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A Reappraisal of Variation in Hominid Mandibular Corpus Dimensions

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ABSTRACT The relationship between breadth and height of the mandibular corpus has been investigated in a sample of 77 hominid mandibles. An interspecific allometric increase in robusticity with size occurs between four taxonomic subgroups of *Australopithecus,* but subgroups of *Homo* vary in robusticity while differing little in size. Within taxonomic subgroups, variation in breadth is not significantly related to variation in height among the "gracile" australapithecines; however, it is isometrically related to height in the "robust " australopithecines and bears an allometric relationship to height in *Homo.* Thus, robusticity, in conjunction with size, may provide a useful indicator of the taxonomic affinities of hominid mandibles.

Wolpoff (1977) investigated the relationship between the height and breadth of the mandibular corpus at M_1 by examining data from 43 adult early hominid mandibles from sites in south, east, and northeast Africa. He noted both a high degree of heterogeneity in the data and that this heterogeneity was not significantly reduced in a taxonomically and geographically restricted subsample of australopithecine mandibles from Koobi Fora. Correlation surface regressions of breadth on height for the raw and logarithmically transformed data were calculated, yielding the following solutions: $B = 0.83\ (H) - 7.45$ from regression of the raw data and $B = 0.201\ (H)^{1.316}$ from regression of the log-transformed data.

The negative intercept of the linear regression and the positive allometric exponent of the regression of the log-transformed data were taken as evidence that robusticity increased with size in these mandibles. Separate linear regressions of the Koobi Fora australopithecines, and of male and female subsamples of the total data, gave results similar to those derived from the complete data. No error estimates were provided for the regression coefficients; thus, the null hypothesis of isometry between breadth and height was not shown to be invalid. Nevertheless, Wolpoff concluded that variation in robusticity *"is an artifact of a single scaling process applied across a wide size range"* and that *"variation in this index does not, by itself, indicate the mixture of taxonomically distinct groups"* (Wolpoff, 1977, p.6). This evidence presumably formed the basis for the suggestion that it was corpus size, rather than corpus proportion (robusticity), that was adaptively significant among the Hominidae. The present study, which includes European and Asian material and incorporates African fossils discovered since 1977, attempts to replicate Wolpoff's findings on a larger sample of 77 adult hominid mandibles.

MATERIALS AND METHODS

Measurements of the mandibular corpus at M_1 were taken from Wood (in preparation) and White and Johanson (1982): many of the mandibles in Wolpoff's analysis have been included in this study and are indicated by an asterisk in Table 1. Where left and right mandibles of the same individual were available, only measurements of the left side were used. The taxonomic attribution of specimens generally follows that of White (1977) and Howell (1978) with the exception that whereas Omo 860 is referred by White and

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TABLE 1. Mandibular corpus measurements (asterisk indicates a specimen included in Wolpoff [1977])[1]

Gracile australopithecines

A. afarensis (n = 11)					*A. africanus* (n = 4)				
Specimen	Br	Ht	Rob	Area	Specimen	Br	Ht	Rob	Area
AL 145-35	21.1	27.8	76	461	*Sts 36	20	36	56	565
*AL 198-1	15.8	31.1	51	386	*MLD 18	20.5	34	60	547
AL 207-13	18.1	28.4	64	404	*MLD 34	19.5	32	61	490
*AL 266-1	21.7	30.5	71	520	*MLD 40	23.5	36	65	664
AL 277-1	17.9	37.0	48	520					
*AL 288-1	17.1	30.0	57	403					
AL 333-1	19.2	35.5	54	535					
AL 333-12	17.4	30.6	57	418					
AL 333-32	23.6	38.4	61	712					
AL 400-1	18.7	35.4	53	520					
LH 4	19.2	31.4	61	474					

Robust australopithecines

A. boisei (n = 24)					*A. robustus* (n = 5)				
Specimen	Br	Ht	Rob	Area	Specimen	Br	Ht	Rob	Area
*ER 403	30.5	47	65	1126	SK 6	24	37.5	64	707
*ER 725	29.5	41	72	950	*SK 12	33	44	75	1140
*ER 726	30	46	65	1084	*SK 23	24.5	37	66	712
*ER 727	24	35	69	660	*SK 34	22	40	55	691
*ER 728	26	37	70	756	*TM1517	24	35	69	660
*ER 729	29	43.5	67	991					
*ER 733a	27	39.5	68	838					
*ER 801	29.5	43.5	68	1008					
*ER 805	29	41	71	934					
*ER 810a	26	40	65	817					
*ER 818	36	50	72	1414					
*ER 819	27	38	71	806					
*ER 1468	36	48	75	1357					
*ER 1469	37	46	80	1337					
*ER 1482	20	31	64	487					
ER 1803	25	42	59	825					
ER 1806	29	44	66	1002					
ER 3229	28	39	72	858					
ER 3230	28	42	67	924					
ER 3729	28	38	74	836					
*Peninj 1	30	40.5	74	954					
*Omo 18	26	35	74	715					
*Omo 74	25	43.5	57	854					
*Omo 7	36	48	75	1357					

Homo

East African (n = 17)					N. Africa/Asia/Europe (n = 15)				
Specimen	Br	Ht	Rob	Area	Specimen	Br	Ht	Rob	Area
*ER 730	19	31.5	60	470	Sangiran 1B	16.5	35.8	46	464
ER 731	19	27	70	403	Sangiran 5	20	38	53	597
*ER 817	18	29	62	410	Sangiran 8	20	35.5	56	558
*ER 992	20	31	64	487	Sangiran 9	23	36	64	650
*ER 1483	26.5	39.5	67	822	Peking AII	15.2	25.6	59	306
*ER 1501	17	29	59	387	Peking GI	16.4	34	48	438
ER 1801	20	34	59	534	Peking HI	15.4	26	59	314
ER 1802	23	38	60	686	Ternifine 1	19	36	53	537
ER 1805	21	30	70	495	Ternifine 2	17	35	49	467
ER 3731	18	30	60	424	Ternifine 3	19	38	50	567
ER 3734	19.5	33	59	505	Arago II	15.5	30	52	365
*OH 13	18	26.5	68	375	Arago XIII	22	32.5	68	562
OH 22	21	28.5	74	470	Mauer	22	34.3	64	593
OH 23	21	33	64	544	Sidi Abder.	17	34.5	49	461
*OH 37	19.5	32	61	490	Montmaurin	16	31	52	390
BK 67	17	33	51	441					
BK 8518	21	30	70	495					

Incertae Sedis (n = 1)				
Specimen	Br	Ht	Rob	Area
Omo 860	21.5	35.5	61	599

[1]Br, breadth; Ht, height; Rob, robusticity.

TABLE 2A. Summary statistics and regressions: All mandibles

	Present study (n = 77)			Wolpoff (1977) (n = 43)		
	Mean	S.D.	C.V. (%)	Mean	S.D.	C.V. (%)
Breadth	22.7	5.42	24	24.5	5.3	21
Height	35.8	5.70	16	38.3	6.4	17
Robusticity	62.9	8.02	13	63.7	7.0	11
	Slope	S.D.	95% Intervals	Slope	S.D.	95% Intervals
Regression log (Br) on log (Ht)	1.20	.093	1.01 to 1.38	1.32[1]	—	—

TABLE 2B. Summary statistics and regressions: Comparison of Australopithecus *with* Homo

	Australopithecus (n = 44)			*Homo* (n = 32)		
	Mean	S.D.	C.V. (%)	Mean	S.D.	C.V. (%)
Breadth	25.3	5.56	22	19.1	2.58	13
Height	38.3	5.69	15	32.4	3.72	11
Robusticity	65.6	7.53	11	59.4	7.49	13
	Slope	S.D.	95% Intervals	Slope	S.D.	95% Intervals
Regression log (Br) on log (Ht)	1.27	0.11	1.04 to 1.50	0.54	0.18	0.17 to 0.91

TABLE 2C. Summary statistics and regressions: Comparison of "gracile" with "robust" australopithecines

	"Gracile" australopithecines (n = 15)			"Robust" australopithecines (n = 29)		
	Mean	S.D.	C.V. (%)	Mean	S.D.	C.V. (%)
Breadth	19.6	2.25	11	28.2	4.27	15
Height	32.9	3.30	10	41.1	4.56	11
Robusticity	59.7	7.40	12	68.6	5.62	8
	Slope	S.D.	95% Intervals	Slope	S.D.	95% Intervals
Regression log (Br) on log (Ht)	0.41	0.29	−0.22 to 1.04	1.10	0.14	0.81 to 1.39

[1]Derived using correlation surface regression.

Howell to *Australopithecus boisei* and *A. africanus,* respectively, we have regarded it as *incertae sedis.* This is because of its apparently primitive premolar root morphology (Abbott and Wood, in press) and because the computed crown area of the preserved M_2 crown in this specimen is outside the range of *A. boisei* and *A. africanus* (Wood and Abbott, 1983). All the Koobi Fora australopithecines, together with the Peninj mandible and three of the four Omo mandibles, are regarded as *A. boisei* for the purposes of this study. Corpus cross-sectional area has been estimated by treating the corpus section as an ellipse, and using the formula Ht × Br × $\pi/4$. Simple data parameters (e.g., mean, S.D., etc.) were calculated using the raw data of the whole sample and of the subgroups; least-squares regression and allometry coefficients were computed using logarithmically transformed data. The present sample is larger than Wolpoff's, and contains a larger proportion of *Homo,* mainly as a result of including European and Asian hominids in the sample.

RESULTS

Summary statistics of the mandibular corpus data are given in Table 2. In Table 2A, Wolpoff's data are compared to the present sample. The coefficients of variation of breadth and height are similar in the two data sets; the marginally lower means of breadth and height in the present study probably reflect the inclusion of more *Homo*

specimens. The regression of log (breadth) on log (height) has a slope of 1.20. Though less than the value derived by Wolpoff, the slope is significantly greater than unity, and thus positive allometry between breadth and height is confirmed. However, subdivision of the data by taxa reveals that whereas in *Australopithecus* the relationship between breadth and height is positively allometric, in *Homo* the relationship between breadth and height is negatively allometric (Table 2B). Furthermore, the two "gracile" taxa within *Australopithecus* exhibit no significant covariation between breadth and height, whereas the "robust" australopithecines show a significant relationship between breadth and height (Table 2C). However, the 95% confidence intervals of the slope of the logarithmic regression of the "robust" australopithecines include unity; thus, the null hypothesis of isometry is not invalidated for the latter group.

Thus, within taxonomic subgroups of the present sample, the relationship of breadth to height varies from being non-significant ("gracile" australopithecines), to being significant, but isometric ("robust" australopithecines) and to being significantly allometric *(Homo)*. The apparent positive allometry between breadth and height, observed in the combined sample, is attributable to variation between, rather than within, taxa. To illustrate this, robusticity indices and elliptical cross-sectional areas are given for six taxonomic subgroups in Table 3 and Figure 1. There is a clear trend for robusticity to increase with corpus size amongst the four australopithecine taxa, and the relationship is indeed positively allometric (Table 2B). Specimens assigned to the genus *Homo* have been subdivided into East African and North Africa/Asia/Europe groups. This emphasises the greater robusticity of East African *Homo,* and avoids the recognised difficulty of classifying the latter remains at the species level (Wood, 1985a). It is of interest that while the difference in corpus size between these subgroups of *Homo* is negligible, the proportional difference in robusticity between them is virtually as great as that found between *A. boisei* and *A. afarensis,* which (in terms of the mandibular corpus) are, respectively, the most robust and the most gracile species of *Australopithecus.*

More detailed analysis of the "robust" australopithecine mandibles suggests that jaw

TABLE 3. Robusticity and cross-sectional area for the six hominid subgroups

	A. afarensis (n = 11)		A. robustus (n = 5)		E. African *Homo* (n = 17)		A. africanus (n = 4)		A. boisei (n = 24)		Other *Homo* (n = 15)	
	Robusticity	Area	Robusticity	Area	Robusticity	Area	Robusticity	Area	Robusticity	Area	Robusticity	Area
Mean	59.4	487	65.8	782	63.5	496	60.5	567	69.2	954	54.8	485
S.D.	8.5	93	7.3	201	5.7	111	4.0	73	5.2	232	6.6	107
C.V.	14%	19%	11%	26%	9%	22%	7%	13%	8%	24%	12%	22%

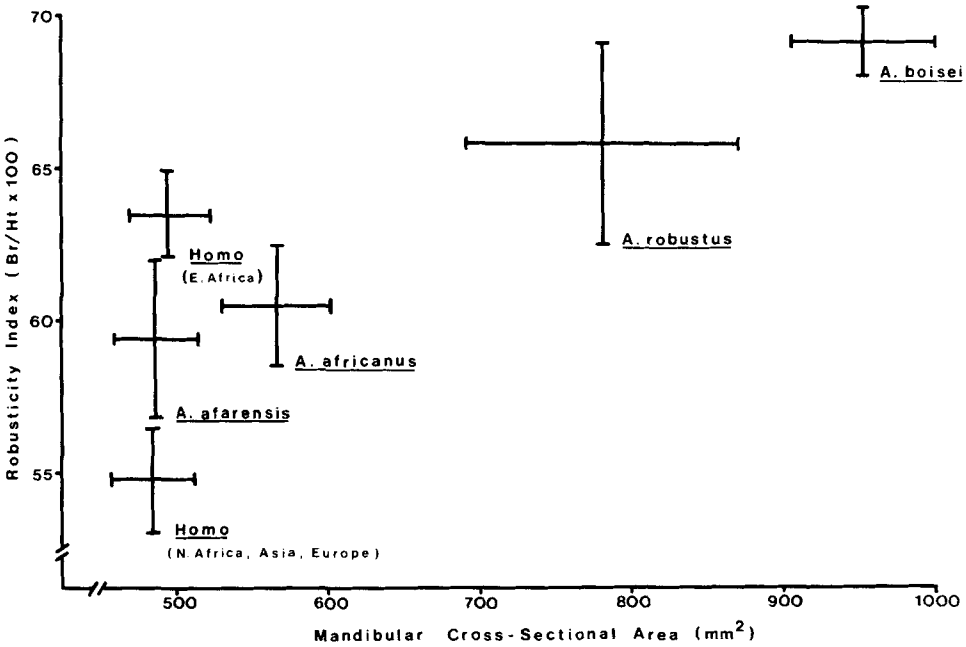

Fig. 1. Mandibular robusticity versus cross-sectional area (means ± S.E.) for the six hominid taxa.

size (expressed as the corpus cross-sectional area) is bimodally distributed in both *A. boisei* and in the much smaller sample of *A. robustus* (Fig. 2). We consider this pattern to reflect sexual dimorphism. Although there is no statistical test for bimodality, the distribution of robusticities in the "male" and "female" subgroups of each species can be seen to follow the australopithecine interspecific trend of increased robusticity with size (Fig. 3) and the estimated degree of dimorphism is similar in each species as is the proportion of "female" to "male" mandibles. A high degree of dimorphism has been proposed for the crania of *A. boisei* (Wood, 1981, 1985b). We estimate the dimorphism in the jaw area to be 61% in *A. robustus* and 66% in *A. boisei* (dimorphism is defined as female/male expressed as a percentage). For comparison, the corresponding measurements on the mandibles of extant primates noted for their dimorphism give values of 77% for *Gorilla* and 68% for *Papio* (Wood, 1975). The overrepresentation of "females" in the fossil sample requires some comment: differential predation and unequal socionomic sex ratios are two possible explanations.

DISCUSSION

The findings of this study contradict those of Wolpoff (1977). In particular there is no evidence for a single scaling process relating robusticity to size among this sample of hominid mandibles. Within the genus *Australopithecus,* there is a clear trend for robusticity to increase with corpus size between species (and perhaps between sexes in the "robust" species *A. robustus* and *A. boisei*). Conversely, within *Homo* there is a marked difference in mean robusticity between early (East African) and later populations, despite there being little variation between these groups in mean corpus size. Biomechanical analysis suggests that while the principal stress regime in the primate mandibular corpus is in the sagittal plane, the shape of the corpus in cross-section is determined by the need to resist a combination of vertical, horizontal, and torsional forces generated in mastication (Hylander, 1979; Smith, 1983). The pattern of increasing robusticity with corpus size, which we observe between the species of *Australopithecus,* is also apparent in data from a wider study of extant primate species

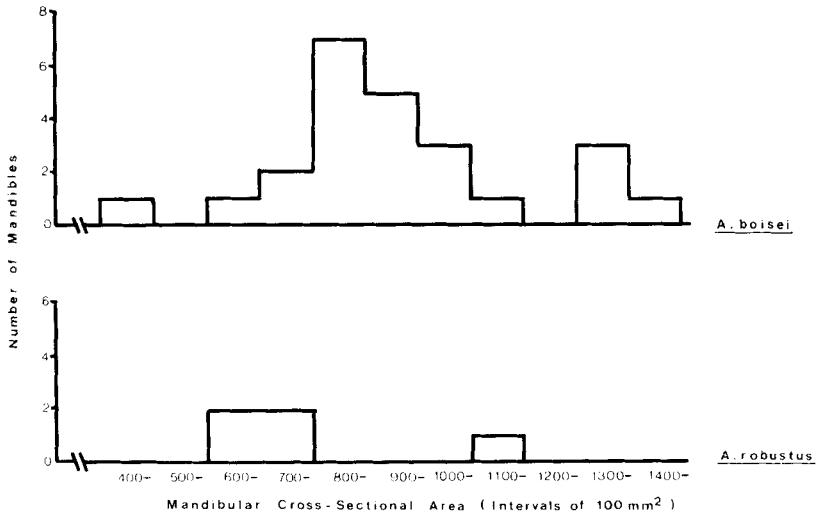

Fig. 2. Mandibular cross-sectional area in *A. boisei* and *A. robustus.*

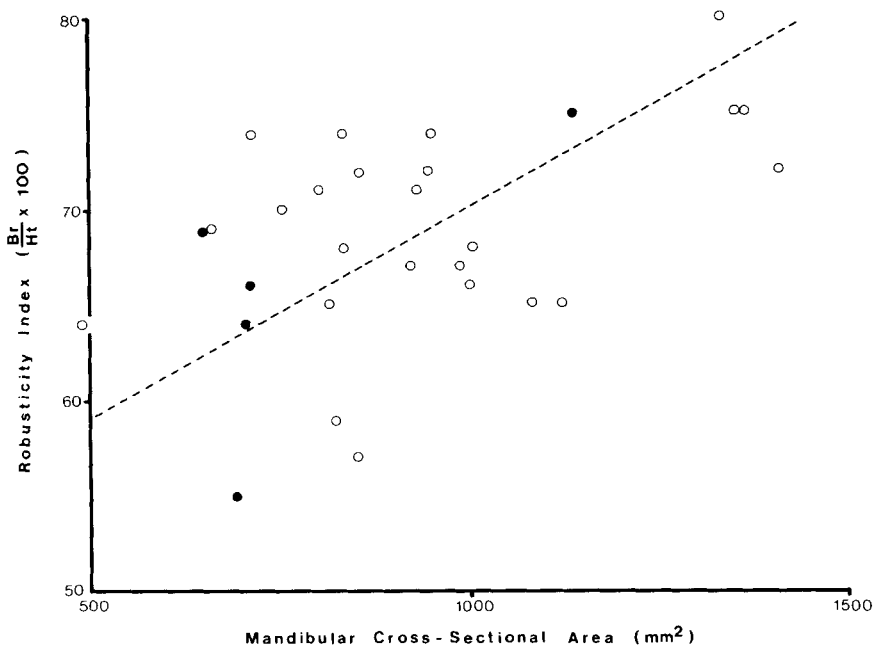

Fig. 3. Robusticity and cross-sectional area at M_1 in 29 "robust" australopithecine mandibles. Open circles indicate *A. boisei;* solid circles, *A. robustus.* The dashed line is the interspecific trend of robusticity with size in all four species of *Australopithecus* (i.e., *A. afarensis, A. africanus, A. robustus* and *A. boisei*).

(Smith, 1983). In the latter study it is notable that while robusticity increased with body size, there was no correlation between robusticity and diet. We must, therefore, accept as the null hypothesis that within *Australopithecus* the differences in mandibular robusticity between species, and perhaps between sexes in the "robust" taxa, are determined by the requirements for geometric scaling to body size rather than by differences in dietary adaptation. Within *Homo,* the mandible exhibits changes in proportion with little

change in size. Body weight, however, is believed to have increased from early East African "habilines" to later *H. erectus* and *H. sapiens* forms (McHenry, 1982). It is tempting to speculate that within *Homo* dietary diversification, with or without diathermic food preparation, has allowed a more gracile mandible to accompany an increase in body size. Others have associated variations in the degree of tooth wear with different cultural patterns of food preparation (Brace, 1962; Smith, 1984), and it would be intriguing to know if the size and robusticity of the mandible were related to cultural practices in recent and sub-recent populations.

The pattern of sexual dimorphism in corpus robusticity within the two "robust" australopithecine taxa, with the presumed males (on the basis of corpus size) having more "robust" mandibles, is notable because it is the reverse of the tendency observed in extant primate taxa (Wood, 1975). One of us has argued elsewhere that evidence of sexual dimorphism must rely on analogies with patterns of dimorphism in extant taxa (Wood, 1979). However, in this case two lines of evidence are in conflict: cross-sectional area follows the extant model (males larger than females), but the pattern of robusticity does not. The explanation may relate to the absolutely and relatively small canines in the "robust" australopithecines, for the extant primate taxa that have more gracile male mandibles are those in which the canines are relatively larger and dimorphic (Kay et al., 1981). In such male mandibles it may be that the length of the canine root determines the height, and thus the proportions, of the mandibular corpus (Wood, 1978; Smith, 1983). It is noteworthy that modern humans, with their absolutely and relatively smaller canines, show either no dimorphism in robusticity, or are dimorphic, but with males having more robust mandibular corpora than females (Wood, 1975).

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