

Does Phenotypic Plasticity Confound Attempts to Identify Hominin Fossil Species?

An Assessment Using Extant Old World Monkey Craniodental Data

Mark Collard^{a, b} Stephen J. Lycett^c

^aLaboratory of Human Evolutionary Studies, Department of Archaeology, Simon Fraser University, Burnaby, B.C., Canada; ^bAHRC Centre for the Evolution of Cultural Diversity, University College London, London, and ^cBritish Academy Centenary Research Project, SACE, University of Liverpool, Liverpool, UK

Key Words

Phenotypic plasticity · Hominins · Taxonomy · Species identification · Strain · Mastication · Old World monkeys

Abstract

It has been hypothesised recently that masticatory strain-induced phenotypic plasticity complicates efforts to delineate species in the hominin fossil record. Here, we report a study that evaluated this hypothesis by subjecting craniodental data from 8 Old World monkey species to ANOVA and discriminant analysis. The study does not support the hypothesis. Characters associated with high masticatory strains were found to exhibit significantly higher levels of variability than low-to-moderately strained characters and dental characters, but the three sets of characters did not differ markedly in taxonomic utility. Moreover, the best discrimination was achieved when all variables were employed. These results suggest that phenotypic plasticity likely plays only a minor confounding role in hominin taxonomy, and that, rather than attempting to exclude phenotypically plastic characters, researchers should simply maximise the number of characters examined.

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Introduction

Reconstructions of human evolutionary history must be based on reliable hypotheses about the origin, nature and fate of species groups [Tattersall, 1986, 1992; Wood, 1992; Kimbel and Martin, 1993; Tattersall and Mowbray, 2005]. However, currently

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Mark Collard, Department of Archaeology
Simon Fraser University, 8888 University Drive
Burnaby, B.C. V5A 1S6 (Canada)
Tel. +1 778 782 8166, Fax +1 778 291 5666
E-Mail mark.collard@sfu.ca

there is little consensus regarding the number and composition of fossil hominin species. Some researchers argue that the known hominin fossil record samples less than 5 species [Wolpoff, 1999; Curnoe and Thorne, 2003], while others contend that more than 20 species are represented among the fossil hominin specimens that have been recovered over the last 150 years [Wood and Richmond, 2000; Foley, 2005].

Recently, Wood and Lieberman [2001] have argued that in order to make progress with the task of developing a robust species-level taxonomy for the fossil hominins researchers need to take into account the possibility that some hard-tissue characters are more reliable indicators of species diversity than others. Phenotypic plasticity – the expression by a genotype of different phenotypes in response to different environmental conditions – is of particular significance in this regard, they suggest. According to Wood and Lieberman [2001, p. 21], ‘variables which demonstrate a high degree of phenotypic plasticity because of epigenetic strain are especially liable to provide misleading tests of intraspecific variation’. Such characters, Wood and Lieberman [2001] aver, are likely to be particularly prevalent in the masticatory system. This is because they experience high levels of strain, and high levels of strain have been found to stimulate bone growth [Currey, 1984; Lanyon and Rubin, 1985; Frost, 1998; Lieberman and Crompton, 1998; Martin et al., 1998; Sylvester et al., 2006]. Wood and Lieberman [2001, pp. 20–21] contrast phenotypically plastic variables with variables that ‘consistently and predictably [have] low levels of within-species variation in appropriate reference taxa’. These, they suggest, are ‘especially useful for testing hypotheses about taxonomic heterogeneity’ [Wood and Lieberman, 2001, p. 21].

Wood and Lieberman [2001] tested their hypothesis with measurement data recorded on crania, mandibles and teeth of 5 species, *Colobus guereza*, *Gorilla gorilla*, *Homo sapiens*, *Pan troglodytes* and *Pongo pygmaeus*. They divided the measurements into 3 groups based on their likelihood of exhibiting phenotypic plasticity, computed the coefficient of variation (CV) for each measurement for each species, and then statistically compared the mean CV for each group of measurements on a species-by-species basis. Wood and Lieberman’s [2001] analyses partially support their hypothesis. The prediction that measurements with a moderate probability of exhibiting phenotypic plasticity should be more variable than characters with a low probability of exhibiting phenotypic plasticity was fulfilled in all 5 cases. However, the prediction that measurements with a high probability of exhibiting phenotypic plasticity should be more variable than characters with a moderate probability of exhibiting phenotypic plasticity and characters with a low probability of exhibiting phenotypic plasticity was fulfilled in only 2 cases. In the other 3 cases, the average CV of the high probability characters was significantly higher than either the average CV of the moderate probability characters or the average CV of the low probability characters but not both.

While Wood and Lieberman [2001] contend that their analyses support the hypothesis that strongly phenotypically plastic characters are less reliable for taxonomic discrimination than characters that are less phenotypically plastic, their analyses in fact only shed light on the relationship between phenotypic plasticity and morphological variability. They do not examine the relationship between phenotypic plasticity and taxonomic utility. Here, we report a study in which the inverse relationship between phenotypic plasticity and taxonomic utility hypothesised by Wood and Lieberman [2001] was tested directly with data from several Old World monkey species.

Materials and Methods

An extensive review of published *in vivo* mastication-induced strain gauge analyses was undertaken [Hylander, 1975, 1977, 1979a, 1979b, 1984, 1986, 1988; Hylander and Bayes, 1979; Brehnan et al., 1981; Demes, 1984; ; Hylander and Crompton, 1986; Hylander et al., 1987, 1991a, 1991b, 1992, 1998, 2000; Herring and Mucci, 1991; Daegling, 1993; Hylander and Johnson, 1994, 1997, 2002; Herring et al., 1996; Ross and Hylander, 1996, 2000; Daegling and Hylander, 1997, 1998, 2000; Spencer, 1998; Rafferty and Herring, 1999; Wall, 1999; Dechow and Hylander, 2000; Herring and Teng, 2000; Ravosa and Profant, 2000; Ravosa et al., 2000a, 2000b; Ross, 2001; Meyer et al., 2002]. The purpose of this review was to identify features of the primate skull that experience different levels of strain during mastication. Particular attention was paid to regions that routinely experience strain gradients in the order of $\geq 1,000 \mu\text{m/m}$ during incision, biting and mastication as strains of this magnitude are known to induce bone growth [Currey, 1984; Martin and Burr, 1989; Martin et al., 1998].

Based on the information recovered during the literature review, a list of 60 interlandmark measurements was compiled (table 1). Twenty-two of the measurements were included because they relate to features that according to strain gauge analyses experience high levels of strain ($\geq 1,000 \mu\text{m/m}$) during mastication. These high strain measurements are located on the mandible, mandibular fossa, zygoma, and zygomatic arch. A further 22 measurements were included because they are associated with features of the primate skull that experience low to moderate levels of strain ($<1,000 \mu\text{m/m}$) during mastication according to the available strain gauge data. These low-to-moderate strain measurements are located on the viscerocranium, neurocranium and basicranium. The remaining 16 measurements are labiolingual and buccolingual diameters of teeth. These were included because teeth, unlike osseous features, do not remodel in response to mechanical loading. Labiolingual and buccolingual diameters were employed instead of mesio-distal diameters to avoid the potentially confounding effects of interstitial wear [Hinton, 1982].

Values for the 60 measurements were obtained from specimens that belong to 8 Old World monkey species. The species sampled were *Cercocebus torquatus*, *Cercopithecus mitis*, *Colobus polykomos*, *Lophocebus albigena*, *Macaca fascicularis*, *Mandrillus leucophaeus*, *Papio anubis* and *Theropithecus gelada*. The measurements were taken on 20 wild-shot adult specimens from each species (10 males, 10 females per taxon). A specimen was judged adult if its third molars had erupted and it exhibited closure of the spheno-occipital synchondrosis. Specimens were deemed male or female based on museum records and visual assessment of secondary sexual characteristics. Cranial and mandibular measurements were recorded to the nearest 1 mm, and dental measurements to the nearest 0.1 mm. All data were collected by S.J.L. with sliding digital calipers and analogue spreading calipers.

The data set was employed in two sets of analyses. The first evaluated the prediction that measurements of osseous structures subject to high levels of mastication-related strain should be more variable than measurements of osseous structures that are subject to low-to-moderate levels of mastication-related strain, and that the latter should in turn be more variable than measurements of teeth. We recognise that the variability of many cranial traits will often be affected by environmental factors other than strain. However, in contrast to certain other sources of epigenetic variation, fluctuation in strain levels can potentially cause significant bone remodeling throughout ontogeny and beyond the normal phase of somatic growth [Lanyon and Rubin, 1985; Martin and Burr, 1989; Herring, 1993]. More importantly, we do not assume that traits outside those we have designated 'high strain' will not vary. Rather, in line with Wood and Lieberman [2001], we predict that, on average, high strain traits will be significantly more variable than traits that experience low-to-moderate levels of strain and dental traits, which do not remodel. Following Wood and Lieberman [2001], phenotypic variability was assessed using the Coefficient of Variation (CV). CVs were determined for each trait, and mean CVs for each group of measurements (i.e. high strain, low-to-moderate strain and dental traits) were computed. In order to test for statistically significant differences between the mean CVs of each trait group, analysis of variance (ANOVA) with post hoc least significant difference pairwise comparisons was employed. With the latter test, there is no need to reduce the critical p value below 0.05 for pairwise comparisons when the ANOVA is significant [Dytham, 2003], which was the

Table 1. Measurements used in this study

Measurement	Description	Source of description
<i>High strain traits (n = 22)</i>		
Mandibular corpus height at M ₁	Minimum distance between the most inferior point on the base and the lingual alveolar margin at the midpoint of M ₁	Wood [1991] (150)
Mandibular corpus width at M ₁	Maximum width at right angles to measurement 1, taken at midpoint of M ₁	Wood [1991] (151)
Height of mandibular symphysis	Minimum distance between the base of the symphysis and infradentale	Wood [1991] (141)
Depth of mandibular symphysis	Maximum depth at right angles to symphyseal height	Wood [1991] (142)
Condylar height	Maximum distance between base of ramus and superior point of condyle	Wood [1975] (36)
Coronoid height	Maximum distance between base of ramus and superior point of coronoid process	Wood [1975] (38)
Ramus breadth	Maximum width of the body of ramus in the anterior-posterior plane	Wood [1975] (42)
Mandibular condyle head length	Maximum length in anterior-posterior plane	Wood [1975] (41)
Mandibular condyle head width	Maximum width in medial-lateral plane	Wood [1975] (40)
Bigonial width	Minimum distance between the inner margins of left gonion and right gonion	Wood [1975] (44)
Inner alveolar breadth at M ₃	Minimum chord distance between the walls of the lingual mandibular alveoli at the midpoint of M ₃	Wood [1975] (49)
Height of zygomatic arch	Maximum height at zygomatico-temporal suture	This study
Thickness of zygomatic arch	Maximum width at zygomatico-temporal suture	This study
Mandibular fossa length	Minimum chord distance between the tympanic plate and the most inferior projection of the articular eminence; taken midway along breadth measurement (see below)	Wood [1991] (80)
Mandibular fossa breadth	Minimum chord distance in the coronal plane between the tip of the entoglenoid process and the most lateral extent of the articular eminence	Wood [1991] (82)
Orbitale to zygomaxillare	Chord distance between orbitale and zygomaxillare	Wood [1991] (58)
Mandibular corpus thickness at M ₃	Minimum distance between the most inferior point on the base and the lingual alveolar margin at the midpoint of M ₃	Wood [1991] (157)
Mandibular corpus height at M ₃	Maximum width at right angles to measurement 17, taken at midpoint of M ₃	Wood [1991] (158)
Inter lower canine distance	Minimum chord distance between the walls of the mandibular canine alveoli	Wood [1991] (166)
Upper ramus breadth	Distance between midpoint of the articular surface of the condyle (instrumentally determined – see measurements 8 and 9) and the most superior point of coronoid process	This study
Bicondylar breadth	Right condylion laterale to left condylion laterale	Wood [1975] (37)
Height of ramus to sigmoid notch	Maximum distance between base of ramus and the most inferior point of sigmoid notch	This study
<i>Low-to-moderate strain traits (n = 22)</i>		
Orbital breadth	Distance between maxillofrontale and ectoconchion	Wood [1991] (56)
Orbital height	Maximum distance between the superior and inferior orbital margins in a direction perpendicular to orbital breadth	Wood [1991] (57)
Interorbital breadth	Chord distance between maxillofrontale	Wood [1991] (55)
Biorbital breadth	Chord distance between ectoconchion	Wood [1991] (50)
Glabella to rhinion	Chord distance between glabella and rhinion	This study
Rhinion to nasospinale	Chord distance between rhinion and nasospinale	Wood [1991] (70)
Nasion to inion	Chord distance between nasion and inion	This study

Table 1 (continued)

Measurement	Description	Source of description
Basion to bregma	Chord distance between basion and bregma (in specimens with a sagittal crest 'bregma' was taken to be the plane of the surrounding vault surface)	Wood [1991] (4)
Biparietal breadth	Maximum breadth across homologous points on the left and right parietal bones	Wood [1991] (9)
Biporionic breadth	Chord distance between left porion and right porion	Wood [1991] (11)
Opisthion to lambda	Chord distance between opisthion and lambda	This study
Hormion to basion	Chord distance between hormion and basion	This study
Opisthion to inion	Chord distance between opisthion and inion	Wood [1991] (37)
Porion to basion	Chord distance between porion and basion	This study
Pterion to bregma	Chord distance between pterion and bregma	This study
Basion to opisthion	Minimum distance between basion and opisthion	Wood [1991] (76)
Width of foramen magnum	Maximum distance in the coronal plane between the inner margins of the foramen magnum	Wood [1991] (77)
Pterion to lambda	Chord distance between pterion and lambda	This study
Porion to opisthion	Chord distance between porion and opisthion	This study
Staphylion to hormion	Chord distance between staphylion and hormion	This study
Pterion to pterion	Chord distance between left pterion and right pterion	This study
Hormion to porion	Chord distance between hormion and porion	This study
<i>Dental traits (n = 16)</i>		
I ₁ labiolingual diameter	Maximum crown diameter perpendicular to the basal part of the labial enamel surface	Wood [1991] (248)
I ₂ labiolingual diameter	Maximum crown diameter perpendicular to the basal part of the labial enamel surface	Wood [1991] (251)
C ₁ labiolingual diameter	Maximum diameter of the crown in the labiolingual axis of the tooth	Wood [1991] (254)
P ₃ buccolingual diameter	Maximum distance between the buccal and lingual borders taken at right angles to the longitudinal axis of the crown	Wood [1991] (258)
P ₄ buccolingual diameter	Maximum distance between the buccal and lingual borders taken at right angles to the longitudinal axis of the crown	Wood [1991] (272)
M ₁ buccolingual diameter	Maximum distance between the buccal and lingual borders taken at right angles to the longitudinal axis of the crown	Wood [1991] (286)
M ₂ buccolingual diameter	Maximum distance between the buccal and lingual borders taken at right angles to the longitudinal axis of the crown	Wood [1991] (314)
M ₃ buccolingual diameter	Maximum distance between the buccal and lingual borders taken at right angles to the longitudinal axis of the crown	Wood [1991] (342)
I ¹ labiolingual diameter	Maximum crown diameter perpendicular to the basal part of the labial enamel surface	Wood [1991] (187)
I ² labiolingual diameter	Maximum crown diameter perpendicular to the basal part of the labial enamel surface	Wood [1991] (189)
C ¹ labiolingual diameter	Maximum diameter of the crown in the labiolingual axis of the tooth	Wood [1991] (191)
P ³ buccolingual diameter	Maximum distance between the buccal and lingual borders taken at right angles to the longitudinal axis of the crown	Wood [1991] (194)
P ⁴ buccolingual diameter	Maximum distance between the buccal and lingual borders taken at right angles to the longitudinal axis of the crown	Wood [1991] (203)
M ¹ buccolingual diameter	Maximum distance between the buccal and lingual borders taken at right angles to the longitudinal axis of the crown	Wood [1991] (212)
M ² buccolingual diameter	Maximum distance between the buccal and lingual borders taken at right angles to the longitudinal axis of the crown	Wood [1991] (224)
M ³ buccolingual diameter	Maximum distance between the buccal and lingual borders taken at right angles to the longitudinal axis of the crown	Wood [1991] (236)
Figures in parentheses indicate the original code.		

Table 2. Mean CV values and results of one-way ANOVA

Taxon	CV			ANOVA		
	high	LM	dental	high vs. LM	high vs. dental	LM vs. dental
<i>Macaca</i>	13.3	9.3	10.5	0.004**	0.052	0.450
<i>Lophocebus</i>	9.7	6.7	7.8	0.001**	0.069	0.184
<i>Cercocebus</i>	13.0	8.4	8.7	0.000**	0.002**	0.884
<i>Theropithecus</i>	13.3	9.0	10.4	0.005**	0.035*	0.602
<i>Papio</i>	13.6	9.2	11.5	0.000**	0.107	0.083
<i>Mandrillus</i>	20.1	11.5	12.9	0.000**	0.001**	0.416
<i>Cercopithecus</i>	11.7	9.2	8.4	0.013*	0.014*	0.844
<i>Colobus</i>	10.0	6.6	6.2	0.001**	0.001**	0.873

LM = Measurements subject to low-to-moderate mastication-related strains. * $p \leq 0.05$; ** $p \leq 0.005$.

case here. Since ANOVA assumes that data are normally distributed [Sokal and Rohlf, 1995], the CVs were logarithmically transformed before analysis. It was predicted that the CVs for the high strain measurements would be significantly higher than the CVs for the low-to-moderate strain measurements, and that the CVs for the latter would be significantly higher than the CVs for the dental measurements. The ANOVA was carried out using SPSS 12.0.1.

The second set of analyses tested the prediction that characters subject to high levels of strain will be markedly worse in distinguishing between taxa than low-to-moderately strained characters or dental characters. This was accomplished by separately subjecting the three groups of characters to discriminant analysis (DA). The form of DA employed separates groups on the basis of canonical discriminant functions [Huberty, 1994; Hair et al., 1998; Quinn and Keough, 2002; Manly, 2005]. The prediction for the DAs was that high strain characters would show markedly less taxonomic discriminatory efficacy than low-to-moderately strained measurements or dental measurements. For comparative purposes, a further DA was undertaken in which all 60 characters were included. The DAs were carried out using SPSS 12.0.1. with stepwise insertion.

Results

Table 2 shows the mean CV for each trait group for each taxon. Table 2 also shows the results of the least significant difference pairwise comparisons following a one-way ANOVA. The results are generally consistent with the prediction that high strain levels will induce greater epigenetic variability in certain characters compared to moderately strained characters or non-remodeling characters. However, it should be noted that not all results were significant when dental measurements and high strain measurements were compared, which indicates that strain does not always result in higher levels of morphological variability.

The results of the DAs are summarised in figures 1–4. The DAs show that high strain measurements (fig. 1) were less effective at distinguishing the species than the low-to-moderately strained measurements (fig. 2) or the dental measurements (fig. 3). In the case of the high strain measurements, 94.9% of specimens were cor-

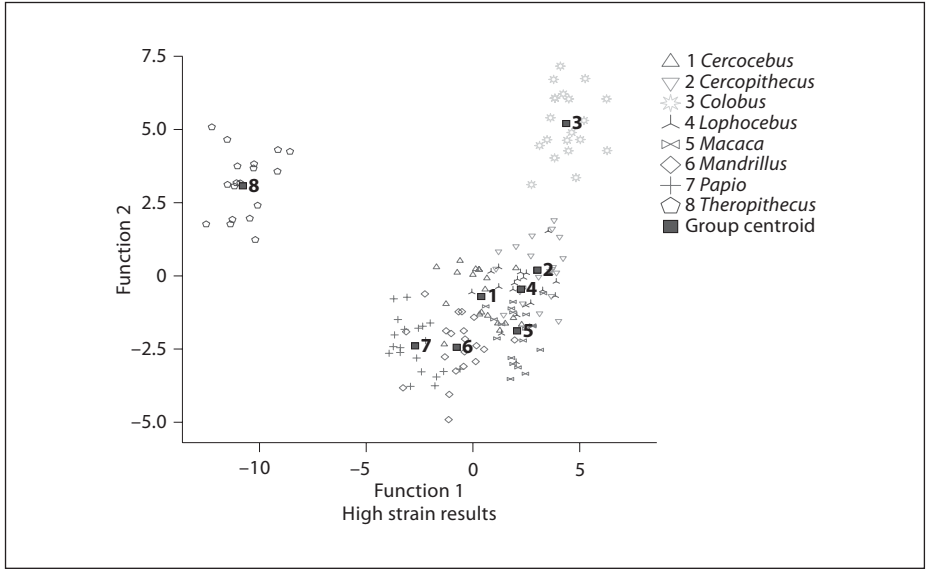


Fig. 1. Results of DA of high strain measurements. 94.9% of specimens correctly classified to species.

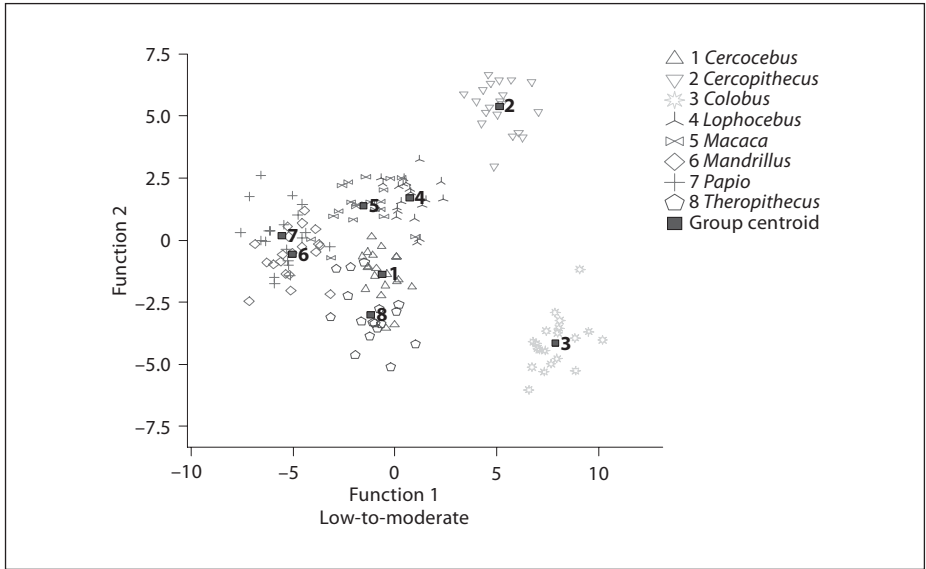


Fig. 2. Results of DA of low-to-moderate strain measurements. 97.5% of specimens correctly classified to species.

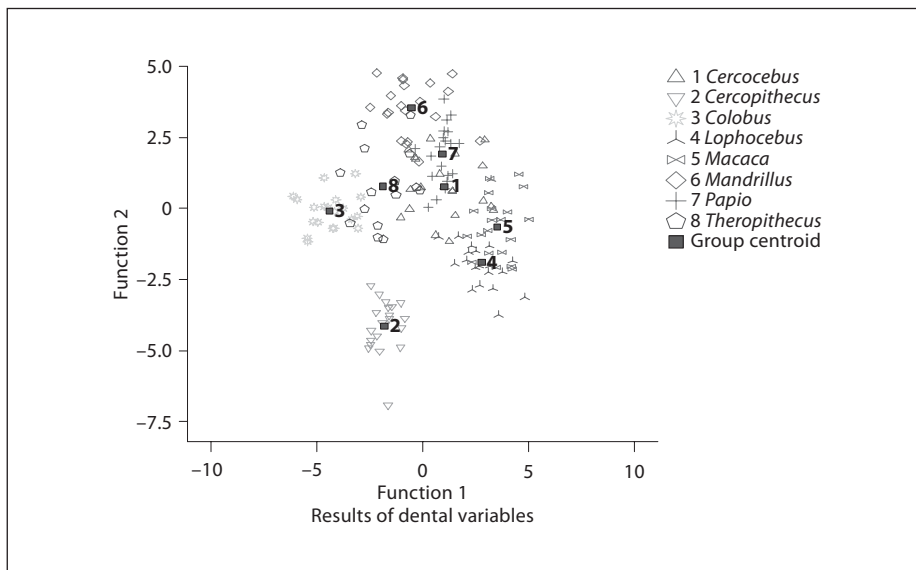


Fig. 3. Results of DA of dental measurements. 97.4% of specimens correctly classified to species.

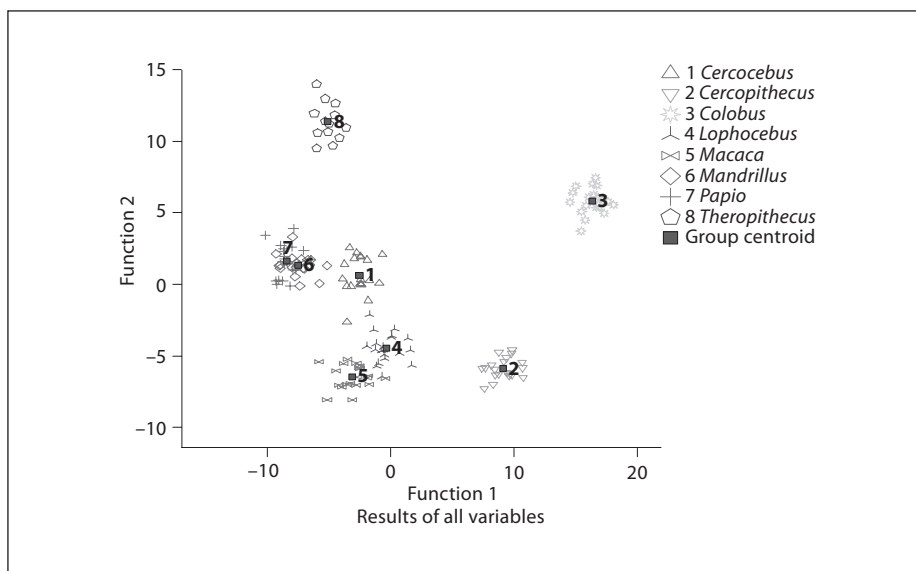


Fig. 4. Results of DA of all 60 measurements. 100% of specimens correctly classified to species.

rectly classified, while 97.5% of the specimens were correctly classified when the low-to-moderately strained measurements were analysed, and 97.4% of the specimens were correctly classified when the dental measurements were employed. When all 60 craniodental characters were included, 100% of specimens were correctly classified to taxon (fig. 4). Hence, while the prediction that high strain characters should have the least discriminatory efficacy is supported, the difference between the three groups in terms of overall taxonomic discriminatory power is less than 3%. Moreover, the most effective means of discriminating taxa was simply to ignore concerns regarding potential epigenetic variability and include all available morphometric data.

Discussion and Conclusions

At first glance, the results of our analyses support Wood and Lieberman's [2001] hypothesis. The results of our CV analyses generally suggest that masticatory strain results in morphological variability, and the results of our DAs suggest that characters that are particularly prone to phenotypic plasticity are less useful for taxonomic discrimination than characters that are less prone to phenotypic plasticity.

However, there are reasons to be cautious about this interpretation. First, the results of the dental/high strain CV comparisons suggest that the relationship between masticatory strain and morphological variability is more complicated than Wood and Lieberman [2001] suggest. Masticatory strain may be an important source of variability in primate craniodental characters, but evidently other factors can override it. Second, the results of the DA suggest that better taxonomic discrimination can be achieved by maximising character number rather than by discriminating between characters on the basis of their likelihood of exhibiting phenotypic plasticity.

In sum, our study supports Wood and Lieberman's [2001] hypothesis that phenotypic plasticity negatively impacts the taxonomic utility of craniodental characters, but it does not support their suggestion that excluding characters that are especially likely to exhibit phenotypic plasticity will lead to more reliable taxonomic hypotheses. It appears that selecting characters on the basis of their likelihood of exhibiting phenotypic plasticity is less effective as an approach to taxonomic discrimination than simply maximising the number of characters examined. We therefore conclude that, while phenotypic plasticity likely contributes to the variation observable in the hominin fossil record, excluding phenotypically plastic characters is an unnecessary course of action for researchers attempting to group fossil hominin specimens into species. Better results can be obtained by ignoring the impact of phenotypic plasticity and evaluating as many characters as possible.

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References

- Brehnan K, Boyd RL, Laskin JL, Gibbs CH, Mahan PE (1981). Direct measurement of loads at the temporomandibular joint in *Macaca arctoides*. *Journal of Dental Research* 60: 1820–1824.
- Curnoe D, Thorne A (2003). Number of ancestral human species: a molecular perspective. *Homo* 53: 201–224.
- Currey JD (1984). *The Mechanical Adaptation of Bones*. Princeton, Princeton University Press.
- Daegling DJ (1993). The relationship of in vivo bone strain to mandibular corpus morphology in *Macaca fascicularis*. *Journal of Human Evolution* 25: 247–269.
- Daegling DJ, Hylander WL (1997). Occlusal forces and mandibular bone strain: is the primate jaw 'overdesigned'? *Journal of Human Evolution* 33: 705–717.
- Daegling DJ, Hylander WL (1998). Biomechanics of torsion in the human mandible. *American Journal of Physical Anthropology* 105: 73–87.
- Daegling DJ, Hylander WL (2000). Experimental observation, theoretical models, and biomechanical inference in the study of mandibular form. *American Journal of Physical Anthropology* 112: 541–551.
- Dechow PC, Hylander WL (2000). Elastic properties and masticatory bone stress in the macaque mandible. *American Journal of Physical Anthropology* 112: 553–574.
- Demes B (1984). Mechanical stresses at the primate skull base caused by the temporomandibular joint force. In *Food Acquisition and Processing in Primates* (Chivers DJ, Wood BA, Bilsborough A, eds.), pp 407–413. London, Plenum.
- Dytham C (2003). *Choosing and Using Statistics: A Biologist's Guide*, 2nd ed. Oxford, Blackwell.
- Foley R (2005). Species diversity in human evolution: challenges and opportunities. *Transactions of the Royal Society of South Africa* 60: 67–72.
- Frost HM (1998). From Wolff's law to the mechanostat: a new 'face' of physiology. *Journal of Orthopedic Science* 3: 282–286.
- Hair JF, Anderson RE, Tatham RL, Black WC (1998). *Multivariate Data Analysis*, 5th ed. Upper Saddle River, Prentice Hall.
- Herring SW (1993). Epigenetic and functional influences on skull growth. In *The Skull* (Hanken J, Hall BK, eds.), vol 1, pp 153–206. Chicago, Chicago University Press.
- Herring SW, Mucci RJ (1991). In vivo strain in cranial sutures: the zygomatic arch. *Journal of Morphology* 207: 225–239.
- Herring SW, Teng S (2000). Strain in the brain case and its sutures during function. *American Journal of Physical Anthropology* 112: 575–593.
- Herring SW, Teng S, Huang X, Mucci RJ, Freeman J (1996). Patterns of bone strain in the zygomatic arch. *The Anatomical Record* 246: 446–457.
- Hinton RJ (1982). Differences in interproximal and occlusal tooth wear among prehistoric Tennessee Indians: implications for masticatory function. *American Journal of Physical Anthropology* 57: 103–115.
- Huberty C (1994). *Applied Discriminant Analysis*. New York, Wiley.
- Hylander WL (1975). The human mandible: lever or link? *American Journal of Physical Anthropology* 43: 227–242.
- Hylander WL (1977). In vivo bone strain in the mandible of *Galago crassicaudatus*. *American Journal of Physical Anthropology* 46: 309–326.
- Hylander WL (1979a). An experimental analysis of temporomandibular joint reaction force in macaques. *American Journal of Physical Anthropology* 51: 433–456.
- Hylander WL (1979b). Mandibular function in *Galago crassicaudatus* and *Macaca fascicularis*: an in vivo approach to stress analysis of the mandible. *Journal of Morphology* 159: 253–296.
- Hylander WL (1984). Stress and strain in the mandibular symphysis of primates: a test of competing hypotheses. *American Journal of Physical Anthropology* 64: 1–46.
- Hylander WL (1986). In vivo bone strain as an indicator of masticatory bite force in *Macaca fascicularis*. *Archives of Oral Biology* 31: 149–157.

- Hylander WL (1988). Implications of in vivo experiments for interpreting the functional significance of 'robust' australopithecine jaws. In *Evolutionary History of the 'Robust' Australopithecines* (Grine FE, ed.), pp 55–83. New York, Aldine de Gruyter.
- Hylander WL, Bays R (1979). An in vivo strain-gauge analysis of the squamosal-dentary joint reaction force during mastication and incisal biting in *Macaca mulatta* and *Macaca fascicularis*. *Archives of Oral Biology* 24: 689–697.
- Hylander WL, Crompton AW (1986). Jaw movements and patterns of mandibular bone strain during mastication in the monkey *Macaca fascicularis*. *Archives of Oral Biology* 31: 841–848.
- Hylander WL, Johnson KR (1994). Jaw muscle function and wishboning of the mandible during mastication in macaques and baboons. *American Journal of Physical Anthropology* 94: 523–547.
- Hylander WL, Johnson KR (1997). In vivo bone strain patterns in the zygomatic arch of macaques and the significance of these patterns for functional interpretations of craniofacial form. *American Journal of Physical Anthropology* 102: 203–232.
- Hylander WL, Johnson KR (2002). Functional morphology and in vivo bone strain patterns in the craniofacial region of primates: beware of biomechanical stories about fossil bones. In *Reconstructing Behavior in the Primate Fossil Record* (Plavcan JM, Kay RF, Jungers WL, van Schaik CP, eds.), pp 43–72. New York, Kluwer Academic/Plenum.
- Hylander WL, Johnson KR, Crompton AW (1987). Loading patterns and jaw movements during mastication in *Macaca fascicularis*: a bone strain, electromyographic and cinefluorographic analysis. *American Journal of Physical Anthropology* 72: 287–314.
- Hylander WL, Johnson KR, Crompton AW (1992). Muscle force recruitment and biomechanical modeling: an analysis of masseter muscle function during mastication in *Macaca fascicularis*. *American Journal of Physical Anthropology* 88: 365–387.
- Hylander WL, Picq PG, Johnson KR (1991a). Function of the supraorbital region of primates. *Archives of Oral Biology* 36: 273–281.
- Hylander WL, Picq PG, Johnson KR (1991b). Masticatory stress hypotheses and the supraorbital region of primates. *American Journal of Physical Anthropology* 86: 1–36.
- Hylander WL, Ravosa MJ, Ross CF, Johnson KR (1998). Mandibular corpus strain in primates: further evidence for a functional link between symphyseal fusion and jaw-adductor muscle force. *American Journal of Physical Anthropology* 107: 257–271.
- Hylander WL, Ravosa MJ, Ross CF, Wall CE, Johnson KR (2000). Symphyseal fusion and jaw-adductor muscle force: an EMG study. *American Journal of Physical Anthropology* 112: 469–492.
- Kimbel WH, Martin L (1993). Species and speciation: conceptual issues and their relevance for primate evolutionary biology. In *Species, Species Concepts, and Primate Evolution* (Kimbel WH, Martin L, eds.), pp 539–553. New York, Plenum Press.
- Lanyon LE, Rubin CT (1985). Functional adaptation in skeletal structures. In *Functional Vertebrate Morphology* (Hildebrand M, Bramble DM, Liem KF, Wake DB, eds.), pp 1–25. Cambridge, Harvard University Press.
- Lieberman DE, Crompton AW (1998). Responses of bone to stress. In *Principles of Biological Design: The Optimization and Symmorphosis Debate* (Wiebel E, Taylor C, Bolis L, eds.), pp 78–86. Cambridge, Cambridge University Press.
- Manly BFF (2005). *Multivariate Statistical Methods: A Primer*, 3rd ed. Boca Raton, Chapman & Hall/CRC.
- Martin R, Burr D (1989). *Structure, Function, and Adaptation of Compact Bone*. New York, Raven.
- Martin RB, Burr DB, Sharkey NA (1998). *Skeletal Tissue Mechanics*. New York, Springer.
- Meyer C, Kahn JL, Boutemi P, Wilk A (2002). Photoelastic analysis of bone deformation in the region of the mandibular condyle during mastication. *Journal of Cranio-Maxillo-Facial Surgery* 30: 160–169.
- Quinn GP, Keough MJ (2002). *Experimental Design and Data Analysis for Biologists*. Cambridge, Cambridge University Press.
- Rafferty KL, Herring SW (1999). Craniofacial sutures: morphology, growth, and in vivo masticatory strains. *Journal of Morphology* 242: 167–179.
- Ravosa MJ, Johnson KR, Hylander WL (2000a). Strain in the galago facial skull. *Journal of Morphology* 245: 51–66.
- Ravosa MJ, Noble VE, Hylander WL, Johnson KR, Kowalski EM (2000b). Masticatory stress, orbital orientation and the evolution of the primate postorbital bar. *Journal of Human Evolution* 38: 667–693.
- Ravosa MJ, Profant LP (2000). Evolutionary morphology of the skull in Old World monkeys. In *Old World Monkeys* (Whitehead P, Jolly CJ, eds.), pp 237–268. Cambridge, Cambridge University Press.
- Ross CF (2001). In vivo function of the craniofacial haft: the interorbital 'pillar'. *American Journal of Physical Anthropology* 116: 108–139.

- Ross CF, Hylander WL (1996). In vivo and in vitro strain in the owl monkey circumorbital region and the function of the postorbital septum. *American Journal of Physical Anthropology* 101: 183–215.
- Ross CF, Hylander WL (2000). Electromyography of the anterior temporalis and masseter muscles of owl monkeys (*Aotus trivirgatus*) and the function of the postorbital septum. *American Journal of Physical Anthropology* 112: 455–468.
- Sokal RR, Rohlf FJ (1995). *Biometry*, 3rd ed. New York, Freeman.
- Spencer MA (1998). Force production in the primate masticatory system: electromyographic tests of biomechanical hypotheses. *Journal of Human Evolution* 34: 25–54.
- Sylvester AD, Christensen AM, Kramer PA (2006). Factors influencing osteological changes in the hands and fingers of rock climbers. *Journal of Anatomy* 209: 597–609.
- Tattersall I (1986). Species recognition in human paleontology. *Journal of Human Evolution* 15: 165–175.
- Tattersall I (1992). Species concepts and species identification in human evolution. *Journal of Human Evolution* 22: 341–349.
- Tattersall I, Mowbray I (2005). Species and paleoanthropology. *Theory in Biosciences* 123: 371–379.
- Wall CE (1999). A model of temporomandibular joint function in anthropoid primates based on condylar movements during mastication. *American Journal of Physical Anthropology* 109: 67–88.
- Wolpoff MH (1999). *Paleoanthropology*. New York, McGraw-Hill.
- Wood BA (1975). *An Analysis of Sexual Dimorphism in Primates*. PhD dissertation, University of London.
- Wood BA (1991). *Koobi Fora Research Project, vol 4: Hominid Cranial Remains*. Oxford, Clarendon Press.
- Wood BA (1992). Early hominid species and speciation. *Journal of Human Evolution* 22: 351–365.
- Wood BA, Lieberman DE (2001). Craniodental variation in *Paranthropus boisei*: a developmental and functional perspective. *American Journal of Physical Anthropology* 116: 13–25.
- Wood B, Richmond BC (2000). Human evolution: taxonomy and paleobiology. *Journal of Anatomy* 196: 19–60.