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Wood, Bernard

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A PALAEONTOLOGICAL MODEL FOR DETERMINING THE LIMITS OF EARLY HOMINID TAXONOMIC VARIABILITY

by

Bernard Wood

Hominid Palaeontology Research Group, Department of Human Anatomy and Cell Biology, University of Liverpool, PO Box 147, LIVERPOOL L69 3BX, United Kingdom

ABSTRACT

This paper has examined the utility and implications of using *Australopithecus boisei* as a model for assessing the limits of intraspecific variation in early hominid species. When compared to variation in a sample of lowland gorilla, the coefficient of variation values of the 25 cranial and mandibular, and 44 dental measurements taken on the *A. boisei* hypodigm were not excessive; the main difference between the two samples was the higher levels of canine variability within *gorilla*.

Levels of variability in *A. boise*i were compared with those in the hypodigms of *A. robustus* and *A. africanus*. In neither case did comparisons demonstrate that those hypodigms were excessively variable. This suggests that if more than one taxon is present within these collections, then any differential diagnosis needs to be based on excessive variation in shape and not size.

INTRODUCTION

The problem of deciding the point at which phenotypic variation exceeds that which can be tolerated within a single species is one that is widely recognised in both palaeontology in general (Mayr, Linsley and Usinger 1953; Sylvester-Bradley 1956; Simpson 1961), and in hominid palaeontology in particular (e.g. Weidenreich 1946; Campbell 1962; Zwell and Pilbeam 1972; Pilbeam 1978; Wolpoff 1978). Some have linked these difficulties with attempts to equate fossil species with neontological ones. Resolutions proposed in the past have included redefining the meaning that is conveyed when a fossil species is erected. For example, the 'palaeospecies' and 'chronospecies' concepts of Cain (1954) and George (1956), respectively, are deliberately intended to invoke a wider concept, i.e. the whole (George 1956), or part (Pilbeam 1972), of an evolutionary lineage. Campbell (1972) is the latest to espouse an alternative solution, which suggests that dating information should supplant morphological evidence as a means of defining species, but it is a view that has attracted few supporters. A third approach leaves the classificatory categories untouched, but suggests that Bayesian probability theory might offer a formal scheme for determining whether fossil site samples are likely to be derived from one, or more, early hominid species (Pilbeam and Vaisnys 1975; Pilbeam 1978).

One strategy for making judgements about the boundaries of palaeontological species has been to base criteria for species variability on variation observed within living taxa. The extent of variation within one, or more, variables in a reference sample is usually compared with that in the fossil sample, and a recent study has proposed that the 'degree' and the 'pattern' of variation should be given separate consideration (Wood, Li and Willoughby 1991). The same study used an 'outgroup' approach, and investigated the pattern of variation in modern humans and the African higher primates. Molecular, and other, evidence have consistently shown these to be the extant taxa most closely related to modern humans, and thus to fossil hominids (Sibley and Ahlquist 1984, 1987; Miyamoto, Slightom and Goodman 1987; Miyamoto *et al.* 1988; Caccone and Powell 1989; Saitou 1991). Univariate and multivariate methods were employed to compare patterns of variation, and the results suggest that the most appropriate extant analogue for assessing the pattern of dental variation is modern *Homo sapiens*, whereas, apparently, both *Homo* and *Pan* provide suitable pattern analogues for assessing cranial and mandibular variation.

Extant reference taxa which can usefully serve as analogues for the degree of variation are more difficult to identify. Several authors have pointed out that no neontological species provides an apt model because the time spanned by palaeontological samples introduces an additional, unquantifiable, source of variation (Pilbeam 1978; Lieberman, Pilbeam and Wood 1988; Wood and Xu 1991). Within the higher primates the degree of intraspecific variation is lowest in *Homo sapiens* and *Pan*. Although these two taxa are judged to be the forms most closely related to early hominids (e.g. Caccone and Powell 1989) many workers have erred on the side of caution and selected a more dimorphic ape, usually *Gorilla*, with the intention of trying to allow for the extra, temporal, influence on variation that is implicit in a fossil sample (e.g. Lieberman *et al.* 1988; Wood *et al.* 1991).

An alternative to using extant analogues is to compare the variation within the test sample with that observed within another hominid species. This strategy has the advantage that both reference and test samples would include the elusive temporal element which is lacking in extant analogues, as well as ensuring that the reference sample provides a type which is genetically closely-related to the test sample. Any fossil taxon used as a reference sample should preferably be defined by autapomorphies (Table 1), so that disagreement about the nature of the reference hypodigm is reduced to a minimum. The fossil taxon should also have a similar, or equivalent, geographical range to the material being evaluated. This serves to eliminate yet another confounding factor, namely the influence of geographical variation.

In the light of these criteria, it was decided to investigate *Australopithecus boisei* as a possible early hominid reference taxon. This paper reports an investigation which sought to explore whether the diagnostic criteria for *A. boisei* could be utilised to identify samples large enough to estimate population parameters. The latter were then computed, as were equivalent parameters generated from extant analogues and the two sets were compared. The results of the investigation were then reviewed to see if they have implications for the assessment of variation within material which has been assigned to other fossil hominid taxa.

TABLE 1
Probable Autapomorphies of *Australopithecus Boisei*

1. **Overall size, shape and form of the cranium.**
   - i. Massive, but orthognathic viscerocranium, with a mean cranial capacity of around 500 ml.
   - ii. Substantial overlap at the parietotemporal suture, with *striae parietalis*.
   - iii. Glabella located on a rounded projection.
2. **Face**
   - iv. Great absolute and relative width of the midface, combined with modest alveolar and midfacial prognathism.
   - v. Nasal bones broader superiorly than inferiorly, combined with well-defined nasal margins.
3. **Cranial base**
   - vi. 'Heart-shaped' foramen magnum.
   - vii. Narrow cranial base, combined with coronally-orientated petrous bones with vertically-inclined posterior faces.
   - viii. Laterally-expanded mandibular fossa, combined with a deep glenoid fossa, short postglenoid process, articular eminence with a steep face and bounded laterally by a substantial articular tubercle and a posteriorly-situated entoglenoid process.
4. **Mandible**
   - ix. Large, robust, corpus, with marked lateral prominence, wide, extramolar sulcus, vertical inner wall and "bulging" lateral wall.
   - x. Long alveolar planum, with both a superior, and a relatively larger inferior, transverse tori.
5. **Dentition**
   - xi. Modest sized incisors and canines combined with massive premolar and molar crowns.
   - xii. Absolutely large-crowned, but relatively buccolingually-narrowed, P_4s.
   - xiii. Absolutely and relatively large premolar and molar talonids.
   - xiv. Molariform P_3 roots.
   - xv. Mesial to distal gradient of increasing root size and robusticity from P_3 - M_3.
   - xvi. Retention in the adult premolars and molars of the deciduous mode of enamel formation.

MATERIALS AND METHODS

The data used in this investigation were gathered by the author as part of a larger study of Plio-Pleistocene hominid evolution (Wood, 1991). The main sample included all the Plio-Pleistocene remains from the East African sites of Koobi Fora, Omo, Olduvai, Peninj, Chesowanja and West Turkana which had been assigned to, or likened to, *A. boisei* (Table 2). The *A. africanus* and *A. robustus* samples include some of the more recently reported additions to the respective hypodigms (Clarke 1988; Grine 1988a). Details of the provenance of the *Gorilla* sample are given in Wood *et al.* (1991).

Metrical data form the core of the evidence, but several non-metrical observations were also included. The cranial and mandibular measurements included in this study are listed in Table 3, and maxillary and mandibular dental measurements are set out in Tables 4 and 5; detailed

TABLE 2
Probable Autapomorphies of *Australopithecus Boisei*

1.	*KOOBI FORA* (KNM-ER)			N=51	
	403	404	405	406	407
	725	726	727	728	729
	732	733	801	802	805
	810	812	814	818	1170
	1171	1467	1468	1469	1477
	1479	1509	1803	1804	1806
	1816	1819	1820	3229	3230
	3729	3737	3885	3886	3890
	3954	5429	5679	5887	6082
	13750	15930	15940	15950	16841
	17760				
2.	*WEST TURKANA* (KNM-WT)			N=2	
	17396	17400			
3.	*PENINJ*			N=1	
	Mandible				
4.	*CHESOWANJA* (KNM-CH)			N=3	
	1	302		304	
5.	*OLDUVAI* (OH)			N=3	
	5	26		30	
6.	*OMO*			N=14	
	F203-1	L64-2	L74A-21	L338y-6	
	L427-7	L628-1	L628-2	L628-5	
	L704-2	L726-11	Omo 47-46	Omo76-37	
	Omo141-2	Omo323-896			

Total Number of Specimens = 74

definitions are to be found in Wood (1991). With the exception of OH5, the remains from West Turkana and a few specimens from the Omo Shungura Formation, all measurements were made on original specimens.

Parameters of taxon hypodigms were calculated using standard formulae except that Coefficient of Variation (CV) calculations for samples of less than ten were based on a formula for small samples (Sokal and Rohlf 1987). Methods are available for assessing the statistical significance of differences in variability (e.g. Sokal and Braumann 1980; Schultz 1985), but the small sample sizes do reduce confidence in any conclusions based on these tests, and in this study no attempt has been made to assess the statistical significance of any CV differences.

RESULTS

The process of assembling a hypodigm of *A. boisei* began by reviewing the characteristics of the type specimen, OH5, employing suitable casts as well as information contained in Tobias (1967). Specimens showing clear resemblances to OH5 were evident in the site collections from Koobi Fora (eg KNM-ER 406 and 733), Chesowanja and the Omo. This expansion of the cranial hypodigm enabled both qualitative and quantitative estimates to be made of the likelihood that smaller crania (eg KNM-ER 407 and 732) may be smaller-bodied, presumably female, representatives of *A. boisei* (Wood 1991).

The absence of a mandible from the type specimen (OH5) means that the mandibular morphology of *A. boisei* has to be inferred. The tooth dimensions of *A. boisei* crania and maxillary/mandibular tooth area ratios of extant higher primates provide a suitable starting point, for the null hypothesis would suggest that the dental dimensions of the mandibles of *A. boisei* should be within the range of mandibular tooth size predicted from the maxillary dentition of *A. boisei*. Such a calculation does indicate that mandibles such as that from Peninj and several from Koobi Fora (eg KNM-ER 729, 3230 etc) most likely belong to *A. boisei*. Likewise, studies of tooth crown and root morphology (Wood and Abbott 1983; Wood, Abbott and Graham 1983; Wood and Uytterschaut 1987; Wood Abbott and Uytterschaut 1988; Wood and Engleman 1988) and of the enamel microstructure (Beynon and Wood 1986, 1987) of teeth associated with cranial and mandibular remains diagnostic of *A. boisei*, have provided criteria for allocating partial dentitions, and even single, isolated, tooth crowns, to the

TABLE 3

Parameters of Selected Cranial and Mandibular Dimensions for *Australopithecus boisei* compared with the CVs of *Gorilla gorilla* and the Hypodigms of *Australopithecus africanus* and *Australopithecus robustus*.

		Australopithecus boisei					*Gorilla* (N=64)	*Australopithecus africanus*		*Australopithecus robustus*	
		N	X	RANGE	CV	95%CL	CV	N	CV	N	CV
Glabella-opisthocranion	(1)	4	158	130-173	12,7	-	11,8	-	-	-	-
Posterior cranial length	(3)	3	47	46-48	2,3	-	17,9	3	7,3	-	-
Minimum frontal breadth	(8)	6	66	60-74	8,2	2,1-14,3	6,2	-	-	3	6,0
Maximum parietal breadth	(9)	6	98	90-110	8,0	2,0-14,0	4,7	-	-	-	-
Biporionic breadth	(11)	5	119	103-134	10,9	1,2-20,6	10,5	4	2,4	-	-
Bimastoid breadth	(13)	4	128	110-144	14,3	-	11,1	-	-	-	-
Biorbital breadth	(50)	3	93	82-100	11,0	-	8,7	3	5,3	3	14,6
Bijugal breadth	(51)	3	124	107-135	13,0	-	10,5	-	-	3	7,0
Interorbital breadth	(55)	4	24	23-27	8,8	-	21,7	4	7,4	-	-
Alveolar breadth (outer)	(54)	3	73	62-81	14,8	-	7,3	-	-	4	5,1
Orbital breath	(56)	3	37	30-38	12,3	-	7,1	3	1,8	-	-
Orbital height	(57)	3	33	30-36	10,2	-	6,9	-	-	-	-
Nasal width	(68)	4	31	28-34	10,3	-	10,2	7	13,6	-	-
Palate length	(90)	3	61	52-71	16,8	-	12,7	3	4,7	3	6,7
Intercanine distance (U)	(98)	3	29	28-31	5,6	-	10,8	8	5,5	10	7,4
Palate height	(103)	3	20	19-20	3,2	-	13,9	6	20,7	8	22,0
Alveolar breadth (inner)	(93)	3	32	31-34	5,1	-	9,2	-	-	4	8,1
Cranial capacity	(-)	6[2]	501	427-530	7,9	3,4-12,4	14,1	6[3]	11,7	1[4]	-
Symphyseal height	(141)	11	47	40-57	15,0	7,7-22,3	13,4	-	-	-	-
Symphseal depth	(-)	11	28	24-32,5	9,5	5,0-14,1	13,1	-	-	-	-
Corpus height (M_1)	(150)	25	42	34-50	9,9	7,0-12,8	11,8	6	11,7	5	7,9
Corpus width (M_1)	(151)	25	29	24-37	11,8	8,3-15,3	9,8	5	10,2	5	14,5
Corpus area (M_1)	(152)	25	960	660-1414	21,3	14,8-27,8	18,7	5	11,6	5	21,5
Robusticity (M_1)	(-)	25	69	57-80	7,5	5,3-9,7	10,0	5	16,9	5	10,6
Intercanine distance (L)	(166)	5	21	20-22,5	5,0	0,6-9,4	14,3	-	-	-	-

NB:

(1) Numbers in parentheses refer to the measurement number in Wood (1991).
(2) Specimens included in *A. boisei* cranial capacity sample = KNM-ER 406,407, 732, 13750; 0h5; Omo L338y-b.
(3) Specimens included in *A. africanus* cranial capacity sample = Sts 5, 19, 60, 71; MLD 37/38; Taung.
(4) Specimen included in *A. robustus* cranial sample = SK 1585.

TABLE 4

Parameters of Maxillary Tooth Crown Dimensions for *Australopithecus boisei* compared with the CVs of *Gorilla gorilla* and of the Hypodigms of *Australopithecus africanus* and *Australopithecus robustus.*

		Australopithecus boisei					*Gorilla* (N=64)	*Australopithecus africanus*		*Australopithecus robustus*	
		N	X	RANGE	CV	95%CL	CV	N	CV	N	CV
I^1	LL	-	-	-	-	-	8,8	3	2,4	13	5,4
	MD	-	-	-	-	-	12,5	3	15,1	15	7,6
I^2	LL	5	6,4	5,6-7,5	13,1	1,4-24,8	11,5	5	10,6	8	10,4
	MD	5	6,5	6,2-6,9	6,5	0,8-12,2	12,9	5	8,8	9	14,5
C	LL	6	8,9	7,6-9,9	10,5	2,6-18,4	20,4	6	5,2	19	7,4
	MD	7	8,8	8,2-10,7	10,6	3,6-17,6	20,9	7	4,2	19	5,9
	CA	6	75,5	63,0-87,0	13,6	3,3-23,9	39,0	6	9,1	19	11,9
P^3	BL	8	15,4	13,9-17,0	8,0	3,2-12,8	8,3	14	6,4	16	5,0
	MD	8	10,9	10,2-12,0	5,7	2,3-9,1	9,1	14	2,2	17	4,0
	CA	8	168,0	142,0-185,5	9,6	3,9-15,3	15,5	14	7,8	16	8,5
P^4	BL	7	16,3	14,3-18,0	8,3	2,8-13,8	7,6	9	5,3	18	5,2
	MD	7	11,7	10,6-12,1	4,5	1,6-7,5	8,4	9	5,1	18	5,6
	CA	7	191,0	151,5-212,5	12,0	4,0-20,0	13,9	9	9,0	18	10,0
M^1	BL	8	16,3	14,9-17,7	6,9	2,8-11,0	7,2	12	5,1	20	4,7
	MD	8	14,8	13,5-15,7	5,6	2,3-8,9	7,1	12	3,9	20	3,0
	CA	8	241,0	212,0-269,0	11,0	4,4-17,6	13,3	12	7,7	20	6,4
M^2	BL	8	18,2	16,4-21,0	10,2	4,1-16,3	7,6	15	6,5	17	5,6
	MD	8	16,1	14,7-17,3	7,0	2,8-11,2	8,3	15	6,5	17	5,6
	CA	8	295,0	242,5-361,0	16,1	6,3-25,9	14,3	15	13,1	17	9,1
M^3	BL	4	18,9	16,2-21,5	14,0	-	9,8	14	8,4	19	4,1
	MD	4	15,7	14,2-16,6	7,4	-	10,2	14	9,5	19	6,0
	CA	4	298,0	230,0-366,0	17,7	-	19,4	14	17,2	19	9,2

NB: LL = Labiolingual diameter; MD = Mesiodistal diameter; CA = Computed crown area: BL = Buccolingual diameter,

TABLE 5

Parameters of Maxillary Tooth Crown Dimensions for *Australopithecus boisei* compared with the CVs of *Gorilla gorilla* and of the Hypodigms of *Australopithecus africanus* and *Australopithecus robustus*

		Australopithecus boisei					*Gorilla* (N=64)	*Australopithecus africanus*		*Australopithecus robustus*	
		N	X	RANGE	CV	95%CL	CV	N	CV	N	CV
I_1	LL	7	6,8	6,1-8,0	12,3	4,1-20,5	8,8	3	10,6	11	9,8
	MD	7	5,4	4,5-5,9	9,7	3,3-16,1	12,5	3	14,0	10	3,6
I_2	LL	4	6,9	6,4-8,1	12,3	-	11,5	3	9,1	8	5,7
	MD	5	6,4	6,1-6,6	3,3	0,4-6,2	12,9	4	13,0	8	6,5
C	LL	9	8,8	7,5-9,7	9,4	4,3-14,6	20,4	7	9,8	12	7,6
	MD	8	8,0	7,3-9,3	9,1	3,7-14,5	20,9	7	6,5	12	7,9
	CA	8	69,0	57,0-83,5	14,2	5,6-22,8	39,0	7	16,5	12	14,2
P_3	BL	7	12,9	11,6-13,9	7,3	2,5-12,1	8,3	6	6,2	7	7,7
	MD	7	10,9	9,6-12,1	7,6	2,6-12,6	9,1	6	6,3	17	4,0
	CA	7	140,5	119,0-165,0	12,8	4,3-21,3	15,5	6	9,7	17	9,7
P_4	BL	14	14,7	12,7-16,5	7,7	4,5-10,9	7,6	6	4,2	16	7,8
	MD	14	13,9	12,2-15,7	7,3	4,3-10,3	8,4	6	7,9	17	4,4
	CA	14	205,0	170,0-240,0	13,1	7,7-18,5	13,9	6	11,7	16	11,2
M_1	BL	11	14,7	12,8-16,0	6,9	3,6-10,2	7,2	11	7,6	26	6,5
	MD	11	16,1	14,6-17,0	5,1	2,7-7,5	7,1	11	5,8	26	5,3
	CA	11	238,5	187,0-262,0	10,3	5,4-15,2	13,3	11	11,2	26	10,9
M_2	BL	14	17,0	14,5-19,0	7,8	4,6-11,0	7,6	10	5,6	22	6,7
	MD	14	18,6	16,0-20,8	8,8	5,2-12,4	8,3	13	4,5	21	5,5
	CA	14	317,5	232,0-384,0	16,4	9,5-23,3	14,3	11	9,5	21	11,9
M_3	BL	18	16,7	15,0-20,0	8,5	5,5-11,5	9,8	11	5,0	20	6,8
	MD	18	19,5	17,2-23,5	8,8	5,7-11,9	10,2	12	8,4	21	5,2
	CA	18	327,0	273,0-470,0	17,2	11,0-23,4	19,4	10	13,5	20	11,1

A. boisei hypodigm (e.g. KNM-ER 802, 1479, 2607). By proceeding in this manner, from what is known to what is unknown, probable autapomorphies of *A. boisei* have been assembled. These are summarised in Table 1, and further details are provided in Wood (1991). These presumed auta-pomorphies, together with apparently unique combinations of characters possessed by *A. boisei*, have allowed the specimen listed in Table 2 to be identified as the hypodigm of *A. boisei*. This relatively restricted hypodigm of *A. boisei* does not include material others have assigned to *Australopithecus aethiopicus* or *Australopithecus aff. aethiopicus* (Howell, Haesaerts and de Heinzelin 1987; Suwa 1988, 1990). The sample size, mean value, range and coefficient of variation for each of the cranial, mandibular, maxillary dental and mandibular dental variables are given in Tables 3-5.

The overall level of variability of cranial and mandibular variables in the *A. boisei* hypodigm matches that in the *Gorilla* sample (Table 3). Alveolar breadth is one of the few variables that show substantially higher levels in the fossil taxon, but the sample size, three specimens only, is small. Despite the major differences in facial and mandibular form between *Gorilla* and *A. boisei*, generally there is remarkable similarity in variability between the two samples. Turning to the dental data, with one exception, variability in *A. boisei* and the *Gorilla* sample is well-matched. The exception is canine size, for while *Gorilla* exhibits high levels of canine variability, reflecting the strong sexual dimorphism in canine size, in the *A. boisei* hypodigm the samples of between six and nine in number have CV values which are half, or less, those of the *Gorilla* sample.

DISCUSSION

Attempts to apply phylogenetic analytical techniques to early hominid taxa have demonstrated that *A. boisei* is the most distinctive of the early hominid taxa (Skelton, McHenry and Drawhorn 1986; Chamberlain and Wood 1987; Wood 1991). This distinctiveness has, however, not been sufficient to insulate it from controversy about its taxonomic status. Such problems relate to judgements about the 'degree' of variation which is admissable within the taxon, and one also impinges on a more general discussion about the meaning of palaeontological species (Bown and Rose 1987). The latter debate, concerning the extent to which the *A. boisei* hypodigm should be expanded to embrace all hyper-megadont East African hominids (Walker *et al.* 1986) will not be reviewed here. Nonetheless, it is relevant to comment on the proposals that the main *A. boisei* hypodigm may subsume two species which differ mainly in size. The basis for these proposals are, firstly, the extent of the multivariate mahalanobis D^2 morphological distance between crania included in the *A. boisei* hypodigm, namely KNM-ER 406 and 732 (Bilsborough and Wood 1988), and, secondly, the extent of variation in mandibular corpus size of juvenile (e.g. KNM-ER 1477 and 1820) and adult (e.g. KNM-ER 729 and 1469) mandibles assigned to *A. boisei* (Dean 1988). However, the evidence from the data in table 3 suggests that neither cranial variables, nor dimensions of the adult mandibular corpus, show levels of variability that obviously exceed those in an extant *Gorilla* sample.

The parameters of the *A. boisei* sample given in tables 3-5 can be usefully compared with parameters for *A. africanus* and *A. robustus*. Such comparisons are justified, for while differences in body size is one of the factors known to be correlated with levels of intraspecific variability (Leutenegger and Cheverud 1985), the most recent estimates suggest that the body sizes of the three taxa are similar, with mean values restricted to between 45-50 kg (Jungers 1988; McHenry 1988). When the parameters of the two 'robust' australopithecines are compared, with the exception of the mesiodistal diameter of the I^2, the CV values of *A. robustus* are similar to those of *A. boisei*. These data thus underscore the taxonomic integrity of the *A. robustus* hypodigm, despite the complexities of deposition at the main Swartkrans site of the hypodigm (Brain 1988). These data do not support the claim that *A. robustus* shows unusually low levels of intraspecific, specifically sexually dimorphic, variation (Robinson 1956). Nor do they suggest that the 'degree' of variability within the *A. robustus* hypodigm provides evidence that the taxon subsumes two taxa, *A. robustus* sensu stricto and *A. crassidens* (Grine 1988b). Such claims will need to demonstrate significant morphological distinctions between the two subsets of *A. robustus*.

It has recently also been suggested that the hypodigm of *A. africanus* from Member 4 at Sterkfontein may comprise not one, but two, taxa (Clarke 1988; Kimbel and White 1988). With the exception of some of the diameters of the mandibular incisor teeth (Table 5), there is, however, no evidence that the Sterkfontein Member 4 hypodigm considered in this study is excessively variable, as judged by either fossil, *A. boisei*, or extant, *Gorilla*, reference samples.

CONCLUSIONS

These results suggest that a hypodigm of *A. boisei* cranial, mandibular and dental remains, assembled using morphological criteria, is not excessively variable when compared to a sample of extant *Gorilla* crania. It is proposed that this fossil taxon has greater utility as a comparator for assessing variation within putative early hominid taxa because its orthognathic face and relatively small canines are among the important shared-derived features which distinguish hominids from pongids.

Proposals that what we presently assume to be 'good' palaeontological species samples, *A. africanus* and *A. robustus*, may instead be an amalgam of several species must rest on evidence that the hypodigms in question are excessively variable in either, or both, the 'pattern' and the 'degree' of their variability. When the 'degree' of variability in the two hypodigms is compared with that in *A. boisei*, there is apparently no evidence that the variability they subsume is excessive.

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