J. Anat. (1991), **174**, pp. 185–205
With 6 *figures*
Printed in Great Britain

Intraspecific variation and sexual dimorphism in cranial and dental variables among higher primates and their bearing on the hominid fossil record

B. A. WOOD, YU LI AND C. WILLOUGHBY

Hominid Palaeontology Research Group, Department of Human Anatomy and Cell Biology, The University of Liverpool, PO Box 147, *Liverpool, L*69 3*BX, UK*

(*Accepted* 18 *July* 1990)

INTRODUCTION

Information about the manner and extent of skeletal and dental variation within extant primate taxa plays an important role in efforts to increase our general understanding of both living and fossil primates. For example, skeletal and dental dimorphisms have proved to be variably reliable indicators of social structure and habitat (Leutenegger & Kelly, 1977; Clutton-Brock & Harvey, 1977; Leutenegger, 1978; Harvey, Kavanagh & Clutton-Brock, 1978; Leutenegger, 1982; Leutenegger & Cheverud, 1982; Jungers, 1985; Leutenegger & Lubach, 1987), and their predictive value has been exploited to reconstruct the probable social organisation of ancient primate communities (e.g. Fleagle, Kay & Simons, 1980).

A knowledge of intraspecific variation is also of value to those engaged in taxonomic analysis. It is an important, if not the primary, task of palaeontologists to make judgements about the significance of the variation they observe within the fossil record. Decisions have to be made as to the likelihood that the remains being studied can be subsumed within a single taxon, or whether the extent of the observed variation demands that several taxa need to be recognised. Palaeontologists have tended to draw on modern analogues to provide a guide to acceptable levels of variation (e.g. Tattersall, 1986, p. 166). These analogues are usually chosen for their genetic propinquity to the study group. While the exact nature of the relationship between modern *Homo sapiens* and the non-human African primates is being debated (see below), there is, nonetheless, abundant evidence to suggest that *Homo*, *Pan* and *Gorilla* comprise a clade distinct from other living primates. This close relationship suggests that it is variation observed within these three taxa which is likely to be the most relevant yardstick for assessing the significance of variation within the hominid fossil record.

Although one can detect a growing consensus about the broad categories of early hominid taxa, there is still vigorous debate about the significance, taxonomic or otherwise, of the variability of remains subsumed within taxa such as *Australopithecus afarensis*, *Australopithecus boisei* and *Homo habilis*. Despite their involving three quite distinct sets of fossil data, all three problems of interpretation hinge on a single question, namely, how much variation is it sensible to tolerate within a single hominid taxon? Clearly, if the members of these three hominid taxa could be identified because they possessed one or more unique features, then there would be less need to seek external criteria for assessing an acceptable degree of intraspecific variation. However, while it may be possible to define *A. boisei* in this way (Wood & Chamberlain, 1987;

Wood, 1991), the definition of the other two taxa is a more complex task than the recognition of autapomorphies (Cracraft, 1981; Wood, 1984, 1989). Thus, there is a pressing need to identify any extant analogues which could help in the task of defining hominid species boundaries.

A third reason for learning more about the nature of intraspecific variation concerns attempts to resolve the phylogenetic relationships between living higher primates. For, while there is strong evidence to suggest that *Homo*, *Pan* and *Gorilla* form a clade distinct from *Pongo* (Andrews, 1987), data which range from traditional morphological observations (Groves, 1986; Andrews, 1988) to information about DNA hybridisation (Sibley & Ahlquist, 1987) and sequencing data (Hasegawa, Kishino & Yano, 1987; Ueda, 1988; Miyamoto *et al.* 1988) have yet to provide conclusive evidence about relationships within the African ape and *Homo* clade. We would contend that the extent and manner in which the members of a taxon vary, in other words the 'structure' of the intraspecific variation, are as much an inherited aspect of the taxon's phenotype as are the form of its teeth or the configuration of its limb bones. That being so, and as long as this internal variation is not obviously especially prone to the confounding effects of convergent evolution, then the pattern of sexual dimorphism is a character that can properly be used as part of the evidence which can be submitted to phylogenetic analysis. Indeed, Oxnard (1987) has pioneered the use of intraspecific variation as a potentially taxonomically valent character (see below).

Until recently, intraspecific variation has been described and assessed relatively crudely. Studies have demonstrated that variation within higher primate taxa can be related, indirectly or directly, to individual variation, geographical variation, often recognised at subspecific level (Groves, 1970, 1986; Courtenay, Groves & Andrews, 1988) and sexual dimorphism. The most telling evidence for the later influence comes from multivariate studies that show that sexual differences apparently dominate those principal components and canonical variates which account for the majority of the within-group variance (e.g. Lieberman, Gelvin & Oxnard, 1985). There is now also evidence to refute the assumption that whereas taxa differ mainly in shape, sexes differ almost exclusively in size (e.g. Van Gerven, 1972). Wood (1976) investigated the basis of dental and skeletal sexual dimorphisms in five catarrhine taxa and showed that sex-discriminating principal components in three higher primate taxa incorporated both size and shape information. Wood (*ibid*) commented on how the pattern of difference in the mean values of individual variables varied between taxa, as well as on apparent sex differences in variance. However, these observations were neither emphasised or pursued, and it was an implicit conclusion of the earlier study that differences in sexual dimorphism between taxa were mainly quantitative and not qualitative.

Oxnard and his colleagues (Wu & Oxnard, 1983; Oxnard, Lieberman & Gelvin, 1985; Lieberman *et al.* 1985; Oxnard, 1987) have subsequently reported studies of dental measurements, taken on much larger samples of higher primates, which apparently show evidence of systematic differences in both means and variances between the sexes. This led them to recognise three apparently distinct patterns of sexual dimorphism. One pattern was seen in *Pongo*, which showed large differences in mean values and none in variances, whereas *Pan* and *Gorilla* exhibited dimorphisms in both means and variances. *Homo sapiens* constitutes the third pattern, with little dimorphism in mean values and no sex differences in sample variances. If the existence of these differences in patterns is confirmed, this would have important implications for palaeontological analysis. For example, which, if any, of the three patterns would be the relevant analogue for assessing variation within fossil hominid taxa? Also, if both qualitative and quantitative differences in sexual dimorphism do exist in higher primates, the tasks of deducing the primitive condition for sexual dimorphism for the great ape and *Homo* clade, and thus predicting its likely expression in the earliest hominids, would be a more complex undertaking than formerly anticipated (Wood, 1985). Thus, for the foregoing series of interconnected reasons, we believe it is an appropriate time to re-examine the nature of sexual dimorphism in higher primate taxa.

The present investigation is based on an expanded sample (Wood, 1976) of *Homo sapiens*, *Pan troglodytes*, *Gorilla gorilla* skeletons, augmented by a sample of *Pongo pygmaeus* skeletons; the sex of all the material used in this analysis is well authenticated from field records. All the skeletal collections are either geographically circumscribed (*Homo sapiens* from Southern Africa), or sample a subspecies only, *Pan troglodytes verus*, *Gorilla gorilla* (Lowland) and *Pongo pygmaeus* (Bornean). A further study is in progress that will explicitly compare the nature and extent of the geographical, subspecific and sexual effects on intraspecific variation.

The present study has several objectives. The first is the documentation of any statistically significant differences in means and distributions between single sex samples of each of the four taxa. The second is to test the hypothesis that any differences in sexual dimorphism between the taxa are qualitative as well as quantitative. The third, and final, objective relates to the use of analogues as tools for assessing the significance of variation in fossil samples. Is intraspecific variation in living groups closely related to hominids qualitatively different from interspecific variation? Do some variables show significant differences within taxa, while differing little between taxa? Conversely, are there variables which are consistently different between taxa, but which seldom vary significantly within taxa, i.e. between the sexes? If some variables consistently appear in either category, this finding would be of potential use to those engaged in hominoid and hominid taxonomy.

MATERIALS AND METHODS

Specimens were chosen using the criteria adopted by Wood (1975). The critical requirement was that individuals were sexed by non-osteological criteria, that is, independently of skeletal and dental characters. Only material sexed in the field, or prior to the preparation of the bones, was analysed for "the logical frailty of using sexual attributions based on osteological or dental criteria to establish the extent of osteological and dental sexual dimorphism is obvious" (Wood, 1976, p. 16). Only specimens with erupted upper and lower third molars were included. Skulls with substantial areas of damage, or those affected by pathological distortions, were not included in the investigation.

The following samples were included in the study.

(1) *Homo sapiens*. Modern human skeletons from the dissecting rooms of the Department of Anatomy and Human Biology of the University of the Witswatersrand. The sample was made up of Bantu-speaking Negroes of the Nguni and Sotho tribes (Wood, 1975).
Total: 40 males/35 females.

(2) *Gorilla gorilla gorilla*. A sample from the Powell-Cotton Museum, Birchington, Kent (Wood, 1975) was supplemented by appropriate specimens from the following institutions: The British Museum (Natural History), London; Rijksmuseum von Natuurlijke Historie, Leiden; Liverpool Museum, Liverpool;

Department of Human Anatomy and Cell Biology, The University of Liverpool; Department of Zoology, Edinburgh University; The Royal Museum of Scotland, Edinburgh.

Total: 34 males/30 females.

(3) *Pan troglodytes verus*. A sample from the Powell-Cotton Museum, Birchington, Kent (Wood, 1975) was supplemented by appropriate specimens from the institutions listed in sample (2).

Total: 18 males/33 females.

(4) *Pongo pygmaeus pygmaeus*. The sample comprised specimens from Borneo from the institutions listed in sample (2) with the exception of the Powell-Cotton Museum.

Total: 21 males/22 females.

Measurements

A total of seventy nine measurements were made on the 233 skulls used in the study. Thirty five dental measurements (nos. 1–35) were included, of which three were crown heights and the remaining thirty two were the buccolingual and mesiodistal diameters of the upper and lower dentition of the right side. Sixteen measurements (nos. 36–51) were recorded from the mandible and twenty eight (nos. 52–79) were taken on the cranium. All the original measurements taken, together with ten compound variables, are listed in Table 1. Details of the measurement definitions and the appropriate technical protocols are given in Wood (1975, 1976).

Measurements were taken by B.W. and C.W. Techniques were checked and confirmed between the two observers and repeated measurements suggest that interobserver and technical errors were well within 2%, with the exception of the mandibular angle measurement which varied by up to 5% even with the same observer. Overall inter-observer error was no greater than that for repeated measurements made by the same observer. Tooth crown dimensions were taken using specially machined dental calipers and recorded to an accuracy of 0·1 mm. Cranial and mandible measurements were made with sliding calipers and were also recorded to 0·1 mm. Measurements made with spreading or co-ordinate calipers were recorded to 1·0 mm and cranial capacity recordings were rounded up or down to the nearest 10 ml.

Mean values, the standard deviation of the mean, the percentage difference between the male and female values and the coefficient of variation (CV) were computed separately for each sex. The means and variances were compared using, respectively, Student's t and F tests using the appropriate degrees of freedom. Distributions were compared to normal using tests for curve symmetry (skewness) and shape (kurtosis).

The pattern of sexual dimorphism was compared using both univariate and multivariate techniques. For the former, the percentage dimorphisms of variables were compared within their regional groupings, e.g. teeth, mandible and cranium. Pattern differences were compared in the multivariate sense using principal components analysis (PCA) computed using both raw and logarithmically transformed data. Differences in intraspecific variation between taxa were examined by comparing the variable loadings for those principal components that are apparently good sex discriminators. The results presented in the next section relate to PCA based on a correlation matrix, but similar results were also obtained using a covariance matrix. In addition to this examination of between-sex variation, the original and logarithmically transformed data for the separate sexes of each taxon were specified as groups for canonical variates analysis (CVA). Analyses of extant remains which include many variables from several different regions of the skull are of limited use to

Table 1. *List of the* 79 *measurements and ten computed variables making up the total of* 89 *variables included in the study*

Variable No.		Measurement	Variable No.	Measurement
1.	I^1	Labiolingual (L/L) diameter	50.	Maximum mandibular length
2.		Mesiodistal (M/D) diameter	51.	Lower intercanine distance
3.	I^2	Labiolingual (L/L) diameter	52.	Orbital breadth
4.		Mesiodistal (M/D) diameter	53.	Orbital height
5.	C	Labiolingual (L/L) diameter	54.	Interorbital breadth
6.		Mesiodistal (M/D) diameter	55.	Biorbital breadth
7.		Labial crown height (LH)	56.	Nasion – rhinion
8.	P^3	Buccolingual (B/L) diameter	57.	Nasion – nasospinale
9.		Mesiodistal (M/D) diameter	58.	Maximum nasal width
10.	P^4	Buccolingual (B/L) diameter	59.	Nasospinale – prosthion
11.		Mesiodistal (M/D) diameter	60.	Bijugal breadth
12.	M^1	Buccolingual (B/L) diameter	61.	Outer alveolar breadth at M^3
13.		Mesiodistal (M/D) diameter	62.	Bizygomatic breadth
14.	M^2	Buccolingual (B/L) diameter	63.	Upper intercanine distance
15.		Mesiodistal (M/D) diameter	64.	Palate length
16.	M^3	Buccolingual (B/L) diameter	65.	Inner alveolar breadth at M^3
17.		Mesiodistal (M/D/) diameter	66.	Palate depth at M^1
18.	I_1	Labiolingual (L/L) diameter	67.	Depth of infratemporal fossa
19.		Mesiodistal (M/D) diameter	68.	Prosthion – M^3
20.	I_2	Labiolingual (L/L) diameter	69.	Glabella – opisthocranion
21.		Mesiodistal (M/D?) diameter	70.	Minimum postorbital breadth
22.	C	Labiolingual (L/L) diameter	71.	Basion – bregma
23.		Mesiodistal (M/D) diameter	72.	Maximum biparietal width
24.		Labial crown height (LH)	73.	Biporionic width
25.	P_3	Buccolingual (B/L) diameter	74.	Mastoid length
26.		Mesiodistal (M/D) diameter	75.	Coronale – coronale
27.	P_4	Buccolingual (B/L) diameter	76.	Opisthion – inion
28.		Mesiodistal (M/D) diameter	77.	Bimastoid width
29.	M_1	Buccolingual (B/L) diameter	78.	Posterior skull length
30.		Mesiodistal (M/D) diameter	79.	Cranial capacity
31.	M_2	Buccolingual (B/L) diameter	80.	Computed upper canine base area (5·6)
32.		Mesiodistal (M/D) diameter		
33.	M_3	Buccolingual (B/L) diameter	81.	Computed lower canine base area (22·23)
34.		Mesiodistal (M/D) diameter		
35.	Maximum cusp height		82.	Length of upper premolar row (9+11)
36.	Vertical height of condylar process		83.	Sum of computed lower premolar crown base areas (8·9)+(10·11)
37.	Bicondylar breadth			
38.	Vertical height		84.	Length of lower premolar row (26+28)
39.	Bicoronoid breadth			
40.	Width of condylar head		85.	Sum of computed lower premolar crown base areas (25·6)+(27·28)
41.	Anteroposterior diameter of condylar head		86.	Length of upper molar row (13+15+17)
42.	Maximum breadth of ascending ramus			
43.	Mandibular angle		87.	Sum of computed upper molar crown base areas (12·13)+(14·15)+(16·17)
44.	Bigonial width			
45.	Corpus height at M_1		88.	Length of lower molar row (30+32+34)
46.	Corpus thickness at M_1			
47.	Symphyseal height		89.	Sum of computed lower molar crown base areas (29·30)+(31·32)+(33·34)
48.	Symphysial thickness			
49.	Inner alveolar breadth at M_3			

palaeontologists who have to deal with fragmentary material. Accordingly, where appropriate, analyses and statistics were computed for five subsets of the data, namely all teeth, mandible, cranium, mandible plus mandibular teeth and cranium plus maxillary teeth. The compound variables were included in the study for their potential utility in taxonomic analysis. Only their parameters have been calculated; they played no part in subsequent multivariate analyses.

Table 2. *Significance of the differences in the mean values and variability between separate sex samples*; *t* = *Student's t for means*, '*F*' = *F ratio for variability* *($P = < 0·05$), **($P = < 0·01$).

Var.	Homo		Pan		Gorilla			Pongo	
no.	*t*	F	*t*	F	*t*	F	F	*t*	F
1.	4·52**	1·44	1·14	1·26	5·04**	1·05		2·51*	1·42
2.	4·61**	1·05	1·40	3·62**	2·84**	2·78**		1·41	1·95
3.	3·15**	1·66	1·38	1·55	4·86**	1·25		2·99**	2·32*
4.	2·93**	1·83*	1·31	1·71	2·84**	1·61		1·53	1·08
5.	5·62**	1·90*	10·88**	2·00	14·10**	1·82		6·89**	2·58*
6.	4·05**	1·41	23·55**	1·61	13·33**	2·07*		6·74**	1·98
7.	1·87	1·47	8·56**	2·21*	14·14**	1·92*		4·60**	1·01
8.	4·61**	1·03	3·15**	1·02	4·33**	1·28		2·85**	1·14
9.	3·63**	1·52	1·23	1·10	4·02**	1·03		1·32	1·01
10.	3·41**	1·04	2·38*	1·58	4·64**	1·42		3·43**	1·00
11.	2·37*	1·73	1·59	1·64	2·07*	1·05		3·78**	1·54
12.	3·72**	1·04	0·60	1·11	5·26**	1·46		4·33**	1·10
13	3·58**	1·33	2·60*	2·13*	2·36*	1·31		4·45**	1·17
14.	3·92**	1·54	0·67	1·72	4·05**	1·94*		5·88**	1·08
15.	2·14*	1·15	1·06	1·45	2·35*	1·47		3·91**	1·12
16.	4·52**	2·53**	1·96	1·33	4·88**	1·26		5·26**	1·43
17.	1·68	1·40	2·01*	2·21*	5·00**	1·30		3·58**	1·27
18.	2·79**	1·04	0·85	1·61	4·12**	2·10*		3·11**	1·24
19.	1·80	1·99*	0·85	3·06**	2·97**	1·02		0·55	1·55
20.	2·79**	1·06	0·86	2·28*	4·48**	1·95*		3·69**	1·50
21.	2·13*	1·24	1·66	1·25	2·60*	1·04		1·65	1·24
22.	6·74**	1·64	8·29**	1·72	13·99**	2·03*		6·35**	1·69
23.	4·81**	1·16	8·12**	2·03*	12·85**	1·59		8·26**	2·75*
24.	2·82**	1·57	4·77**	1·07	14·95**	2·03*		3·95**	1·62
25.	3·89**	2·14*	4·54**	2·28*	3·87**	2·08*		1·60	1·47
26.	2·48*	2·01*	2·00	1·41	5·11**	1·05		2·90**	1·08
27.	3·18**	1·33	2·50*	1·00	3·32**	1·55		2·35*	1·18
28.	3·07**	1·82*	2·22*	1·48	3·44**	1·04		2·01*	1·24
29.	3·30**	1·16	2·99**	1·29	3·61**	1·42		3·09**	1·13
30.	3·52**	1·02	2·70*	1·52	2·66**	1·36		3·46**	1·26
31.	4·27**	2·20*	1·85	1·26	3·70**	1·08		4·84**	1·26
32.	2·93**	1·92*	3·63**	1·71	2·69**	1·45		4·43**	1·36
33.	2·36*	1·01	2·18*	1·79	5·03**	1·91*		4·76**	1·37
34.	2·93**	1·32	2·18*	1·86	3·65**	1·71		3·07**	1·40
35.	2·26*	1·04	0·97*	1·09	3·11**	1·04		1·95	1·95
36.	4·93**	1·41	2·55*	1·24	6·94**	2·77**		5·10**	2·13*
37.	6·67**	1·35	3·93**	1·36	8·49**	1·05		4·35**	1·35
38.	4·47**	1·44	2·45*	1·26	8·99**	2·41**		5·59**	1·94
39.	4·68**	1·99*	1·50	1·66	8·26**	1·68		3·65**	1·27
40.	6·52**	1·42	3·33**	1·03	7·34**	1·54		4·53**	1·07
41.	0·28	1·04	0·08	1·89	6·19**	1·21		2·35*	2·32*
42.	3·49**	1·18	2·53*	1·07	11·36**	1·12		5·15**	2·03
43.	1·48	1·58	1·71	1·63	1·68	1·23		0·84	1·59
44.	6·35**	1·65	1·22	1·21	8·04**	1·96*		5·04**	1·42
45.	1·31	1·15	0·57	1·39	6·77**	1·10		3·71**	2·05
46.	1·98	1·69	0·55	1·82	4·68**	2·75**		4·24**	1·36
47.	2·77**	1·50	3·70**	2·30*	9·84**	1·03		5·05**	1·57
48.	2·32*	1·61	1·48	2·09*	6·48**	1·49		3·42**	1·77
49.	2·87**	1·36	0·18	1·30	2·13*	2·64**		2·34*	1·54
50.	4·05**	1·72	1·96	2·23*	13·59**	1·02		5·94**	2·18*
51.	0·47	1·62	1·00	1·33	1·55	1·65		0·98	2·78*
52.	3·83**	1·81*	0·68	1·00	5·43**	1·30		3·16**	1·78
53.	0·53	1·70	0·45	1·59	1·35	1·76		3·28**	1·68
54.	4·93**	1·22	3·43**	1·47	6·32**	2·89**		1·27	2·12*
55.	5·84**	1·92*	2·74**	1·24	9·24**	1·28		3·34**	1·18
56.	0·30	1·34	2·89**	1·14	3·18**	2·40**		2·96**	2·50*

Table 2. (*continued.*)

Var.	Homo		Pan		Gorilla		Pongo	
no.	*t*	F	*t*	F	*t*	F	*t*	F
57.	3·83**	1·21	3·39**	1·06	6·65**	1·37	4·54**	1·82
58.	3·41**	1·60	3·94**	1·66	6·20**	1·88*	4·22**	3·00**
59.	0·49	1·01	0·28	1·12	3·62**	1·73	4·16**	3·18**
60.	6·80**	1·64	4·77**	1·81	11·23**	1·88*	3·83**	1·16
61.	4·17**	1·64	1·27	1·60	5·14**	1·46	4·12**	1·20
62.	8·22**	1·46	6·73**	1·53	10·62**	1·20	5·00**	1·53
63.	3·78**	1·26	0·66	1·72	3·00**	2·04*	2·70**	2·34*
64.	4·07**	1·38	2·73**	1·78	11·49**	1·08	5·72**	3·59**
65.	4·13**	1·09	1·14	1·54	2·46*	1·75	2·46*	1·84
66.	0·26	1·03	2·89**	1·57	1·72	1·58	4·28**	1·59
67.	3·26**	1·01	9·00**	1·87	9·15**	1·81	3·42**	1·63
68.	4·87**	2·05*	2·48*	1·11	7·36**	2·03*	5·19**	1·68
69.	5·94**	1·45	2·15*	1·31	11·74**	2·29*	4·74**	1·64
70.	4·48**	2·03*	0·19	1·16	2·33*	1·14	0·72	1·83
71.	4·47**	1·12	1·00	1·14	6·39**	1·51	3·21**	2·42*
72.	4·10**	1·56	2·11*	1·99	3·20**	1·59	1·78	1·60
73.	3·74**	1·16	0·70	1·02	10·25**	1·10	4·70**	1·24
74.	5·42**	2·35**	1·60	1·05	5·70**	2·06*	1·94	2·08
75.	3·60**	1·05	0·45	1·18	2·98**	1·24	0·68	2·38*
76.	0·85	2·42**	0·86	1·97*	10·31**	3·11**	2·73**	3·21**
77.	6·32**	1·05	4·29**	1·23	7·26**	2·42**	4·57**	2·34*
78.	2·32*	1·97*	0·69	1·93	6·28**	1·31	0·95	1·83
79.	5·94**	1·93*	2·27*	1·06	6·56**	1·94	4·17**	1·69
80.	5·73**	1·75	12.68**	3·29**	14·29**	3·34**	7·08**	2·21*
81.	6·55**	1·66	8·55**	3·15**	14·02**	3·19**	7·47**	1·58
82.	3·58**	1·14	1·58	1·50	3·75**	1·09	2·90**	1·60
83.	4·75**	1·08	2·44*	1·09	4·80**	1·32	3·37**	1·15
84.	3·10**	2·51**	1·44	1·61	4·99**	1·31	2·68**	1·31
85.	3·75**	2·50**	2·50*	1·55	5·33**	1·74	2·40*	1·76
86.	3·01**	1·00	2·00	2·41*	3·75**	1·34	4·62**	1·32
87.	4·17**	1·33	1·89	2·16*	4·63**	1·55	5·42**	1·10
88.	3·89**	1·35	3·06**	1·61	3·69**	1·26	3·97**	1·47
89.	3·97**	1·76	3·06**	1·81	4·50**	1·13	4·51**	1·02

RESULTS

The means, standard deviations and coefficients of variation for each of the 79 original, and ten compound, variables were computed for the separate sex samples; the data were also used to compute a percentage dimorphism index (PDI). The statistical significance of the sex differences in means and dispersions are presented in Table 2. In all four taxa there are more significant differences in mean values of the raw measurements between the sexes than would be expected by chance alone. However, the extent of significant differences in male/female means varies from taxon to taxon. Approximately half the sex differences in *Pan* reach significance at the 95 % level, whereas in *Gorilla* the majority of variables are significantly different; *Homo* and *Pongo* have an intermediate incidence of approximately 80 %. When the incidence of significant differences is broken down into dental, mandibular and cranial categories (Table 3) it is evident that, with two exceptions relating to mandibular variables, the significant differences are distributed proportionally among the anatomical regions. The two exceptions are the relatively lower levels of significant differences in the means of mandibular variables in *Homo* and *Pan*.

When sample variability is compared, the picture is a comparable one overall. All

Table 3. *Percentage of significant differences of means* (*M*) *and variability* (*V*) *for each major regional category of variables.*

	Homo		*Pan*		*Gorilla*		*Pongo*	
	M	V	M	V	M	V	M	V
All measurements (n = 79)	84	23	51	15	95	32	81	22
Teeth (n = 35)	91	26	54	23	100	29	80	9
Mandible (n = 16)	69	6	38	19	88	31	88	25
Cranium (n = 28)	82	29	54	4	93	36	79	36

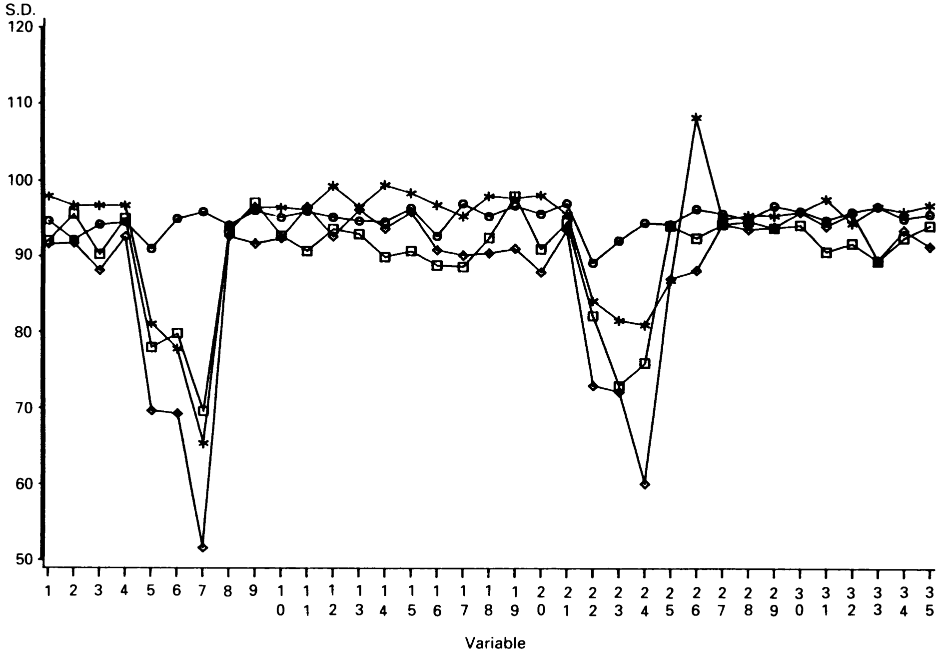

Fig. 1. Plots of the Percentage Dimorphism Indices (SD) for maxillary and mandibular dental measurements (nos. 1–35). *, *Pan*; □, *Pongo*; ◇, *Gorilla*; ○, Homo.

four taxa have more variables with different sex dispersions than would be expected by chance alone. The results for sample dispersions correspond to those of mean differences, with *Pan* (n = 12), *Pongo* (n = 17), *Homo* (n = 18) and *Gorilla* (n = 25) having increasing numbers of variables with dimorphic variance (Table 3). Only two regional subsets of original variables show as many, or fewer, sex differences in sample dispersions than would be expected by chance alone; these are measurements of the *Homo* mandible and the *Pan* cranium (Table 3). The single sex distributions have been tested for departures from a normal distribution with respect to shape (kurtosis) and symmetry (skewness). There were more departures from normality due to shape than would be expected by chance alone, but with the exception of the *Homo* female sample (n = 14), the number of departures was consistently low (n = 7–11). Asymmetrical distributions were, however, more common, especially so in the female samples of *Gorilla* (n = 19) and *Pongo* (n = 27).

The investigation of whether higher primate sexual dimorphisms vary qualitatively as well as quantitatively between taxa was undertaken by comparing patterns of

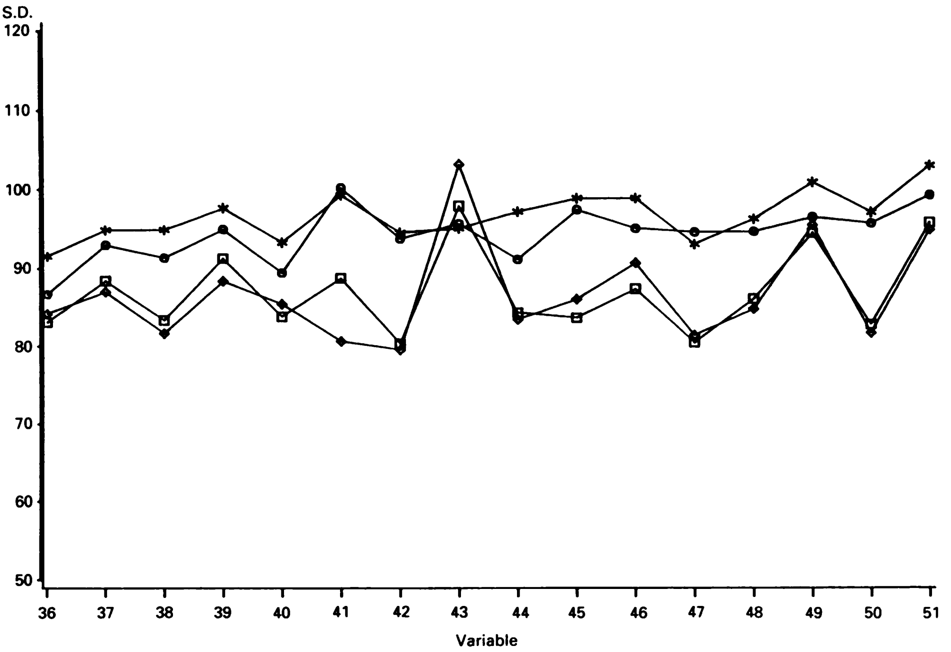

Fig. 2. Plots of Percentage Dimorphism Indices (PDIs) for mandibular measurements (nos. 36–51). *, *Pan*; □, *Pongo*; ◇, *Gorilla*; ○, *Homo*.

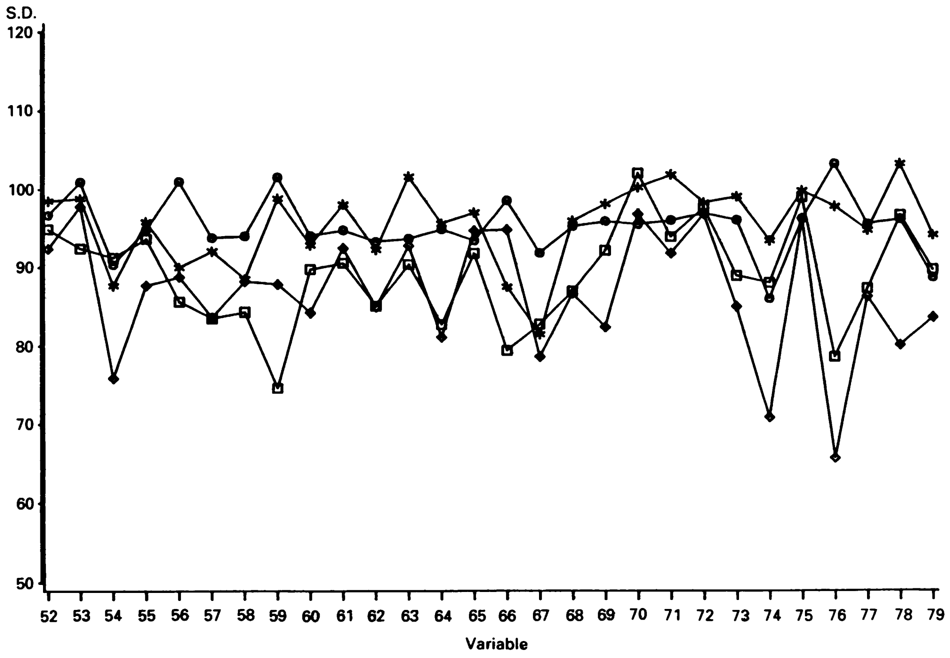

Fig. 3. Plots of the Percentage Dimorphism Indices (PDIs) for cranial measurements. *, *Pan*; □, *Pongo*; ◇, *Gorilla*; ○, *Homo*.

Table 4. *Comparison by taxa of the variables that have the highest loadings of sex-discriminating principal components, computed from a correlation matrix constructed from the raw data*

	Homo	*Pan*	*Gorilla*	*Pongo*
Teeth				
No. of 'sex' PC	I	I	I	I
Variance	49%	40%	57%	61%
Variables with high loadings	31, 5, 25, 14, 27, 12, 8, 29, 32, 26, 33, 6	22, 31, 13, 10, 28, 30, 29, 23, 5, 27, 8	23, 12, 31, 17, 22, 1, 6, 29, 33, 22, 29, 17, 20	32, 16, 31, 14, 33, 6, 10, 12
Mandibles				
No. of 'sex' PC	I	I	I	I
Variance	36%	28%	62%	65%
Variables with high loadings	38, 44, 37, 39, 42, 40	42, 40, 38, 37, 36, 47	50, 47, 38, 40, 37, 42	42, 38, 44, 50, 37, 47
Cranium				
No. of 'sex' PC	I	I	I	I
Variance	38%	32%	49%	52%
Variable with high loadings	62, 60, 55, 69, 79, 61, 70, 77, 54, 74	60, 62, 77, 55, 61, 69, 79, 57, 65, 64	62, 60, 69, 55, 73, 64, 76, 77, 67, 79	62, 73, 77, 64, 55, 60, 69, 59, 67, 68

taxonomic variation as revealed by both univariate and multivariate techniques. The plots of the sexual dimorphism indices for the three major anatomical regions for each taxon are a simple, but effective, means of comparing the nature of the sex differences. The data for the dental variables (Fig. 1) suggest that any qualitative differences are relatively minor, with between-taxon variation mainly evident in the mesiodistal dimensions. *Gorilla*, *Pongo* and *Pan* share a broadly similar pattern of canine sex difference; *Homo* lacks any substantial dimorphism in canine crown height or length. The distributions of the mandibular variables (Fig. 2) apparently form two versions of the same basic pattern, one in *Gorilla* and *Pongo* and the other in *Homo* and *Pan*. The two pairs of plots shadow each other, except for two variables, mandibular angle (V = 43) and inner alveolar breadth (V = 49). The pattern of cranial variation can likewise be subdivided into the same two pairs of taxa with only the variables from the palate and infratemporal fossa departing from the general pattern (Fig. 3).

The pattern of intragroup variation was also examined in a multivariate sense. In the first of these examinations the structure of the groups was compared using principal components analysis. The loadings for each component were examined to see if any one was acting as the primary sex discriminator; in all cases it was PCI. A subroutine then listed the variable loadings on that component in rank order, and the top third for each of the variable subsets (e.g. teeth, mandible and cranium) were extracted and compared between the four taxa. The raw and log-transformed data gave similar results; the results for the raw data are given in Table 4. In the case of the mandible and cranium half of the variables with high loadings appear in the listings for all four taxa; the degree of communality is less for dental variables, for only one third appear in all four taxon lists.

Group structure was also examined in multivariate space using canonical variates analysis; logarithmically transformed data conformed best to the distribution criteria demanded by CVA and results for these data are presented. The locations of the canonical variate means with respect to the first three axes are given in Figures 4–6. The critical comparison to be made is the inclination of the line joining the male and

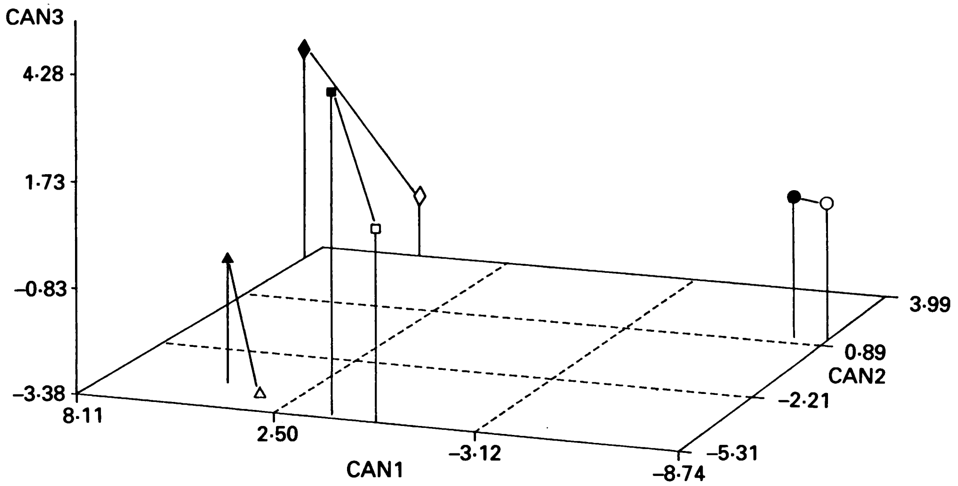

Fig. 4. Plots of canonical variate means for separate male and female samples of the dental measurements from the four extant taxa. ■, *Pan*; ▲, *Pongo*; ◆, *Gorilla*; ●, *Homo*.

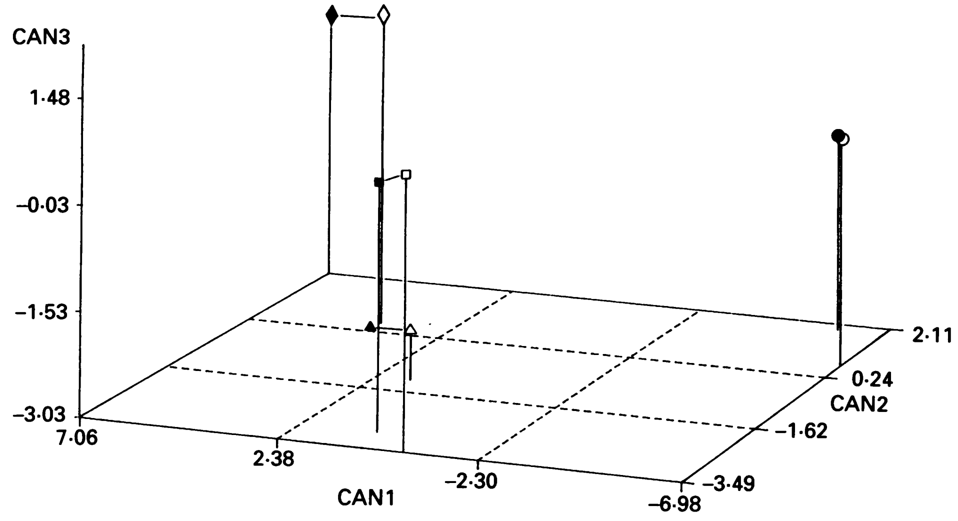

Fig. 5. Plots of canonical variate means for separate male and female samples of the mandibular measurements from the four extant taxa. ■, *Pan*; ▲, *Pongo*; ◆, *Gorilla*; ●, *Homo*.

female means with respect of multivariate space. This has been done by calculating the angles the four slopes make with the first three canonical axes; these are set out in Table 5. It is apparent that for each of the dental, mandibular, and to a lesser extent, the cranial data sets, the lines joining the non-human primate sex means are orientated similarly, and in a direction that differs from the axis that connects the separate sex centroids of *Homo*.

The third objective of the study was to examine and compare the ways in which individual variables differed within and between the sample taxa. This was done by comparing, for each variable, the sums of the squared differences between the taxa with those between the sexes. A ratio of unity indicates that the sums of squares are

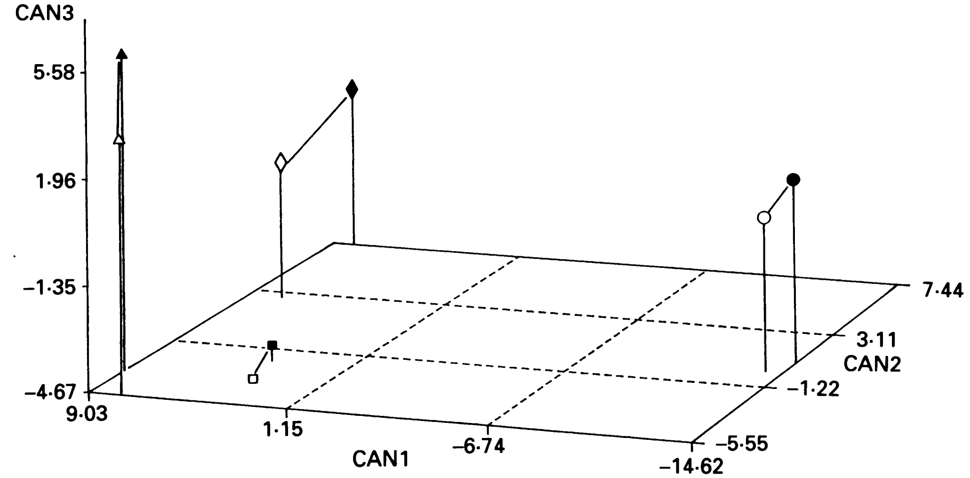

Fig. 6. Plots of canonical variate means for separate male and female samples of the cranial measurements from the four extant taxa. ■, *Pan*; ▲, *Pongo*; ◆, *Gorilla*; ●, *Homo*.

Table 5. *Angles subtended by the canonical axes joining the male and female group means; canonical axes are extracted from a variance–covariance matrix constructed from the logarithmically-transformed data*

	Teeth			Mandible			Cranium		
	I = 69 %	II = 19 %	III = 6 %	I = 79 %	II = 13 %	III = 6 %	I = 79 %	II = 13 %	III = 7 %
Homo	−82·8	1·5	−7·0	−41·5	−46·1	11·8	29·6	−33·6	−42·2
Pan	−24·5	−3·2	−65·3	−61·3	−23·4	15·6	−13·0	−66·0	−19·8
Gorilla	−35·5	8·5	−53·2	−60·5	−27·4	10·1	−6·6	−76·0	−10·5
Pongo	−21·6	−5·9	−67·5	−56·1	−30·8	12·8	−26·5	−36·5	−41·9

N.B. (i) Angles are given with respect to the corresponding canonical variate axes so that 0° is perpendicular to, and 90° parallel to, the respective canonical axis.

(ii) The percentage variance subsumed into each canonical axis is indicated.

equal; less than one, that taxonomic variation exceeds sex variation; greater than one, the converse. Variables with low values are thus likely to be more reliable taxonomic discriminators than variables with ratios that are high (e.g. > 0·4) or which exceed unity. The variables which are highly correlated with the sex-discriminating principal component are unlikely to be variables with a high potential for taxonomic discrimination, and there is considerable overlap between such variables (Table 4) and those with a high F ratio (Table 6). There is a detectable pattern among the variables listed as potentially poor taxonomic discriminators in Table 6. Canine measurements are strongly represented in this category, and it is notable that breadth measurements dominate among the mandibular and cranial variables. In contrast, there is an apparent trend for the mesiodistal diameters of the pre- and postcanine teeth to be above-average taxonomic discriminators.

Table 6. *Comparison of ratios of squared distances between taxa with squared distances between sexes (i.e. 'F' ratio)*

(A) > 0·4 i.e. lower potential for taxonomic discrimination	
Teeth:	C L/L*; C M/D; C CH*; C L/L; C M/D*; C CH*
Mandible:	Bicondylar breadth*; bicoronoid breadth; bigonial width*; maximum mandibular length
Cranium:	Interorbital breadth: biorbital breadth; maximum nasal width*; bijugal breadth; outer alveolar breadth at M^{3*}; bizygomatic breadth*; inner alveolar breadth at M^3; depth of infratemporal fossa; biporionic width; mastoid length*; opisthion-inion; bimastoid width*
(B) < 0·15 i.e. higher potential for taxonomic discrimination	
Teeth:	I^1 L/L; P^3 B/L; P^3 M/D; P^4 B/L; P^4 M/D; M^1 M/D; M^2 M/D; M^3 M/D; I_1 L/L; I_1 M/D; P_3 M/D; P_4 B/L; P_4 M/D; M_1 M/D; M_2 M/D; M_3 M/D
Mandible:	Mandibular angle; lower intercanine distance
Cranium:	Orbital height; nasion-rhinion; upper intercanine distance; minimum postorbital breadth; basion-bregma; maximum biparietal width; coronale-coronale; cranial capacity.

N.B. *indicates an 'F' ratio of > 0·75.

DISCUSSION

Since the important early study by Owen (1848), anatomists and physical anthropologists have continued to explore the nature of intraspecific variation in extant hominoids by taking and collecting measurements from sexed skulls and dentitions. The majority of these investigations have concentrated on documenting the sexual differences occurring within geographically-restricted samples of *Homo sapiens*. The cranium (Fawcett, 1902; Pearson & Davin, 1924; Giles & Elliot, 1963; Crichton, 1966; Howells, 1966; Kajanoja, 1966; De Villiers, 1968; Rightmire, 1970*a*, *b*; Calcagno, 1981; Uytterschaut, 1986), mandible (Martin, 1936; Morant, 1936; Giles, 1964; De Villiers, 1968; Hunter & Garn, 1972) and dentition (Mijsberg, 1931; Yamada, 1932; Seipel, 1946; Selmer-Olsen, 1949; Thomsen, 1955; Moorrees, 1957; Moorrees, Thomsen, Jensen & Yen, 1957; Barrett, Brown, Arato & Ozols, 1964; Jacobson, 1968) have usually been studied separately, although a few investigators (e.g. Wood, 1975, 1976) have included all three regions within the same study.

While relatively large numbers of studies of non-human primates have recorded the measurements of males and females separately, much smaller numbers have incorporated samples which are reliably sexed, large enough to provide a reliable estimate of population parameters, or which contain data from more than one or two variables. Numerous studies of *Pan troglodytes* satisfy two or more of these criteria (Hrdlicka, 1923; Gregory & Hellman, 1926; Schultz, 1940; Ashton & Zuckerman, 1950; Schuman & Brace, 1954; Ashton, 1956, 1957; Remane, 1960; Pilbeam, 1969; Mahler, 1973; Robinson & Steudel, 1973; Almquist, 1974; Fenart & Deblock, 1974; Wood, 1976; Dierbach, 1986; Luboga & Wood, 1990). Other studies have given comparable information for *Pan paniscus* (Johnson, 1974; Luboga & Wood, 1990), *Gorilla gorilla* (Randall, 1943; Ashton & Zuckerman, 1950; Ashton, 1956, 1957; Remane, 1960; Schultz, 1962; Pilbeam, 1969; Booth, 1970; Greene, 1973; Frayer, 1973; Mahler, 1973; Robinson & Steudel, 1973; Wood, 1976; McCown, 1982; Sakka, 1985; Schmid & Stratil, 1986), and for *Pongo pygmaeus* (Hrdlicka, 1923; Gaul, 1933; Schultz, 1941; Hooijer, 1948; Ashton & Zuckerman, 1950; Remane, 1960; Schultz, 1962; Mahler, 1973; Robinson & Steudel, 1973; Winkler, Conroy & Vannier, 1988; Leutenegger & Masterson, 1989).

The vast majority of these studies are relatively straightforward exercises in documenting the extent of sexual variation in mean values for cranial, mandibular or dental variables. The small number of studies that did record estimates of population variation did not go on to explore the implications of any sexual dimorphisms in variance. A few investigators have partitioned variation into size and shape components (e.g. Wood, 1976; Uytterschaut, 1986) and Wood (1976) used relative growth techniques to explore the extent to which allometric growth may have determined the magnitude of any shape differences between males and females. That study investigated cranial, mandibular and dental sexual dimorphism in *Homo sapiens* and four Old World primates. Its conclusions, in relation to the nature of sexual dimorphism, can be summarised as follows: (i) Between-taxon differences in sexual dimorphism were interpreted as being ones "of degree of dimorphism rather than due to a different pattern of dimorphism" (Wood, 1976, p. 32). (ii) Sex differences in variance were found to be notably higher in *Gorilla* (29 % of all variables) compared to *Pan* and *Homo*. (iii) The sexes differed in both size and shape. These conclusions remained untested for nearly a decade until the nature of sexual dimorphism in the dentition of higher primates was re-examined by Oxnard *et al.* (1985). He and his colleagues analysed the buccolingual and mesiodistal diameters of the maxillary and mandibular dentitions of 367 specimens of *Homo sapiens*, *Pan*, *Gorilla* and *Pongo*, and considered the results in terms of three tooth categories, incisors, canines and postcanine teeth (excluding the third molar); in a companion paper they investigated the multivariate structure of the data (Lieberman *et al.* 1985). Their results suggested that in none of the three dental categories were the patterns of sexual dimorphism consistent across the four taxa; indeed the only shared pattern was that of incisor and canine variation between *Pan* and *Gorilla*. These two taxa were interpreted as sharing significant sexual dimorphism in both means and variance for incisors and canines, whereas *Pongo* is dimorphic for means only and *Homo* sexually monomorphic for both mean values and dispersions. In the postcanine teeth three apparently distinct patterns occurred. Their *Gorilla* sample exhibited dimorphic means and variances, in *Pongo* only means were dimorphic, whereas *Pan* and *Homo* were sexually monomorphic for both means and variances (Oxnard *et al.* 1985, Table IV, p. 138). In their exploration of the multivariate structure of the same data, the use of high dimensional plots (Andrews, 1972), apparently revealed additional differences in the pattern of sexual dimorphism, between the two jaws, for example (Lieberman *et al.* 1985, p. 314). The authors concluded that "sexual dimorphism in hominoid teeth is not a simple unidimensional phenomenon related to size differences but is complex and involves a different pattern in each species" (Lieberman *et al.* 1985, p. 323).

When the relevant, dental, results of the present study are compared with those of Oxnard *et al.* (1985), there are some similarities, but a greater number of contrasts. The results are similar in that the samples used in both studies suggest that their parent populations show significant differences in the mean values of the variables, but thereafter the similarities end. Whereas in Oxnard *et al.* (1985) few *Homo* means are sexually dimorphic, in the present study the numbers of significant mean differences in *Homo* are high, similar to those in *Pongo* and greatly exceeding the number in *Pan* (Table 3). This would suggest that the parent populations of the *Homo sapiens* samples used in the two studies have different degrees, and perhaps also patterns, of sexual dimorphism; this conclusion is compatible with the results of recent studies of modern *Homo sapiens* populations (Calcagno, 1981; Ricklan & Tobias, 1986; Uytterschaut, 1986; van Vark, van der Sman, Dijkema & Buikstra, 1989). Jacobson's (1968) earlier study of Bantu dental sexual dimorphism also suggested that virtually all measurements showed significant (> 95 %) differences between the sexes. The same is the case for most other studies of anatomically-modern *Homo sapiens* (see above), the exceptions being the highly unusual Tristanites (Thomsen, 1955) and the Aleuts (Moorrees, 1957). It is also possible that Oxnard's *Homo sapiens* sample, which was obtained from an orthodontic practice, may not be comparable with those used in earlier studies.

Similar discrepancies exist when the results relating to dispersion are compared in the two studies. In the present investigation, although the overall number of sexually dimorphic dispersions is greatest in *Gorilla*, for dental variables alone the incidence in *Gorilla* is matched by those in both *Pan* and *Homo*. This contrasts with the study of Oxnard *et al.* (1985), which suggested that sexual dimorphism in dispersions across all categories of dental variables was a phenomenon confined to *Gorilla* and that *Homo sapiens* was uniformly monomorphic for variance. In the present study both *Gorilla* and *Pongo* have the highest levels of dispersion dimorphism for cranial and mandibular variables (Table 3).

Further comparisons of the pattern of sex difference between the taxa can be made by inspection of the sexual dimorphism indices (Figs. 2–4). Such plots will not reveal the subtle interactions between variables that are uncovered by the high dimensional plots (Lieberman *et al.* 1985), but their interpretation is both direct and simple. The dental data conform to two basic patterns, with the major distinction relating to dimorphism in canine dimensions. *Homo* constitutes one pattern which exhibits little size dimorphism, while the three non-human higher primate taxa show varying degrees of sexual canine dimorphism. This is not to suggest that there is no evidence of differences between data collected from *Pan*, *Gorilla* and *Pongo*, but these results, and those of Wu & Wang (1987), indicate that such variation is relatively minor compared to the presence or absence of canine dimorphisms. There are, for example, differences in canine dimorphism between the upper and lower canines so that whereas *Pan* and *Pongo* have similar upper canine sexual dimorphisms, for the lower canines the sex differences within *Pongo* exceed those for *Pan*. For non-dental variables, the major divisions in the pattern of sexual dimorphism are between *Homo* and *Pan* on the one hand and *Gorilla* and *Pongo* on the other.

When the interactions between variables are taken into account by investigating the variable loadings on the major sex-discriminating principal component for each taxon (Table 4) it is evident that the dentition is the region where any differences in the pattern of sexual dimorphism are most marked, for only one third of the variables with highest loadings are common to the lists of the four taxa. However, comparison of the angles subtended by the axes which connect the single-sex mean values of the dental variables in canonical space suggests, as did the simple inspection of the percentage dimorphism indices, that the pattern of multivariate dental sexual dimorphism in *Pan*, *Gorilla* and *Pongo* is essentially similar and that it contrasts with the pattern in *Homo* (Table 5). Similar contrasts between *Homo* and the non-human primates exist for the slopes of the lines connecting the sex means of the mandibular and cranial variables (Table 5), but only the cranial slopes suggest any subdivision within the non-human higher primates, with the slope patterns of *Pan* and *Gorilla* being more similar to each other than either is to *Pongo*.

The canonical analysis results can be directly compared with the results of previous investigations among higher primates made by Robinson & Steudel (1973) and Oxnard (1985, 1987, 1988). The relevant results from Robinson & Steudel (1973) suggest that the group structure is different for mandibular and maxillary teeth. For the mandibular dentition (*ibid*, Fig. 3, p. 516) there is a basic similarity in the direction of the sex discriminating axes among all four extant genera (*Homo sapiens*, *Pan*, *Gorilla* and *Pongo*) when results based on C-M_1 measures are compared. A different pattern, and one which is closer to the one observed in the present study, is seen when equivalent measures of maxillary teeth are considered (*ibid*, Fig. 4, p. 517) and this shows a contrast between the direction of the sex discriminating axis for *Homo* and the axes for the non-human samples.

Oxnard (1987) based his analysis on data from incisors, canines, premolars and molars, and he also provided a three-dimensional plot of the position of the separate male and female samples for each taxon with respect to the first three canonical axes (*ibid*, Fig. 2: 17, p. 59). This result is similar to that obtained for maxillary teeth by Robinson & Steudel (1973) and has been summarised by the author as showing that "all three apes share a similar direction from female to male that is quite different from that in *Homo*" (Oxnard, 1987, p. 59). Thus, at this level of analysis there is considerable agreement between the three sets of results. This suggests that, for the vast majority (in this study $> 95\%$) of the variance subsumed within the first three canonical analyses, there are two basic patterns of dental sexual dimorphism for the higher primates, one for *Homo* and another for *Pan*, *Gorilla* and *Pongo*. The results of the canonical studies incorporated in the present study suggest that two basic patterns also underly sexual dimorphisms in the mandible and cranium, although univariate comparisons suggested that mandibular, and to a lesser extent, cranial sexual dimorphisms were similar in *Homo* and *Pan*. A *Homo/Pan* and *Gorilla/Pongo* dichotomy is also apparent when canine measurements are considered in more detail. Whereas in *Homo* and *Pan* the coefficients of variation are similar in the two sexes, this is not so for *Gorilla* and *Pongo*, in which female canine measurements are substantially more variable than male measurements. The implications of these results for the analysis of fossil hominoids are evident. Parsimony would suggest that fossil hominoids would share the basic pattern of the non-human primates, but the nearer the fossils approached a *Homo-Pan* clade (if such exists) then one would expect more subtle shifts in the pattern of sexual dimorphism (see Figs. 1, 2). These results do not fully resolve the problems facing those workers who are attempting to predict the pattern of sexual dimorphism in fossil hominids, but they may offer help. The inference is that the more general pattern of sexual dimorphism is strongly correlated with canine size. It is probably fair to assume that hominids which share canine and facial reduction with *Homo*, whether as an apomorphy or a homoplasy, are more likely to share its pattern of sexual dimorphism, but predictions about the probable pattern of sexual dimorphism in the relatively larger canine-bearing, more primitive, hominids still lack a sound basis.

The final part of the study sought to identify variables which, within the range of taxa being tested, were consistently either good sex discriminators and poor taxonomic discriminators or *vice versa*. Previous studies among primates have suggested that within-taxon differences are dominated by size whereas between-taxon variation has a larger shape component (van Gerven, 1972; Albrecht, 1978). If this is so then it would be logical to assume that variables which are highly correlated with body size would, in turn, be effective sex discriminators. Gingerich (1977) demonstrated that the mesiodistal diameter of M_2 is highly correlated with body size over a range of primates. Steudel (1980) investigated the relationship of twenty five variables with body size in primates ranging from *Macaca* to *Gorilla*, but only listed the three variables with correlations at levels of $r = > 0{\cdot}95$; they were palate breadth, bizygomatic breadth and orbital width. However, both these studies only investigated variable/body size correlations between species and not within species, and previous experience suggests that intra- and intertaxonomic relationships may be quite different (Bauchot & Stephan, 1964; Gould, 1975; Wood & Stack, 1980).

Within the present study, indications of the relative utility of variables for sexual and taxonomic discrimination can be found in the variable loadings for sex-discriminating principal components (Table 4) and by considering the ratios of the within-to-between group sums of squared distances (Table 6); in each case the variables have been subdivided into dental, mandibular and cranial categories. Several trends emerge in each regional category of variables. Canine variables and tooth crown breadth (buccolingual) measurements are generally good sex-discriminating variables, whereas central incisor crown dimensions and tooth crown length (mesiodistal) measures are better taxonomic discriminators; the efficacy of dental breadth measures as sexual discriminators is consistent with the conclusions of earlier studies of modern man and the great apes (Garn, Lewis, Swindler & Kerewsky, 1967). In the mandible, breadth measurements are generally good sex discriminators, whereas mandibular angle and intercanine distance are better taxonomic indicators. Within the cranium, breadth measurements dominate as sex-discriminators, whereas facial heights are apparently stronger taxonomic discriminators (Tables 4, 6).

While there can be no hard and fast allocation of variables to sex and taxon-discriminating categories, the results of this study may help in the resolution of some of the more intractable taxonomic problems that engage the interest of hominid palaeontologists. For example, the differences in cranial size and shape between crania such as KNM-ER 406 and OH 5, presumed male *Australopithecus boisei*, and KNM-ER 407 and 732, putative female crania of *A. boisei*, are mainly found in the width measurements of the cranium. This pattern of difference suggests that sexual dimorphism must be regarded as a probable explanation for the dimorphism that exist between these sets of hominid crania (Leakey, 1971, 1973; Wood, 1991).

It should be apparent that the results of this study must be regarded as preliminary until its propositions have been tested on different geographical samples of higher primate taxa. Such tests are in progress and will be reported in due course.

CONCLUSIONS

The results of this study of sexual dimorphism in higher primate taxa are best considered in relation to the objectives that determined the nature of this investigation.

The first was an attempt to test the hypothesis that there are clear distinctions between the patterns of sexual dimorphism seen in *Homo*, *Pan*, *Gorilla* and *Pongo*. In this study, the distinctive patterns of differences in mean values and dispersions noted by Oxnard (1985, 1987, 1988) for dental variables are not evident. Instead, there is apparently more consistency in the patterns of sexual dimorphism of non-human higher primate taxa than was noted in the latter study. It is true that the sample sizes used in the present investigation are much smaller than those used by Oxnard, but the former are still large enough for us to assume that they reflect the structure of the parent population. What possible explanations are there for the different conclusions? They could be due to the heterogenous nature of the Oxnard sample, or simply be an indication that ape as well as human populations show geographical variation in internal structure. Inspection of the pattern of ratios of sex means for mandibular and cranial variables suggests two basic patterns, one shared by *Homo* and *Pan* and the other by *Gorilla* and *Pongo*. However, multivariate comparisons of the same data indicate a dichotomy between a *Homo* and a non-human primate pattern.

The results relevant to the last of the three main objectives suggest that there are sufficient consistencies in the patterns of intra- and interspecific variation to hold out the possibility that palaeontologists can use such associations to help sort intraspecific from interspecific variation within the hominoid and hominid fossil record. Within higher primates, for example, canine variables, postcanine crown breadths, mandibular and cranial breadths are all consistently good sex discriminators, whereas mesiodistal crown dimensions and facial heights are better at discriminating between the sample taxa.

Finally, the results have implications for phylogenetic analysis. Degrees and patterns of sexual dimorphism in this study are a good deal less polyphyletic than was suggested by Oxnard (1987, 1988). Sexual dimorphisms in *Homo sapiens* and *Pan* apparently share some features in common, particularly within the mandibular and cranial categories of variables. However, the polarity of this 'character', if it is such, has yet to be determined by the necessary detailed investigations of the degree and pattern of sexual dimorphism in a wider range of primate taxa.

SUMMARY

The extent and nature of dental and cranial sexual dimorphisms in extant hominoids have been investigated using reliably sexed samples of *Homo sapiens* (n = 75), *Pan troglodytes* (n = 51), *Gorilla gorilla* (n = 64) and *Pongo pygmaeus* (n = 43). Seventy nine measurements (35 dental, 16 mandibular and 28 cranial) formed the basis of the study. The patterns of mean differences and dispersions between the taxa were compared across the anatomical regions and the group structures of the separate sex samples were analysed using multivariate (PCA and CVA) analysis. Within and between group variations were compared across the taxa to investigate whether any variables were consistently effective sex or taxonomic discriminators.

The study confirmed that there were differences in degree and pattern of sexual dimorphism between the extant higher primates, but the results did not substantiate the distribution of patterns as suggested by Oxnard *et al.* (1985); in particular there was no evidence of the dispersion differences noted by those authors. There were sufficient consistencies in the behaviour of variables across the four taxa to suggest that all canine dimensions, postcanine crown buccolingual dimensions and mandibular and cranial breadths are generally good sex discriminators, whereas some incisor dimensions, postcanine crown mesiodistal dimensions and facial heights are more effective at discriminating between the four extant taxa included in this study.

The work reported in this paper grew out of an earlier collaboration between Bernard Wood and Michael Clarke, and the latter's contribution is gratefully acknowledged. Research incorporated in the present study was supported by a grant from The Leverhulme Trust (B.W.), the Academia Sinica (Yu Li), and the support of an MRC Intercalated Studentship award (C.W.). The authors are grateful to Andrew Chamberlain, Craig Engleman and Elizabeth Walker for their help with the preparation of the manuscript.

REFERENCES

Albrecht, G. (1978). The craniofacial morphology of the Sulawesi macaques. *Contributions to Primatology* **13**, 1–151.

Almquist, A. (1974). Sexual differences in the anterior dentition in African primates. *American Journal of Physical Anthropology* **40**, 359–368.

Andrews, D. F. (1972). Plots of high-dimensional data. *Biometrics* **28**, 125–136.

Andrews, P. (1987). Aspects of hominoid phylogeny. In *Molecules and Morphology in Evolution: Conflict or Compromise* (ed. C. Patterson), pp. 21–53. Cambridge: Cambridge University Press.

Andrews, P. (1988). Book review. *Cladistics* **4**, 297–304.

ASHTON, E. H. (1956). Sexual differences in the dimensions of the milk teeth of the chimpanzee and gorilla. *Proceedings of the Zoological Society of London* **126**, 121–125.

ASHTON, E. H. (1957). Age changes in dimensional differences between the skulls of male and female apes. *Proceedings of the Zoological Society of London* **128**, 259–265.

ASHTON, E. H. & ZUCKERMAN, S. (1950). Some quantitative dental characters of fossil anthropoids. *Philosophical Transactions of the Royal Society* **234**, 485–520.

BARRETT, M. J., BROWN, T., ARATO, G. & OZOLS, I. V. (1964). Dental observations on Australian Aborigines: buccolingual crown diameters of deciduous and permanent teeth. *Australian Dental Journal* **9**, 280–285.

BAUCHOT, R. & STEPHAN, H. (1964). Le poids encephalique chez les insectivores malagaches. *Acta zoologica* **45**, 63–75.

BOOTH, S. N. (1970). Observations on the teeth of the mountain gorilla. *American Journal of Physical Anthropology* **34**, 85–88.

CALCAGNO, J. M. (1981). On the applicability of sexing human skeletal material by discriminant function analysis. *Journal of Human Evolution* **10**, 189–198.

CLUTTON-BROCK, T. H. & HARVEY, P. H. (1977). Primate ecology and social organisation. *Journal of Zoology* **183**, 1–39.

COURTENAY, J., GROVES, C. & ANDREWS, P. (1988). Inter- or intra-island variation? An assessment of the differences between Bornean and Sumatran orang-utans. *In Orang-utan Biology* (ed. J. H. Schwartz), pp. 19–29. Oxford University Press.

CRACRAFT, J. (1981). The use of functional and adaptive criteria in phylogenetic systematics. *American Zoologist* **21**, 21–36.

CRICHTON, J. M. (1966). A multiple discriminant analysis of Egyptian and African negro crania. *Papers of the Peabody Museum* **57**, 47–67.

DE VILLIERS, H. (1968). *The Skull of the South African Negro. A Biometrical and Morphological Study*, pp. 1–342. Johannesburg: Witwatersrand University Press.

DIERBACH, A. (1986). Intraspecific variability and sexual dimorphism in the skulls of *Pan troglodytes verus*. *Human Evolution* **1**, 41–50.

FAWCETT, C. D. (1902). A second study of the variation and correlation of the human skull with special reference to the Naqada crania. *Biometrika* **1**, 408–467.

FENART, R. & DEBLOCK, R. (1974). Sexual differences in adult skulls of *Pan troglodytes*. *Journal of Human Evolution* **3**, 123–133.

FLEAGLE, J. G., KAY, R. F. & SIMONS, E. L. (1980). Sexual dimorphism in early anthropoids. *Nature* **287**, 328–330.

FRAYER, D. W. (1973). *Gigantopithecus* and its relationship to *Australopithecus*. *American Journal of Physical Anthropology* **39**, 413–426.

GARN, S. M., LEWIS, A. B., SWINDLER, D. R. & KEREWSKY, R. S. (1967). Genetic control of sexual dimorphism in tooth size. *Journal of Dental Research* **46**, 963–972.

GAUL, G. (1933). Uber die Wachstumsveränderungen am Gehirnschädel des Orang-utan. *Zeitschrift für Morphologie und Anthropologie* **31**, 362–394.

GILES, E. (1964). Sex determination by discriminant function analysis of the mandible. *American Journal of Physical Anthropology* **22**, 129–136.

GILES, E. & ELLIOT, O. (1963). Sex determination by discriminant function analysis of crania. *American Journal of Physical Anthropology* **21**, 53–68.

GINGERICH, P. D. (1977). Correlation of tooth size and body size in living hominoid primates with a note on relative brain size in *Aegyptopithecus* and *Proconsul*. *American Journal of Physical Anthropology* **47**, 395–398.

GOULD, S. J. (1975). Allometry in primates, with special emphasis on scaling and the evolution of the brain. *Contributions to Primatology* **5**, 244–292.

GREENE, D. L. (1973). Gorilla dental sexual dimorphism and early hominid taxonomy. *Symposium of the 4th International Primatological Congress* **3**, 82–100.

GREGORY, W. K. & HELLMAN, M. (1926). The dentition of *Dryopithecus* and the origin of man. *Anthropological Papers of the American Museum of Natural History* **28**, 1–123.

GROVES, C. (1970). Population systematics of the gorilla. *Journal of Zoology* (*London*) **161**, 287–300.

GROVES, C. (1986). Systematics of the great apes. *Comparative Primate Biology* **1**, 187–217.

HARVEY, P. H., KAVANAGH, M. & CLUTTON-BROCK, T. H. (1978). Sexual dimorphism in primate teeth. *Journal of Zoology* (*London*) **186**, 475–485.

HASEGAWA, M., KISHINO, H. & YANO, T. (1987). Man's place in Hominoidea as inferred from molecular clocks of DNA. *Journal of Molecular Evolution* **26**, 132–147.

HOOIJER, D. A. (1948). Prehistoric teeth of man and the orang-utan from Central Sumatra, with notes on the fossil orang-utan from Java and Southern China. *Zoologische mededeelingen* **29**, 175–301.

HOWELLS, W. W. (1966). The Jomon population of Japan. A study by discriminant analysis of Japanese and Ainu crania. *Papers of the Peabody Museum* **57**, 1–47.

HRDLICKA, A. (1923). Variations in the dimensions of lower molars in man and anthropoid apes. *American Journal of Physical Anthropology* **6**, 423–438.

HUNTER, W. S. & GARN, S. M. (1972). Disproportionate sexual dimorphism in the human face. *American Journal of Physical Anthropology* **36**, 133–138.

JACOBSON, A. (1968). Morphological and metrical study of the teeth, the jaws and the bony palate of several large groups of South African Bantu-speaking Negroids. Ph.D. thesis, University of the Witwatersrand.

JOHANSON, D. C. (1974). Some metric aspects of the permanent and deciduous dentition of the pygmy chimpanzee (*Pan paniscus*). *American Journal of Physical Anthropology* **41**, 39–48.

JUNGERS, W. L. (1985). Body size and scaling of limb proportions in primates. *In Size and Scaling in Primate Biology* (ed. W. L. Jungers), pp. 345–381. New York: Plenum.

KAJANOJA, P. (1966). Sex determination of Finnish crania by discriminant function analysis. *American Journal of Physical Anthropology* **24**, 29–34.

LEAKEY, R. E. F. (1971). Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya. *Nature* **231**, 241–245.

LEAKEY, R. E. F. (1973). Australopithecines and hominines: a summary on the evidence from the Early Pleistocene of Eastern Africa. *Symposium of the Zoological Society of London* **33**, 53–69.

LEUTENEGGER, W. (1978). Scaling of sexual dimorphism in body size and breeding system in primates. *Nature* **272**, 610–611.

LEUTENEGGER, W. (1982). Scaling of sexual dimorphism in body weight and canine size in primates. *Folia primatologica* **37**, 163–176.

LEUTENEGGER, W. & CHEVERUD, J. (1982). Correlates of sexual dimorphism in primates: ecological and size variables. *International Journal of Primatology* **3**, 387–402.

LEUTENEGGER, W. & KELLY, J. T. (1977). Relationship of sexual dimorphism in canine size and body size to social, behavioural and ecological correlates in anthropoid primates. *Primates* **18**, 117–136.

LEUTENEGGER, W. & LUBACH, G. (1987). Sexual dimorphism, mating system, and the effect of phylogeny in De Brazza's monkey (*Cercopithecus neglectus*). *American Journal of Primatology* **13**, 171–179.

LEUTENEGGER, W. & MASTERSON, T. J. (1989). The ontogeny of sexual dimorphism in the cranium of the Bornean orang-utans (*Pongo pygmaeus pygmaeus*). 1. Univariate analyses. *Zeitschrift für Morphologie und Anthropologie* **78**, 1–14.

LIEBERMAN, S. S., GELVIN, B. R. & OXNARD, C. E. (1985). Dental sexual dimorphisms in some extant hominoids and ramapithecines from China: a quantitative approach. *American Journal of Primatology* **9**, 305–326.

LUBOGA, S. A. & WOOD, B. A. (1990). Position and orientation of the foramen magnum in higher primates. *American Journal of Physical Anthropology* **81**, 67–76.

MCCOWN, E. R. (1982). Sex differences: the female as baseline for species description. *In Sexual Dimorphisms in Homo sapiens* (ed. R. L. Hall), pp. 37–83. New York: Praeger Scientific.

MAHLER, P. (1973). Metric variation and tooth wear patterns in the pongid dentition. Ph.D. dissertation, University of Michigan.

MARTIN, E. S. (1936). A study of the Egyptian series of mandibles, with special reference to mathematical methods of sexing. *Biometrika* **28**, 149–178.

MIJSBERG, W. A. (1931). On sexual differences in the teeth of the Javanese. *K. Nederlandse akademie van wetenschappen* **34**, 1111–1115.

MIYAMOTO, M. M., KOOP, B. F., SLIGHTOM, J. L., GOODMAN, M. & TENNANT, M. R. (1988). Molecular systematics of higher primates: genealogical relations and classification. *Proceedings of the National Academy of Sciences of the USA* **85**, 7627–7631.

MOORREES, C. F. A. (1957). *The Aleut Dentition: a Correlation Study of Dental Characteristics in Eskimoid People*, pp. 1–196. Cambridge, Mass.: Harvard University Press.

MOORREES, C. F. A., THOMSEN, S. O., JENSEN, E. & YEN, P. K-J. (1957). Mesiodistal crown diameters of the deciduous and permanent teeth of individuals. *Journal of Dental Research* **36**, 39–47.

MORANT, G. M. (1936). A biometric study of the human mandible. *Biometrika* **28**, 84–122.

OWEN, R. (1848). On a new species of chimpanzee. *Proceedings of the Zoological Society of London*, 27–35.

OXNARD, C. E. (1985). Hominids and hominoids, lineages and radiations. In: *Hominid Evolution: Past, Present and Future* (ed. P. V. Tobias), pp. 271–278. New York: Alan R. Liss.

OXNARD, C. E. (1987). *Fossils, Teeth and Sex: New Perspectives on Human Evolution*, pp. 1–281. Seattle and London: University of Washington Press.

OXNARD, C. E. (1988). Fossils, teeth and sex: new perspectives in human evolution. *Proceedings of the Australasian Society for Human Biology* **1**, 23–73.

OXNARD, C. E., LIEBERMAN, S. S. & GELVIN, B. R. (1985). Sexual dimorphisms in dental dimensions of higher primates. *American Journal of Primatology* **8**, 127–152.

PEARSON, K. & DAVIN, A. (1924). On the biometric constants of the human skull. *Biometrika* **16**, 328–363.

PILBEAM, D. R. (1969). Tertiary Pongidae of East Africa: evolutionary relationships and taxonomy. *Bulletin of the Peabody Museum of Natural History*, No. 31, 1–185.

RANDALL, F. E. (1943). The skeleton and dental development and variability of the gorilla. *Human Biology* **15**, 236–254; 307–337: **16**, 23–76.

REMANE, A. (1960). Zahne und Gebiss. *Primatologia* **3**, 637–846.

RICKLAN, D. E. & TOBIAS, P. V. (1986). Unusually low sexual dimorphism of endocranial capacity in a Zulu cranial series. *American Journal of Physical Anthropology* **71**, 285–293.

RIGHTMIRE, G. P. (1970*a*). Iron age skulls from Southern Africa reassessed by multiple discriminant analysis. *American Journal of Physical Anthropology* **33**, 147–168.

RIGHTMIRE, G. P. (1970*b*). Bushman, Hottentot and South African Negro crania studies by distance and discrimination. *American Journal of Physical Anthropology* **33**, 169–196.

ROBINSON, J. T. & STEUDEL, K. (1973). Multivariate discriminant analysis of dental data bearing on early hominid affinities. *Journal of Human Evolution* **2**, 509–527.

SAKKA, M. (1985). Sexual dimorphism in great apes: the skull of the gorilla. In *Human Sexual Dimorphism* (ed. J. Ghesquiere, R. D. Martin & F. Newcombe), pp. 79–103. London and Philadelphia: Taylor & Francis.

SCHMID, P. & STRATIL, Z. (1986). Growth changes, variations and sexual dimorphism of the gorilla skull. In *Primate Evolution* (ed. J. G. Else & P. C. Lee), pp. 239–247. Cambridge: Cambridge University Press.

SCHULTZ, A. H. (1940). The size of the orbit and the eye in primates. *American Journal of Physical Anthropology* **26**, 389–408.

SCHULTZ, A. H. (1941). Growth and development in the orang-utan. *Contributions to Embryology* **29**, 59–110.

SCHULTZ, A. H. (1962). Metric age changes and sex differences in primate skulls. *Zeitschrift für Morphologie und Anthropologie* **52**, 239–255.

SCHUMAN, E. L. & BRACE, C. L. (1954). Metric and morphologic variations in the dentition of the Liberian chimpanzee: comparisons with anthropoid and human dentitions. *Human Biology* **26**, 239–268.

SEIPEL, C. M. (1946). Variation of tooth position. *Svensk tandläkare tidskrift* **39**, Suppl.

SELMER-OLSEN, R. (1949). An odontological study on the Norwegian Lapps. *Det. Norske Videnskaps-Akademi, Oslo.*

SIBLEY, C. G. & AHLQUIST, J. E. (1987). DNA hybridization evidence of hominoid phylogeny: results from an expanded data set. *Journal of Molecular Evolution* **26**, 99–121.

STEUDEL, K. (1980). New estimates of early hominid body size. *American Journal of Physical Anthropology* **52**, 63–70.

TATTERSALL, I. (1986). Species recognition in human palaeontology. *Journal of Human Evolution* **15**, 165–175.

THOMSEN, S. (1955). Dental morphology and occlusion in the people of Tristan da Cunha. *Results of the Norwegian Scientific Expedition to Tristan da Cunha*, 1937–1938, No. 25.

UEDA, S. (1988). Multiple recombinational events in primate immunoglobulin epsilon and alpha genes suggest closer relationships of humans to chimpanzees than to gorillas. *Journal of Molecular Evolution* **27**, 77–83.

UYTTERSHAUT, H. T. (1986). Sexual dimorphism in human skulls. A comparison of sexual dimorphism in different populations. *Human Evolution* **1**, 243–250.

VAN GERVEN, D. P. (1972). The contribution of size and shape variation to patterns of sexual dimorphism in the human femur. *American Journal of Physical Anthropology* **37**, 49–60.

VAN VARK, G. N., VAN DER SMAN, P. G. M., DIJKEMA, J. & BUIKSTRA, J. E. (1989). Some multivariate tests of differences in sexual dimorphism between human populations. *Annals of Human Biology* **16**, 301–310.

WINKLER, L. A., CONROY, G. C. & VANNIER, M. W. (1988). Sexual dimorphism in exocranial and endocranial dimensions. In *Orang-utan Biology* (ed. J. H. Schwartz), pp. 225–232. Oxford: Oxford University Press.

WOOD, B. A. (1975). An analysis of sexual dimorphism in primates. PhD. thesis, University of London.

WOOD, B. A. (1976). The nature and basis of sexual dimorphism in the primate skeleton. *Journal of Zoology (London)* **180**, 15–34.

WOOD, B. A. (1984). The origin of *Homo erectus*. *Courier Forschungsinstitut Senckenberg* **69**, 99–111.

WOOD, B. A. (1985). Sexual dimorphism in the hominid fossil record. In *Human Sexual Dimorphism* (ed. J. Ghesquiere, R. D. Martin & F. Newcombe), pp. 105–123. London: Taylor and Francis.

WOOD, B. A. (1989). Hominid relationships: a cladistic perspective. *Proceedings of the Australasian Society for Human Biology* **2**, 83–102.

WOOD, B. A. (1991). *Cranial Remains from Koobi Fora, Kenya.* Oxford: Clarendon Press.

WOOD, B. A. & CHAMBERLAIN, A. T. (1987). The nature and affinities of the robust australopithecines: a review. *Journal of Human Evolution* **16**, 625–641.

WOOD, B. A. & STACK, C. G. (1980). Does allometry explain the differences between gracile and robust australopithecines? *American Journal of Physical Anthropology* **52**, 55–62.

WU RUKANG & OXNARD, C. E. (1983). *Ramapithecus* and *Sivapithecus* from China: some implications for higher primate evolution. *American Journal of Primatology* **5**, 303–344.

WU RUKANG & WANG LINGHONG (1987). Sexual dimorphism of fossil apes in Lufeng. *Acta anthropologica sinica* **6**, 169–174.

YAMADA, E. (1932). An anthropological study of the Japanese teeth. *Journal of The Japanese Dental Association* **25**, 15 *et seq.*