

Craniodental Variation in *Paranthropus boisei*: A Developmental and Functional Perspective

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ABSTRACT What levels and patterns of craniodental variation among a fossil hypodigm are necessary to reject the null hypothesis that only a single species is sampled? We suggest how developmental and functional criteria can be used to predict where in the skeleton of fossil hominins we should expect more, or less, within-species variation. We present and test three hypotheses about the factors contributing to craniodental variation in extant primate taxa, and then apply these results to the interpretation of the *P. boisei* hypodigm. Within the comparative samples of extant *Homo*, *Pan*, *Gorilla*, *Pongo*, and *Colobus*, variables from the cranial base, neurocranium, and face that are not subject to high magnitudes of strain have consistently lower levels of intraspecific variation than variables from regions of the face subject to high levels of strain. Dental

size variables are intermediate in terms of their reliability. *P. boisei* is found to have a low degree of variability relative to extant primates for variables shown to be generally useful for testing taxonomic hypotheses. Contrary to the claims of Suwa et al. ([1997] *Nature* 389:489–492), the recently discovered material from Konso falls within the range of variation of the “pre-Konso” hypodigm of *P. boisei* for available conventional metrical variables. Those aspects of the Konso material that appear to extend the range of the *P. boisei* hypodigm involve regions of the skull predicted to be prone to high levels of within-species variation. The approach used in this study focuses on craniodental data, but it is applicable to other regions of the skeleton. *Am J Phys Anthropol* 116:13–25, 2001.

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A sound, species-level, or alpha, taxonomy, based on reliable inferences about the taxonomic significance of morphological variation, is a prerequisite for reconstructing human evolutionary history. Because of taphonomic factors, the majority of the hominin fossil record is cranial, mandibular, and dental (hereafter referred to as “craniodental”). Thus, hominid paleontologists must devise effective methods for sorting craniodental remains into species. No hominin fossils are alike, but how different do crania, jaws, and teeth have to be for researchers to reject the hypothesis that they are conspecific?

Conventionally, the fossil record is sorted into hypothetical species by using modern species taxa as analogues. Analyses of the degree and pattern of within-species variation in modern human and closely related nonhuman primate populations are typically used as the sources of empirical evidence about intraspecific craniodental variation in hominins. However, the utility and testability of these models is limited because all but the modern human comparative analogues lack the unique craniodental features, such as relatively small canines, reduced prognathism, and centrally-located foramen magnum, that set hominins apart from the other apes. Moreover, even *Homo sapiens* is of limited utility as a comparator because generally low levels of sexual dimorphism, and the presence of unique features

(e.g., a large brain, a retracted face, and small canines), along with unique combinations of plesiomorphic features, make modern human craniodental material distinctive. Thus, the pattern of intraspecific variation in the most closely related extant primate taxa (e.g., Wood et al., 1991) may not always be appropriate for investigating the taxonomic significance of variation among hominin fossils.

This paper explores another approach for predicting the pattern of intraspecific variation within extinct early hominin taxa. Specifically, we use developmental and functional information to generate hypotheses about the regional distribution of intraspecific variation. We then test those hypotheses by analyzing variation across a range of extant anthropoid primates, including those that are often used as comparators for fossil hominins. Are there variables that one would predict, on the basis of developmental and functional criteria, to show rela-

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tively little within-species variation? If so, substantial levels of variation in these variables in a fossil hypodigm would strongly suggest taxonomic heterogeneity. Conversely, are there classes of variables that, for developmental or functional reasons, one would expect to show higher levels of intraspecific variation? If so, high levels of variation in these variables would not be reliable indicators of taxonomic heterogeneity. Newly discovered fossil evidence of existing species can then be used to “test” these hypotheses. Variability within a distinctive fossil species should be concentrated on morphology that is prone to higher than average levels of intraspecific variation in extant comparators. For reasons set out above and below, this study applies these principles to the craniodental remains attributed to *Paranthropus boisei*.

For a given feature, the total sum of variation within a living species, σ_{total} , can be broken down into several contributory factors (Vaisnys et al., 1984):

$$\sigma_{\text{total}} = \sigma_{\text{ontogenic}} + \sigma_{\text{geographic}} + \sigma_{\text{temporal}} \\ + \sigma_{\text{intersexual}} + \sigma_{\text{intrasexual}}$$

For a fossil species, taphonomy also contributes to the observed variation (Wood, 1991; Silverman et al., 2001). The extent to which these factors contribute to intraspecific variation is expected to differ for each fossil species. In the case of *P. boisei*, variation due to sampling individuals from different ontogenetic stages can be controlled for by including only mature adult specimens in an analysis. Variation due to sampling individuals from geographically dispersed populations is probably not a significant problem for *P. boisei* because the hypodigm is restricted to a reasonably small geographic area, East Africa, with only one specimen coming from a site elsewhere, in Malawi. Variation due to sampling individuals from different time periods is a potential problem for all fossil taxa. There is reason, however, to suspect that time is apparently not a major source of variation in *P. boisei*. Wood et al. (1994) demonstrated that, with the exception of the P_4 crown, there is little change in size of most craniodental variables among *P. boisei* fossils dated to between 2.0 and 1.4 Myr, which is most of the hypodigm. The final components of σ_{total} , i.e., the variation between and within sexes that is attributable to factors other than ontogeny, geography, and chronological age, are more problematic. Within the higher primates, the main sources of such intraspecific variation are sexual dimorphism, phenotypic responses to differences in behavior, the allometric and other effects of differences in body mass, and other factors not accounted for by differences between the sexes.

Many, if not most, taxonomic studies attempt to deal with these sources of variation by comparing variation in a fossil sample with variation within closely related, extant analogue species. If the variation is significantly larger in the fossil hypodigm

than in the extant species, then the null hypothesis that the specimens sample one species is rejected. A fundamental problem with this type of comparative analysis is the choice of analogue species, which is usually determined on the basis of observations of, or inferences about, genetic propinquity. Thus modern humans, and the other African great apes, are traditionally the preferred analogues for investigations of intraspecific variation within fossil hominins. However, the specialized nature of the hominin cranium and dentition mean that nonhuman extant higher primate analogues are not always an appropriate model. Most early hominin species probably have unique patterns and components of their variation that result in both type I and type II statistical errors. For example, *P. boisei* was probably considerably sexually dimorphic in body mass (including skull size), but not for canine size (Wood, 1991; Wood et al., 1991; Plavcan and van Schaik, 1992). Such a pattern of sexual dimorphism is not present in any extant higher primate species.

VARIATION IN *PARANTHROPUS BOISEI*

The epistemological problem of which craniodental characters are more, or less, reliable as indicators of species diversity is a general one for all fossil hominin taxa. However, this study focuses on *Paranthropus boisei sensu stricto* (hereafter referred to as *P. boisei*) for several, related reasons. Most importantly, *P. boisei* is a distinctive, relatively well-sampled, early hominin taxon, whose hypodigm includes several substantially complete fossil crania. Although the type specimen of *P. boisei* is the well-preserved OH5 cranium from Olduvai Gorge, discoveries made subsequently at Koobi Fora and West Turkana comprise the majority of the craniodental hypodigm of *P. boisei* (Wood, 1991). The first good evidence of a mandible from the same taxon as OH5 came with the recovery of the well-preserved Peninj 1 mandible from Lake Natron in 1964 (Leakey and Leakey, 1964). Since then, an impressive mandibular sample has been accumulated from collections made at the Shungura Formation, in the Omo region, and from Koobi Fora (Wood, 1991). The dentitions of OH5 and the Peninj mandible, together with evidence from associated and isolated teeth from the Shungura Formation and Koobi Fora, have provided a substantial amount of information about the distinctive features of the gross morphology and microstructure of the dentition of *P. boisei* (Wood and Abbott, 1983; Wood et al., 1983, 1988; Wood and Uytterschaut, 1987; Suwa, 1988; Suwa et al., 1996; Ramirez Rozzi, 1993). Wood (1991) summarizes further details about the craniodental hypodigm of *P. boisei*.

Variation within the craniodental hypodigm of *P. boisei* has been the subject of recent reviews (e.g., Wood, 1991; Wood et al., 1994; Suwa et al., 1996), which reflect the broad consensus about its taxonomy developed over the last 30 years. The first attempt to quantify the extent of craniofacial variation

in *P. boisei* was an analysis of the shape differences between a presumed male, KNM-ER 406, and a presumed female, KNM-ER 732 (Corruccini, 1974). However, other than a collection of modern human crania, no comparative data were provided to calibrate the multivariate shape distance between the crania. This was remedied in a subsequent analysis that used multivariate allometric methods, in which Corruccini (1976, p. 561) included a comparative sample of *Gorilla* crania to show that KNM-ER 732 differs from OH5 and KNM-ER 406 "in much the same way female gorillas differ from males." Bilsborough and Wood (1988) used a combination of width measurements and distances from porion in order to reflect phenetic variation in the early hominin face, and used uni- and multivariate methods to compare the face of KNM-ER 732 with those of presumed male *P. boisei* specimens. The two morphs were very different according to this analysis. No nonhuman primate comparative taxa were included for calibration, but the D^2 distance between the two presumed *P. boisei* morphs is as great as the distance between the male morph and *Homo habilis*, or *A. africanus* (Bilsborough and Wood, p. 75, their Table 7).

As part of an empirical investigation that compared the nature of intraspecific and interspecific variation of higher primate skulls and dentitions, Wood et al. (1991) included 28 cranial measurements. They found that facial and biporionic widths were more likely to vary within species than between them, and suggested that because many of the differences between the large and small *P. boisei* morphs also involve width measurements, then this reinforced the case for their being in the same taxon. In another publication, Wood (1991) focused on the degree of sexual dimorphism shown by the living higher primates for cranial base dimensions, and compared these with the degree of difference for the same measurements between the proposed large and small *P. boisei* morphs. Wood (1991, p. 61, his Table 3.1) showed that the degree of difference between the two fossil groups does not exceed the within-species variation in the comparative taxa. This study also reported the results of a multivariate analysis based on the measurements that, respectively, KNM-ER 407 and 732 share with OH5 and KNM-ER 406. When the first three canonical variates are plotted, the orientations of the lines joining the large and small morphs, and the distance between those morphs, are similar to those between the males and females of the majority of the comparative taxa, the exception being *Pongo* (Wood, 1991, pp. 63–64, and 70).

The recent discovery at Konso, Ethiopia, of a taxonomically distinctive, ca. 1.4-Myr-old, large, presumably male skull (KGA-10-525), together with other cranial evidence (Suwa et al., 1997), has provided a new test of the ability to predict the nature of intraspecific craniodental variation within *P. boisei*. Suwa et al. (1997, p. 492) suggested that several

aspects of infraorbital and zygomatic morphology depart from previous descriptions of the species (e.g., Rak, 1983; Wood, 1991). They also claimed that a number of cranial features "without functional significance" (and thus presumably of taxonomic significance) lay beyond the existing range of *P. boisei* variation. These features included the posterior development of the sagittal crests, the lateral projection of the temporomandibular joint (TMJ), and the fusion of the postglenoid process with the tympanic. Suwa et al. (1997, p. 489) concluded that the new skull presents hitherto unknown (and presumably unpredicted and unpredictable) information about variation within *P. boisei*, and they suggested that the Konso evidence "cautions against excessive taxonomic splitting."

However, in many ways, the evidence provided by the KGA 10-525 skull, and the other fossils from Konso, seemed to lend support to existing, empirically generated predictions about the likely distribution of polymorphisms and size-related variation within *P. boisei*. For example, the review by Wood et al. (1994) of the observed variation within the "pre-Konso" hypodigm of *P. boisei* emphasized the contrast between the relatively consistent morphology of the mandible (especially the corpus) and the greater variability of the face and cranial vault. It stressed that polymorphism is "particularly marked in the arrangement of the ectocranial crests, but it is also evident in the face" (Wood et al., 1994, p. 130). Walker and Leakey (1988) and Brown et al. (1993) also drew attention to ectocranial polymorphisms within the *P. boisei* hypodigm. Nonetheless, the new information provided by KGA 10-525 underscores the need for a better understanding of the functional and developmental processes which result in the morphological variation researchers must interpret in order to generate durable taxonomic hypotheses and reliable phylogenetic inferences. Can we use functional and developmental information from extant primates to generate hypotheses about the degree and pattern of intraspecific variation in the skull for an extinct hominin taxon as derived in its morphology as *P. boisei*? To what extent are these hypotheses supported by the important new craniodental evidence for *P. boisei* provided by the Konso discoveries? Does the Konso evidence significantly extend the range of observed variation within *P. boisei*? If so, is the "extra" variation randomly distributed, or is it localized in some regions of the skull?

HYPOTHESES

In this study we propose and test three hypotheses regarding the relative taxonomic reliability of craniodental morphology. Two premises underlie all three tests. First, we seek predictions that can be generalized beyond the extant comparative taxa used to test them. Second, variables with lower than average (i.e., more conservative) levels of intraspecific variation (e.g., from sexual dimorphism) are

likely to be more taxonomically valent than those with average, or above average levels of intraspecific variation.

Hypothesis 1

Variables that measure the size and shape of the face and mandible are predicted to exhibit more intraspecific variation, and thus will be poorer at discriminating species, than regions such as the cranial base, neurocranium (excluding ectocranial structures).

Hypothesis 2

Features that have higher coefficients of narrow-sense heritability (h^2) are predicted to show less intraspecific variability, and are thus be more taxonomically valent, than features with lower heritabilities. Specifically, dental morphologies, that tend to have relatively high heritabilities ($h^2 > 0.60$), are predicted to be less variable than other cranial and mandibular morphologies.

Hypothesis 3

Osseous features whose development is weakly influenced by epigenetic stimuli, especially those generated by mechanical loading, are predicted to be less variable, and will thus be more taxonomically informative than more phenotypically plastic features (Herring, 1993; Lieberman, 1995, 1999). In particular, skeletal structures subject to high and frequent magnitudes of masticatory strain will be more variable within species than those that are routinely subjected to lower strain magnitudes.

Note that these hypotheses are not independent in the sense that they do not divide the skull into mutually exclusive subsets of features. For example, most features of the cranial base and neurocranium are also subject to low levels of mechanical loading. Likewise, dental features that are highly heritable are also either unresponsive, or are only weakly responsive, to epigenetic stimuli such as strain.

MATERIALS AND METHODS

Samples

The fossils comprising the *P. boisei* sample are listed in Table 1. All the measurements are taken from Wood (1991) with the exception of those for the Konso fossils, which are taken from Suwa et al. (1997). Variation in the *P. boisei* sample is compared with intraspecific variation in samples of adult males and females from five extant species (see Table 2 for details): *Homo sapiens*, *Pan troglodytes* spp., *Gorilla gorilla* spp., *Pongo pygmaeus*, and *Colobus guereza* spp. These taxa were chosen as analogues because they represent a range of patterns and degrees of intraspecific variation (Wood, 1976; Wood et al., 1991). The comparative data sets come from Collard (1998) and Chamberlain (1987). Criteria given in both data sources limit the sample to individuals with completely erupted permanent

TABLE 1. *Paranthropus boisei* craniodental remains included in the analysis¹

Specimen	Specimen	Specimen
KGA 10-506	KNM-ER 1806	OMO 57-41
KGA 10-525	KNM-ER 1818	OMO 75-14
KGA 10-570	KNM-ER 1819	OMO 84-100
KGA 10-1720	KNM-ER 3229	OMO 136-1
KGA 10-2705	KNM-ER 3230	OMO 136-2
KNM-CH 1	KNM-ER 3729	OMO F22-1
KNM-ER 403	KNM-ER 3731	OMO F203-1
KNM-ER 404	KNM-ER 3737	OMO L7A-125
KNM-ER 405	KNM-ER 3885	OMO L74A-21
KNM-ER 406	KNM-ER 3889	OMO L157-35
KNM-ER 407	KNM-ER 3890	OMO L238-35
KNM-ER 725	KNM-ER 3952	OMO L338
KNM-ER 726	KNM-ER 3954	OMO L338x-39
KNM-ER 727	KNM-ER 5429	OMO L338x-40
KNM-ER 728	KNM-ER 5877	OMO L398-630
KNM-ER 729	KNM-ER 6128	OMO L398-847
KNM-ER 732	KNM-ER 13750	OMO L398-2608
KNM-ER 733	KNM-ER 15930	OMO L628-2
KNM-ER 801	KNM-ER 15940	OMO L628-3
KNM-ER 802	KNM-ER 15950	OMO L628-4
KNM-ER 805	KNM-ER 16841	OMO L860-2
KNM-ER 810	KNM-ER 17760	PENINJ 1
KNM-ER 816	KNM-WT 17396	
KNM-ER 818	KNM-WT 17400	
KNM-ER 1171	OH 5	
KNM-ER 1467	OH 38	
KNM-ER 1468	OMO 18-31	
KNM-ER 1469	OMO 33-9	
KNM-ER 1509	OMO 33-63	
KNM-ER 1803	OMO 33-65	
KNM-ER 1804	OMO 33-508	
	OMO 47-46	

¹ All specimen measurements were taken from Wood (1991), with the exception of the Konso material. For these specimens, data were taken from Suwa et al. (1997).

dentitions, and in both samples, decisions about the sex of the specimens were made using criteria other than skull morphology.

Variables

The 37 variables listed in Table 3 were chosen in order to sample craniodental morphology that potentially differs in the degree and pattern of its intraspecific variation, and which is prevalent in the hominin fossil record. Although the variable list provides relatively comprehensive coverage of the dentition, some regions of the skull, such as the basiocranium, which are not as well-represented in the hominin fossil record, have fewer variables. Assessments of measurement reliability are given in the references for the sources of data. Buccolingual rather than mesiodistal tooth crown dimensions were used in order to avoid the effects of the different degrees of interstitial wear that accrues after the eruption of the permanent dentition. In order to test hypothesis 1, the variables were divided into four regional subsets: 1) dentition, 2) palate and mandible, 3) upper face, and 4) basicranium and neurocranium (Table 3). In order to test hypothesis 2 (the influence of heritability), dental and skeletal variables were divided into two general heritability categories. As demonstrated by Townsend and Brown (1978), Cheverud and Buikstra (1982), and

TABLE 2. Comparative extant primate samples used in the analysis

Species	N	M	F	Reference
<i>Colobus guereza</i>	24	12	12	Collard (1998), Chamberlain (1987)
<i>Gorilla gorilla</i>	37	20	17	Collard (1998), Chamberlain (1987)
<i>Homo sapiens</i>	75	40	35	Collard (1998), Chamberlain (1987)
<i>Pan troglodytes</i>	35	13	22	Collard (1998), Chamberlain (1987)
<i>Pongo pygmaeus</i>	41	20	21	Collard (1998), Chamberlain (1987)

TABLE 3. Craniodental variables measured on extant samples

Variable ¹	Region	Heritability	Plasticity
I ¹ labiolingual crown diameter (187)	Dentition	High	Low
I ² labiolingual crown diameter (189)	Dentition	High	Low
C labiolingual crown diameter (191)	Dentition	High	Low
P ³ buccolingual crown diameter (194)	Dentition	High	Low
P ⁴ buccolingual crown diameter (203)	Dentition	High	Low
M ¹ buccolingual crown diameter (212)	Dentition	High	Low
M ² buccolingual crown diameter (224)	Dentition	High	Low
M ³ buccolingual crown diameter (236)	Dentition	High	Low
I ₁ labiolingual crown diameter (248)	Dentition	High	Low
I ₂ labiolingual crown diameter (251)	Dentition	High	Low
C labiolingual crown diameter (254)	Dentition	High	Low
P ₄ buccolingual crown diameter (272)	Dentition	High	Low
M ₁ buccolingual crown diameter (286)	Dentition	High	Low
M ₂ buccolingual crown diameter (314)	Dentition	High	Low
M ₃ buccolingual crown diameter (342)	Dentition	High	Low
Coronoid process height	Palate-mandible	Low-to-moderate	High
Mandibular corpus height at M ₁ (150)	Palate-mandible	Low-to-moderate	High
Mandibular corpus thickness at M ₁ (151)	Palate-mandible	Low-to-moderate	High
Mandibular symphysis height (141)	Palate-mandible	Low-to-moderate	High
Mandibular symphysis depth (142)	Palate-mandible	Low-to-moderate	High
Mandibular condyle height	Palate-mandible	Low-to-moderate	High
Palate height at M ¹ (103)	Palate-mandible	Low-to-moderate	High
Palate height at incisive fossa	Palate-mandible	Low-to-moderate	High
Anteroposterior condyle	Palate-mandible	Low-to-moderate	High
Nasospinale-prosthion (43)	Upper face	Low-to-moderate	High
Mastoid length (7)	Basi-neurocranium	Low-to-moderate	High
Orbital breadth (56)	Upper face	Low-to-moderate	Moderate
Orbital height (57)	Upper face	Low-to-moderate	Moderate
Biorbital breadth (50)	Upper face	Low-to-moderate	Moderate
Superior facial breadth (49)	Upper face	Low-to-moderate	Moderate
Interorbital breadth (55)	Upper face	Low-to-moderate	Moderate
Glabella-opisthocranium (1)	Basi-neurocranium	Low-to-moderate	Moderate
Minimum frontal breadth (8)	Basi-neurocranium	Low-to-moderate	Moderate
Basion-bregma (4)	Basi-neurocranium	Low-to-moderate	Moderate
Maximum parietal breadth (9)	Basi-neurocranium	Low-to-moderate	Moderate
Parietal coronal breadth (29)	Basi-neurocranium	Low-to-moderate	Moderate
Bicarotid breadth ²	Basi-neurocranium	Low-to-moderate	Moderate

¹ Detailed definitions of the measurements with numbers in parentheses are given in Wood (1991).² Defined in Dean and Wood (1981).

Hunter (1990), crown dimensions in modern humans and nonhuman primates have h^2 estimates of approximately 0.60 or higher, whereas h^2 estimates of almost all skeletal features are considerably lower, ranging between 0.10–0.60. Dental and skeletal variable subsets are referred to as “high” and “low-to-moderate,” respectively, in Table 3. Finally, in order to test hypothesis 3 (the influence of phenotypic plasticity), tooth crowns, skeletal regions subject to low masticatory strains, and skeletal regions subject to high masticatory strains were assigned respectively to three categories of plasticity: 1) low, 2) moderate, and 3) high. Tooth crowns are fully formed prior to eruption and occlusion, and thus the buccolingual dimension of crown-complete teeth should not be affected by the forces generated by mastication, and should manifest minimal pheno-

typic plasticity. Cranial and mandibular variables, on the other hand, change in response to the forces generated by activities such as chewing, and were classified into two groups on the basis of experimentally derived *in vivo* strain magnitudes (Hylander, 1977, 1979a,b, 1984, 1986, 1988; Hylander and Crompton, 1986; Hylander and Johnson, 1992, 1994; Hylander et al., 1991, 1992). Since magnitudes of strain greater than 1,000 $\mu\epsilon$ have been shown to induce bone deposition (see Currey, 1984; Martin and Burr, 1989; Martin et al., 1998), features from regions which experience strains of approximately 1,000 $\mu\epsilon$ and higher were categorized as “high strain.” Also included in this category are features from the TMJ, which has been shown to be a load-bearing joint subject to high strains (Hylander, 1979a), and features that are influenced by the in-

sertions and origins of the major jaw adductor muscles (Herring, 1993). Features in regions of the face typically subject to strains below 250 $\mu\epsilon$ were categorized as moderately phenotypically plastic (Table 3). It should be noted, however, that the extent to which bone forms in response to different mechanical parameters such as the number, frequency, or magnitude of strain-inducing loading events has yet to be resolved.

Statistical tests

This study focuses on the coefficient of variation (CV) because it is a size-independent measure of variation that has been shown to be especially useful for comparing fossil samples in which the determination of sex is problematic (Cope and Lacy, 1994; Sokal and Rohlf, 1995; Donnelly and Kramer, 1999). Since the CVs in fossil hypodigms such as *P. boisei* are likely to be biased by small sample sizes, we also assessed intraspecific variation using the parameter V^* , which is calculated as $(1 + 1/4n) * sd/mean$ (Sokal and Braumann, 1980). CV and V^* were calculated for combined-sex samples to facilitate comparison with the *P. boisei* hypodigm for which the sex can only be inferred.

Recent studies have shown that between-sample comparisons of equal relative variation such as the CV may be misleading because of the high likelihood of type I statistical errors. These comparisons are best made using a modified weighted scores test (Fligner and Killeen, 1976; Donnelly and Kramer, 1999). Consequently, variation in the *P. boisei* hypodigm was compared to variation in each analogue species, using the FK test of Donnelly and Kramer (1999) (modified from Fligner and Killeen, 1976). Briefly, each variable is log-transformed, and size-corrected by subtracting the log-transformed median of the sample. The resulting absolute values are then rank-ordered and converted into weighted scores; significance is determined from normal-distribution z-values (for details, see Donnelly and Kramer, 1999, p. 512). To test which sets of variables have lower, more predictable, patterns of variability (hypotheses 1–3), variation in the pooled-sex V^* was compared within each species using sets of variables divided a priori into nominal categories based on craniodental region, estimated heritability, and predicted phenotypic plasticity (see above, and Tables 5–7). In order to avoid assumptions of normality, assessments of significance were made using Mann-Whitney U-tests. The same test was used to investigate whether the Konso material falls within the range of variation of the pre-Konso *P. boisei* hypodigm (see Tables 1 and 8).

RESULTS

Fossil variation

In Table 4, variation in the *P. boisei* hypodigm is compared with variation in the extant primate taxa for 27 of the 37 variables listed in Table 3. Ten of the

Table 3 variables were omitted because they were not represented on sufficient *P. boisei* specimens to calculate means and standard deviations. It was also only possible to apply the FK test for significance to 10 (6 dental, and 4 mandibular) of the variables in Table 4, because of the need for at least 7 individuals in the sample (Donnelly and Kramer, 1999). For 2 of the 6 dental variables, P^3 B/L and P_4 B/L, variability in the fossil sample exceeded that in all five comparators. Variation in the *P. boisei* sample for the remaining four dental variables consistently exceeded that for *Colobus*. Of the remaining comparators, *P. boisei* was found to be more variable than *Pan* in M_2 B/L, than *Gorilla* in M^2 B/L, and more variable than both *Homo* and *Pan* in M_1 B/L and M_3 B/L. For mandibular corpus height, *P. boisei* is more variable than all the comparators except *Pongo*; in mandibular corpus thickness, variation in *P. boisei* only exceeds that in *Pan* and *Gorilla*. The pattern for mandibular symphyseal dimensions is the same for both height and thickness, with variation in the *P. boisei* fossil sample exceeding variation in *Homo* and *Pan*, but not the variation in *Pongo*, *Gorilla*, and *Colobus*.

Regional effects

Variability in CV and V^* by craniodental region, in both the *P. boisei* hypodigm and in the comparative modern species analogues, is summarized in Table 5, along with estimates of significance. As is evident from Table 5, the results of CV and V^* are virtually identical, and only those for V^* are illustrated (Fig. 1A). These show different levels of variability across regions of the skull. The palate-and-maxillary region has the highest degree of variability, with the basicranial-neurocranial complex displaying the least variability. In particular, in all extant taxa, V^* values among palate and maxilla variables are significantly ($P < 0.05$) greater than in the basicranial-neurocranial complex. V^* in the palatal and maxillary variables is also significantly greater than in dental variables in *H. sapiens*, and in upper facial variables in *Pongo*. In addition, V^* in the dentition is significantly more variable than basicranial and neurocranial variables in *Colobus*, *Homo*, and *Pongo*; and the upper facial variables are significantly more variable than basicranial and neurocranial variables in *Colobus* and *Pongo* (Table 5). Therefore, hypothesis 1 is partially supported in all the extant taxa sampled, since measurements of morphological features in the cranial base and neurocranium are less variable than measurements reflecting the morphology of the palate and mandible within. The dentition and upper face are generally intermediate in terms of variability.

Heritability effects

Variability in CV and V^* sorted by estimated heritability are summarized in Table 6, and the latter are illustrated in Figure 1B. In all extant primates

TABLE 4. Variation in *P. boisei* and comparative primate samples (all measurements in mm)¹

Variable	<i>P. boisei</i>			<i>H. sapiens</i>			<i>P. troglodytes</i>			<i>P. pygmaeus</i>			<i>G. gorilla</i>			<i>C. guereza</i>		
	Range			Range			Range			Range			Range			Range		
	V*	Max	Min	V*	Max	Min	V*	Max	Min	V*	Max	Min	V*	Max	Min	V*	Max	Min
T ¹ l-1 (187)	12.9	8.0	6.1	6.5	8.8	6.0	6.1	10.7	8.0	11.2	15.0	9.7	7.1	12.0	9.0	6.3	5.0	3.7
T ² l-1 (189)	14.1	7.5	5.6	7.7	8.2	5.1	6.4	9.3	7.2	12.9	13.2	7.0	9.2	11.6	8.0	5.4	5.0	4.0
Cl l-1 (191)	9.2	9.8	7.9	7.1	8.7	6.0	15.3	16.6	9.3	15.8	19.2	10.9	19.6	24.5	13.0	16.6	10.4	6.7
P ³ b-1 (194) ²	12.5	17.0	12.0	7.3 ³	11.1	6.8	7.4 ³	11.7	8.3	8.8 ³	14.8	10.5	7.0 ³	18.3	13.5	8.0 ³	6.7	4.7
P ⁴ b-1 (203)	3.0	12.5	11.6	7.4	11.1	6.7	6.6	11.0	8.4	8.9	15.2	10.8	6.2	17.0	13.2	5.6	7.4	6.0
M ¹ b-1 (212)	6.9	17.7	14.9	6.3	13.5	9.6	5.5	12.8	10.0	6.6	15.1	11.6	5.9	17.0	14.0	4.0	7.1	6.1
M ² b-1 (224) ²	9.9	21.0	15.8	7.4	14.5	10.3	6.2	13.0	10.5	8.1	15.9	11.8	6.4 ³	18.9	14.8	4.9 ³	8.0	6.7
M ³ b-1 (236)	12.5	21.4	16.0	8.6	13.8	9.1	5.8	12.7	10.0	9.0	15.1	10.7	9.0	18.6	13.0	4.5	7.6	6.4
Palate height at M1 (#66 Wood, 1975)	3.2	20.0	19.0	22.6	18.5	4.0	19.2	17.0	6.0	23.5	24.0	8.0	14.5	22.0	13.0	21.7	10.0	5.0
Palate height at incisive fossa (#P5 Chamberlain, 1987)	16.9	7.1	5.2	25.0	14.0	5.0	27.7	12.0	3.0	37.9	24.0	5.0	18.7	13.0	7.0	19.5	7.0	3.0
I ₁ l-1 (248)	15.1	8.0	6.2	8.1	7.4	4.8	6.0	9.8	7.4	9.8	11.4	8.1	11.4	13.5	8.0	6.2	4.8	3.7
I ₂ l-1 (251)	14.7	7.5	6.4	14.6	8.0	5.3	5.4	10.0	8.2	11.4	12.4	8.3	5.9	12.0	9.0	5.5	5.8	4.1
Cl l-1 (254)	9.2	9.7	7.7	9.8	9.9	5.5	11.8	15.8	10.3	14.1	18.4	10.5	16.4	20.3	13.0	11.9	9.3	6.4
P ₁ b-1 (272) ²	13.4	18.9	11.5	7.4 ³	10.3	7.1	8.4 ³	10.2	7.3	9.2 ³	13.5	9.5	7.9 ³	16.2	11.5	5.9 ³	5.2	4.2
M ₁ b-1 (286) ²	10.7	18.7	12.8	5.6 ³	12.2	9.3	5.0 ³	10.8	8.9	7.1	13.4	10.2	7.4	16.5	12.0	3.8 ³	5.8	5.1
M ₂ b-1 (314) ²	7.4	18.8	14.5	6.4	12.8	9.3	5.0 ³	11.5	9.3	8.0	14.4	10.9	8.0	19.3	14.0	4.5 ³	7.0	5.8
M ₃ b-1 (342) ²	7.8	19.0	14.1	7.0 ³	12.1	8.1	6.3 ³	11.5	9.1	9.8	15.2	9.9	11.0	19.7	12.5	4.6 ³	7.0	5.9
Mand. corpus height M1 (150) ²	11.5	50.0	30.0	9.4 ³	36.0	23.5	9.0 ³	34.0	24.5	17.1	52.7	28.5	10.1 ³	47.0	31.0	10.4 ³	26.5	18.0
Mand. corpus thickness M1 (151) ²	14.6	37.0	18.0	11.2	16.3	9.5	9.3 ³	18.0	13.2	12.9	21.3	12.6	8.7 ³	24.0	17.0	11.3	10.5	6.6
Mand. symphysis height (141) ²	11.6	57.0	37.0	9.5 ³	42.0	28.4	7.8 ³	50.8	37.5	18.0	84.7	44.3	12.4	78.0	50.0	13.4	33.0	21.5
Mand. symphysis thickness (142) ²	13.7	35.0	20.0	10.4 ³	18.0	11.0	9.3 ³	21.1	14.5	16.2	28.2	14.2	14.6	35.0	20.0	13.4	14.6	9.2
Glabella-opisthocranion (1) (#69, Wood, 1975)	12.8	173.0	130.0	4.0	201.0	170.0	3.7	144.0	120.0	7.0	152.0	115.0	12.2	225.0	142.0	4.1	89.0	77.0
Basion-bregma (4) (#71, Wood, 1975)	6.1	103.0	92.0	4.7	142.0	114.0	5.6	98.0	78.0	7.2	117.0	88.0	7.1	120.0	89.0	4.2	53.0	45.0
Max. biparietal breadth (9) (#72, Wood, 1975)	8.7	110.0	90.0	4.1	147.0	122.0	3.6	105.0	90.0	5.0	115.0	90.0	5.0	114.0	92.0	3.7	62.0	53.0
Upper facial breadth (49) (#F1, Chamberlain, 1987)	14.7	115.0	90.0	5.5	118.0	98.0	5.3	113.0	92.0	12.2	116.0	81.0	10.7	148.0	99.0	8.0	70.0	52.0
Biorbital breadth (50) (#55 Wood, 1975)	11.0	100.0	82.0	4.8	107.3	87.0	5.9	102.0	76.0	7.4	91.0	70.8	8.9	126.0	91.0	5.5	63.0	50.5
Max. orbital breadth (56) (#52, Wood, 1975)	12.3	40.0	32.0	4.2	40.8	33.0	6.8	39.5	31.2	6.2	38.2	30.4	8.4	51.0	35.0	5.4	27.0	21.6
Max. orbital height (#53, Wood, 1975)	9.8	36.0	30.0	6.7	39.0	27.5	7.7	42.5	30.0	10.1	51.2	30.2	6.0	45.0	35.5	4.9	23.2	19.0

¹ Max, maximum; Min, minimum; Mand, mandibular.

² Variables for which sample size of *P. boisei* was large enough ($n \geq 7$) for FK test (see text for details).

³ Variables for which *P. boisei* is significantly more variable according to the FK test (see text for details).

TABLE 5. CV and V* by region (standard deviations in parentheses)¹

Species	CV				V*			
	B-N	DENT.	U-F	P-M	B-N	DENT.	U-F	P-M
<i>Colobus guereza</i>	1.90 (2.18)	3.81 (1.61)	3.73 (3.85)	6.13 (3.83)	1.92 (2.20)	3.85 (1.63)*	3.77 (3.89)*	6.19 (3.87)*
<i>Gorilla gorilla</i>	2.60 (2.44)	3.29 (1.30)	3.83 (1.50)	4.44 (2.01)	2.61 (2.46)	3.31 (1.31)	2.85 (1.51)	4.47 (2.02)**
<i>Homo sapiens</i>	1.59 (1.24)	3.28 (0.59)	2.27 (1.71)	5.86 (3.73)	1.59 (1.25)	3.29 (0.59)*	2.27 (1.71)	5.88 (3.74)***
<i>Pan troglodytes</i>	2.80 (4.29)	2.94 (0.96)	2.63 (1.65)	5.35 (4.62)	2.82 (4.32)	2.96 (0.97)	2.65 (1.66)	5.39 (4.65)*
<i>Pongo pygmaeus</i>	2.43 (2.51)	3.86 (0.98)	4.15 (3.18)	6.63 (4.01)	2.44 (2.52)	3.88 (0.98)*	4.18 (3.20)*	6.67 (4.04)****
<i>Paranthropus boisei</i>	1.83 (0.65)	2.06 (0.86)	2.78 (0.43)	3.32 (1.27)	1.95 (0.68)	2.17 (0.93)	3.01 (0.44)	3.42 (1.29)***

¹ B-N, basicranium and neurocranium; DENT., dentition; U-F, upper face; P-M, palate and mandible. Significance is according to Mann-Whitney U-test results.

* Significantly different ($P < 0.05$) than basicranium and neurocranium.

** Significantly different ($P < 0.05$) than dentition.

*** Significantly different ($P < 0.05$) than upper face.

except *H. sapiens*, dental size variables with higher h^2 tend to be less variable than skeletal variables with lower heritability. However, this trend is not statistically significant in any species. Therefore hypothesis 2 is rejected; dental features are not notably less variable than skeletal features.

Phenotypic plasticity effects

Variability in CV and V* is related to estimated phenotypic plasticity in Table 7, and the latter is illustrated in Figure 1C. In all extant taxa, the skeletal variables that are known to be measuring structures subject to high masticatory strains (and which are thus presumably more phenotypically plastic) have significantly higher levels of variability ($P < 0.05$) than skeletal variables from regions of the skull known to be subject to lower strain magnitudes. Skeletal variables subject to high strains are also significantly more variable than dental characters. In *Colobus* and *Pongo*, skeletal variables known to be subject to high masticatory strains also have significantly more variation than dental variables. Note that dental variables are intermediate in terms of variability between skeletal characters with higher and lower levels of phenotypic plasticity. This tendency, however, is not characteristic of the *P. boisei* hypodigm, which exhibits an unusually low degree of variability among phenotypically plastic characters. Therefore hypothesis 3 is supported. Skeletal features subjected to the high strain magnitudes generated during mastication are considerably more variable among the extant taxa sampled than the variables that capture the form of the skeletal features subject to lower strains.

Variation within *P. boisei*

When the Mann-Whitney U test is applied to the data provided by Suwa et al. (1997), the Konso specimens are apparently not significantly different in terms of their metrical variation from the “pre-Konso” hypodigm of *P. boisei* (Table 8; Fig. 2). In other words, the Konso specimens fit within the population parameters of *P. boisei* predicted by the “pre-Konso” hypodigm.

DISCUSSION

The above results indicate that there are patterns in the distribution of craniodental intraspecific variation among the extant anthropoid primates sampled in this study that are independent of the overall level of within-species variability. Most importantly, variables from skeletal regions known to be subject to low strains from mastication have consistently and significantly lower CVs within species than variables known to be subject to higher magnitudes of strain. In terms of region, variables which measure the size and shape of the neurocranium and basicranium (excluding the temporomandibular joint) tend to be the least variable; and variables which measure the size and shape of the upper face tend to have lower CVs than variables which measure the size and shape of the palate and mandible. Finally, variables which measure dental size tend to have lower CVs than skeletal variables, but this effect is not significant.

These results demonstrate consistent trends in the level and pattern of intraspecific variation among extant anthropoid primates, especially the great apes, that are commonly used as comparators for variation in fossil hominin hypodigms. Intraspecific variation is most consistent in aspects of the basicranium and neurocranium and upper face (whose shape is presumably influenced mostly by brain size and shape), which are not subject to major epigenetic stimuli from mechanical loading. In contrast, skeletal variables that are repeatedly subject to high strains from mastication have much greater levels of intraspecific variation.

From a taxonomic perspective, such patterns are important to consider when using extant species as analogues in order to assess the significance of variation in a fossil hominin hypodigm. Not all variables are equally useful for testing hypotheses about taxonomic heterogeneity without a priori knowledge about what sorts of patterns to expect. As noted above, a variable that consistently and predictably has low levels of within-species variation in appro-

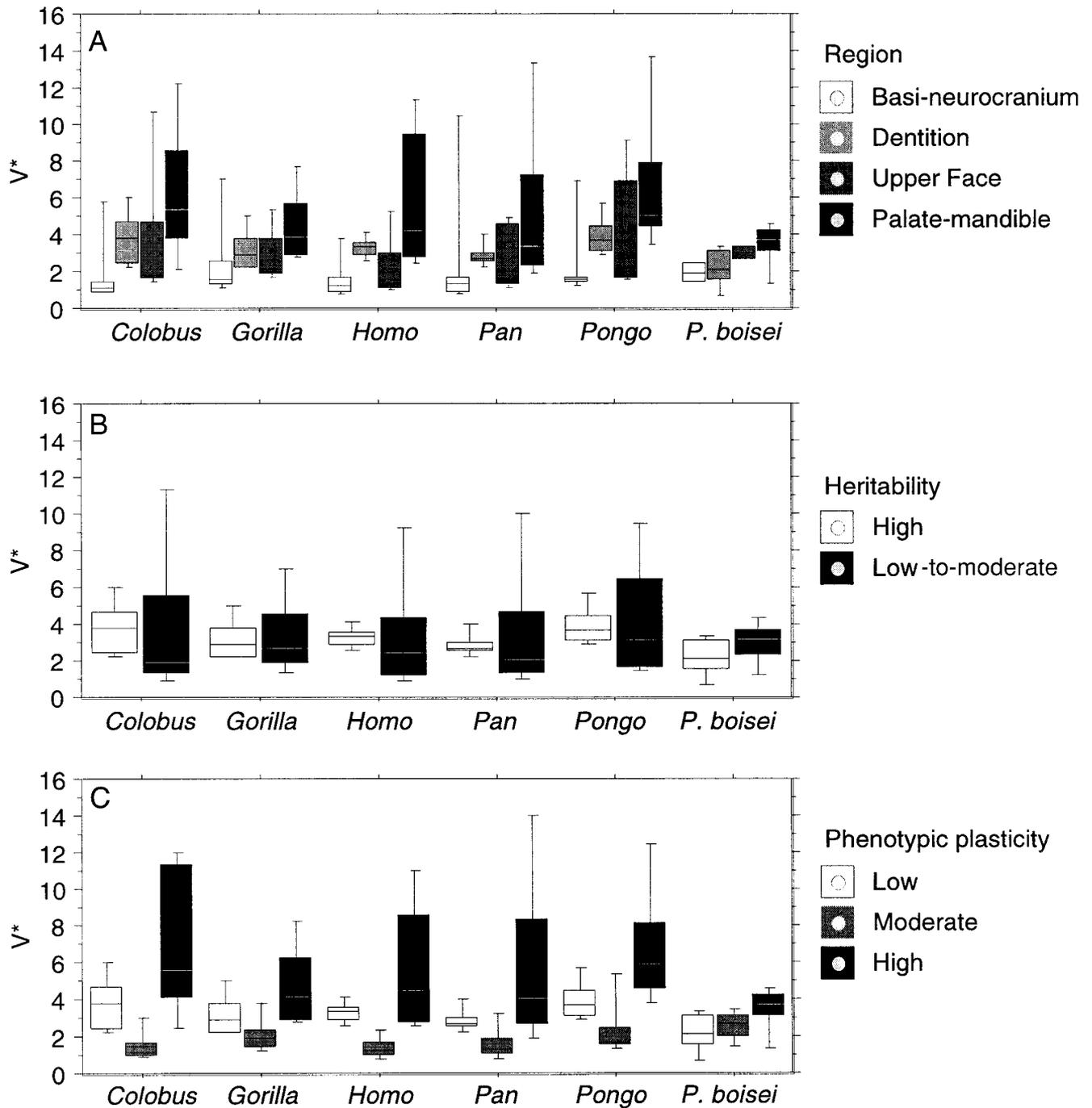


Fig. 1. Box-and-whisker comparison of V^* , a size-corrected estimate of CV (Sokal and Braumann, 1980), for *P. boisei* and extant primate taxa by region (A), heritability (B), and estimated phenotypic plasticity (C). Boxes indicate 50% confidence interval around the mean; whiskers indicate 90% confidence interval for the mean. See Tables 4–7 for tests of significance.

appropriate reference taxa is especially useful for testing hypotheses about taxonomic heterogeneity (Wood et al., 1991). If such a variable has a high degree of variation within a fossil hypodigm, then one can reject with some confidence the null hypothesis that the hypodigm samples one species. In contrast, variables with high levels of within-species variation are less useful for rejecting single species null hypotheses. Variables which demonstrate a high degree of

phenotypic plasticity because of epigenetic responses to strain are especially liable to provide misleading tests of intraspecific variation (Lieberman, 1997). Thus, in addition to the widely accepted requirements for taxonomically valent skeletal characters (that they should be discrete, quantifiable, and independent), we suggest that they should also be relatively unresponsive to nongenetic stimuli such as mechanical loading.

TABLE 6. CV and V* by heritability (standard deviations in parentheses)¹

Species	CV		V*		P ¹
	H	L-M	H	L-M	
<i>Colobus guereza</i>	3.81 (1.61)	4.03 (3.69)	3.85 (1.63)	4.08 (3.73)	0.29
<i>Gorilla gorilla</i>	3.29 (1.30)	3.37 (2.13)	3.31 (1.31)	3.39 (2.14)	0.51
<i>Homo sapiens</i>	3.28 (0.59)	3.41 (3.17)	3.37 (0.59)	3.29 (3.18)	0.17
<i>Pan troglodytes</i>	2.94 (0.96)	3.72 (3.92)	2.96 (0.97)	3.75 (3.95)	0.25
<i>Pongo pygmaeus</i>	3.86 (0.98)	4.52 (3.66)	3.88 (0.98)	4.57 (3.68)	0.68
<i>Paranthropus boisei</i>	2.06 (0.86)	2.81 (1.07)	2.17 (0.93)	2.95 (1.08)	0.07

¹ H, high heritability; L-M, low-to-moderate heritability. Mann-Whitney U-test.

TABLE 7. CV and V* by predicted phenotypic plasticity (standard deviations in parentheses)¹

Species	CV			V*		
	Low	Mod.	High	Low	Mod.	High
<i>Colobus guereza</i>	3.81 (1.61)	1.61 (1.05)	6.70 (3.73)	3.85 (1.63)	1.63 (1.07)*	6.77 (3.77)*:**
<i>Gorilla gorilla</i>	3.29 (1.30)	2.14 (1.21)	4.72 (2.13)	3.31 (1.31)	2.15 (1.22)*	4.75 (2.14)**
<i>Homo sapiens</i>	3.28 (0.59)	1.36 (0.65)	5.66 (3.33)	3.29 (0.59)	1.34 (0.65)*	5.68 (3.34)*
<i>Pan troglodytes</i>	2.94 (0.96)	1.67 (1.15)	5.98(4.68)	2.96 (0.97)	1.69 (1.16)*	6.02 (4.72)**
<i>Pongo pygmaeus</i>	3.86 (0.98)	2.44 (2.32)	6.80 (3.57)	3.88 (0.98)	2.46 (2.34)*	6.84 (3.59)*:**
<i>Paranthropus boisei</i>	2.06 (0.86)	2.37 (0.69)	3.32 (1.27)	2.17 (0.93)	2.55 (0.75)	3.42 (1.29)*

¹ Low, dentition with low predicted phenotypic plasticity; Mod., craniofacial regions subject to lower strain magnitudes, with moderate (Mod.) predicted phenotypic plasticity (see text for details); High, craniofacial regions subject to higher strain magnitudes, with high predicted phenotypic plasticity (see text for details). Significance is according to Mann-Whitney U-test results.

* Significantly different ($P < 0.05$) from regions phenotypically plastic.

** Significantly different ($P < 0.05$) from regions moderately phenotypically plastic.

TABLE 8. Metrical variation in pre-Konso *P. boisei* hypodigm vs. Konso specimens

Variable ¹	<i>P. boisei</i> hypodigm (from Wood, 1991)			Konso specimens (from Suwa et al. 1997)			P ²
	Mean (mm)	SD	N	Mean (mm)	SD	N	
Biporionic breadth (11)	119.0	12.5	5	143.5	na	1	0.14
Maximum bimastroid breadth (13)	128.3	17.3	4	151.0	na	1	0.16
Mandibular corpus height at M ₁ (150)	41.4	4.8	28	41.5	na	1	0.91
Mandibular corpus width at M ₁ (151)	28.3	4.2	28	29.0	na	1	0.72
M ¹ m-d (211)	14.7	0.7	6	14.5	na	1	0.62
M ¹ b-l (212)	16.1	1.1	6	15.9	na	1	0.99
M ² b-l (224)	17.5	1.8	7	19.2	na	1	0.28
M ³ b-l (236)	17.8	2.5	4	19.1	na	1	0.48
M ₁ m-d (285)	16.1	0.9	12	16.2	na	1	0.99
M ₁ b-l (286)	15.2	1.7	9	14.9	na	1	0.86
M ₂ b-l (314)	16.7	1.3	16	17.2	0.5	2	0.67
M ₃ m-d (341)	18.7	1.7	28	19.9	1.8	2	0.38
M ₃ b-l (342)	16.1	1.2	26	16.3	2.0	2	0.99
Minimum molar height (59)	36.2	8.5	3	35.0	na	1	0.65
Maxillo-alveolar breadth at M ² (88)	81.7	2.5	3	82.0	na	1	0.99
Alveolar breadth at M ³ (93)	32.3	1.5	3	47.0	na	1	0.17

¹ Measurement number from Wood (1991) given in parentheses.

² Mann-Whitney U-test results.

With these considerations in mind, how does the pattern of variation in *P. boisei* compare with that of extant primate taxa? This study demonstrates that *P. boisei* is more variable than highly dimorphic extant primate species such as *Gorilla* and *Pongo* in only two palatal and mandibular variables subject to high mechanical loads, and in a few postcanine dental dimensions (Table 4). The same pattern holds when intraspecific variation in *P. boisei* is compared to that of less dimorphic species such as *Homo sapiens*, *Pan troglodytes*, and *Colobus* spp. For these comparisons, *P. boisei* is only more variable in some lower postcanine tooth dimensions and in mandibular corpus and thickness dimensions (for details, see

Table 4). In all other respects, *P. boisei* appears to be unexceptional in its pattern or degree of variation. Most importantly, *P. boisei* does not appear to display more variation than any extant primate species studied here in any craniodental variable that consistently and predictably evinces low levels of within-species variation. Moreover, in terms of which variables tend to have higher CVs than others, the pattern of variability in *P. boisei* is not substantially different from that of any of the extant primates sampled here (Fig. 1). The results of this study do not refute the hypothesis that the hypodigm of *P. boisei* is not especially variable (Chamberlain and Wood, 1985; Wood, 1991).

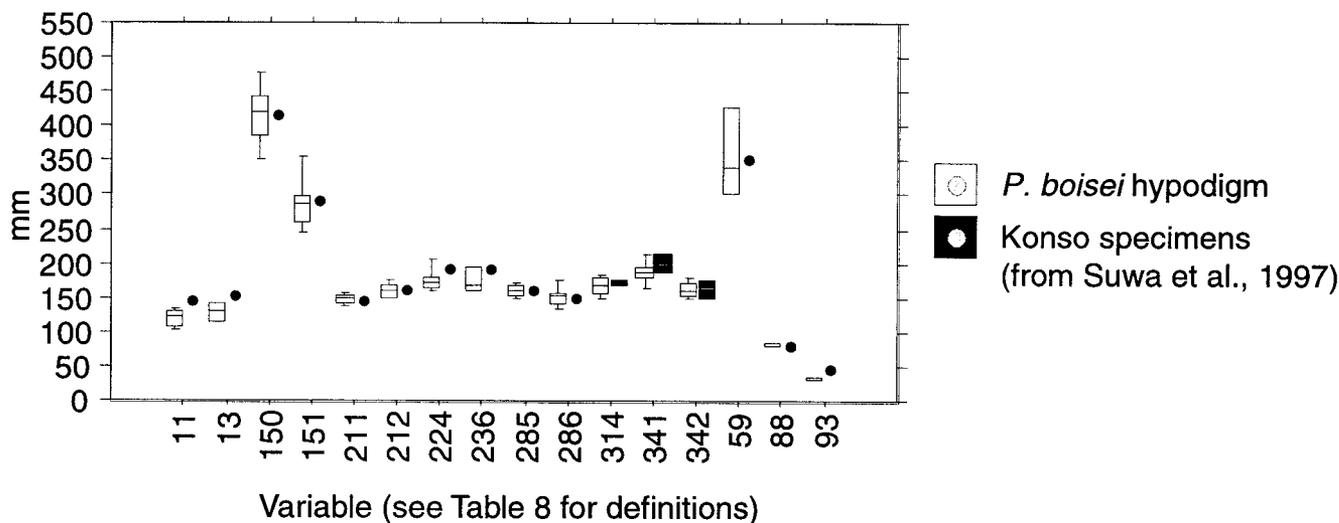


Fig. 2. Box-and-whisker comparison of pre-Konso *P. boisei* hypodigm with metrical data from Suwa et al. (1997). Boxes indicate 50% confidence interval around the mean; whiskers indicate 90% confidence interval for the mean. See Table 8 for definitions of variables and tests of significance.

We now turn to the problem of whether the recently published fossil material from Konso challenges earlier views about taxonomic heterogeneity or variability in the *P. boisei* hypodigm. While we fully endorse the decision to add the Konso material to the *P. boisei* hypodigm, we question the interpretation by Suwa et al. (1997) that the Konso material (and in particular the KGA-10-525 skull) has broader implications for hominin taxonomy. We suggest that, far from exposing the frailty of current taxonomic hypotheses, the evidence from Konso confirms published predictions about craniodental metrical variation within *P. boisei* (Walker and Leakey, 1988; Wood, 1991; Wood et al., 1991, 1994; Brown et al., 1993). In terms of metric variation, the new material from Konso is not significantly different in size than the pre-Konso hypodigm for any variable for which Suwa et al. (1997) present quantitative data. As far as we can tell, the Konso material falls entirely within the range of variation of the pre-Konso hypodigm.

Suwa et al. (1997, their Table 2) single out eight nonmetric features in which KGA 10-525 is said to be beyond the range of observed *P. boisei* variation. These are: the postglenoid merged with the tympanic, occipitomarginal sinus, anterior orientation of the zygomatic frontal process, visor-like zygomatic morphology, zygomatic prominence, zygomaticomaxillary fossa, low position of the infraorbital foramen, and the median maxillary torus. Many of these morphological features can be described quantitatively, and we await further publication of the Konso material to test these claims rigorously. However, with the exception of an occipitomarginal sinus, and the low position of the infraorbital foramen, these features are all part of the lower and midfacial masticatory complex that is well-known to be dynamically responsive to functional demands of the masticatory apparatus (reviewed in Herring, 1993).

According to the data presented above, such features are likely to be unsuitable for making systematic inferences, especially in large, adult males. Moreover, experimental studies of nonhuman primates and other mammals suggest that one should expect to see considerable intraspecific variation in the morphology of features such as the orientation of the zygomatic frontal process and the zygomatic prominence. The masseter generates high strain magnitudes in the zygomatic arch and maxilla (Hylander, 1988; Herring and Mucci, 1991), and this region plays a crucial role in counteracting high bending and twisting forces in the face during mastication (Demes, 1987; Weishampel, 1993; Greaves, 1995). Comparisons of animals raised on soft- vs. hard-food diets show that simple dietary modification can result in substantial morphological differences in these regions of the cranium between the two test groups (Corruccini and Beecher, 1982; Kiliaridis, 1986). Therefore, while we do not dispute the unique nature of the infraorbital and zygomaticomaxillary regions of KGA-10-525, we suggest that they are hardly the sorts of morphological variations which should call into question taxonomic hypotheses about a species that many researchers suggest was morphologically specialized to generate and withstand substantial masticatory forces (e.g., Demes and Creel, 1988; Hylander, 1988).

Finally, it is encouraging to note that the *P. boisei* hypodigm remains well-accepted. The discovery of the Konso material was claimed (paradoxically) to indicate that earlier formulations of the pre-Konso *P. boisei* hypodigm were overly narrow. However, there are no published disagreements over the taxonomic status of the Konso material as *P. boisei* and, as demonstrated above, the Konso material fits within previous predictions of variation and polymorphism with the hypodigm. While fossils are the primary data on which hominin paleontologists

must base their attempts to reconstruct human evolutionary history, advances in our understanding of hominin evolution also come from improvements in the methods we use to interpret fossil evidence and compare it to modern taxa.

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