbreviations: NPP = non-phenotypically-plastic characters; LMS = low-to-moderate-strain characters; MHS = moderate-to-high-strain characters; ALL = all characters; IC = number of parsimony-informative characters; CL = cladogram length; CI = consistency index; RI = retention index.

ontogeny. The analysis compared the branching pattern of a dendrogram summarizing interspecific similarities and differences in estimated early postnatal facial form with the branching pattern of the group's consensus molecular phylogeny (Disotell et al., 1992; Disotell, 1994, 1996; Harris and Disotell, 1998; Harris, 2000), which is widely considered to be accurate (e.g., Groves, 1989; Fleagle and McGraw, 1999, 2002; Lockwood and Fleagle, 1999; Collard and Wood, 2000, 2001; Jolly, 2001). Collard and O'Higgins (2001) found that the branching patterns of the facial-form dendrogram and the molecular cladogram differed, and they interpreted this as evidence that homoplasy in the papionin face is present from a very young age. Given that unweaned individuals are less active and eat softer diets than older individuals, and are therefore less likely to experience behavior-induced phenotypic plasticity, Collard and O'Higgins' (2001) finding is consistent with a relatively minor role for homoiology in analyses of interspecific phylogenetic relationships.

There are two corollaries of this explanation. The first is that we need to test directly the possibility that homoiology affects within-species phylogenetic analyses. This is particularly important given that phylogenetically oriented analyses of population-level samples and even individual specimens are becoming increasingly popular in hominin paleontology (e.g., Brauer and Rimbach, 1990; Caparros, 1997; Hawks et al., 2000; Brace et al., 2001; Kramer et al., 2001; Wolpoff et al., 2001; Asfaw et al., 2002; Cameron et al., 2004). The second is that we must look for other processes to explain the difficulties many researchers have encountered reconstructing phylogenetic relationships among primate species and genera from standard skeletal characters (Hartman, 1988; Harrison, 1993; Corruccini, 1994; Lieberman et al., 1996; Wood and Collard, 1999; Collard and Wood, 2000; Masters and Brothers, 2002; Ackermann and Cheverud, 2002). If phenotypic plasticity does not cause the homoplasy that pervades data sets of cranial characters for the primates, then what does? The main conventional candidates are natural selection and ontogenetic limits on phenotypic diversity (Simpson, 1953; Gould and Lewontin, 1979; Wake, 1991; Lieberman et al., 1996). However, it is also possible that character integration contributes to the homoplasy observed among the fossil hominins (Lieberman, 1999; Lovejoy et al., 1999, 2000; McCollum, 1999; McCollum and Sharpe, 2001; Naylor and Adams, 2001; but see Strait, 2001). Given that a reliable phylogeny is a prerequisite for the successful reconstruction of human evolutionary history, developing methods for assessing the relative importance of these factors should clearly be a priority for hominin paleontologists.

Conclusions

The study described here was undertaken to assess the validity of the hypothesis that homoiology is an important source of homoplasy among fossil hominins. Two analyses were carried out using data from the extant hominoid primates and the group's consensus molecular phylogeny. The first sought to determine whether skeletal features that remodel and are subject to moderate-to-high masticatory strains are significantly more variable (i.e., phenotypically plastic) than skeletal features that remodel and are subject to low-to-moderate masticatory strains, and whether the latter are significantly more variable than skeletal features that do not remodel and therefore are unaffected by phenotypic plasticity. The second investigated whether the non-phenotypically-plastic, low-to-moderate-strain, and moderate-to-high-strain skeletal features differ in their ability to recover the phylogenetic relationships of the extant hominoids.

The results of this study support the suggestion that mechanical loading results in phenotypic plasticity in hominin cranial bones. However, they do not support the hypothesis that homoiology is a major reason why phylogenetic analyses of hominin crania have so far yielded conflicting and weakly supported hypotheses of relationship. There are several possible explanations for the failure of the analyses to support the homoiology hypothesis. We think that the most likely of these is that homoiology is a problem in intraspecific rather than interspecific phylogenetic analyses.

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