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Analysis of the dental morphology of Plio-Pleistocene hominids. III. Mandibular premolar crowns

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INTRODUCTION

This is the third in a series of morphometric studies of early hominid teeth (Wood & Abbott, 1983; Wood, Abbott & Graham, 1983). The series has two principal aims. First, to document and describe, using objective criteria, the dental characteristics of early hominid taxa. Second, to use these characteristics as a guide to the affinities of specimens whose taxonomic designation is unknown, or problematic.

By insisting that specimens have to be complete enough to provide a minimum of detailed morphometric data, these studies are necessarily based on smaller samples than surveys which rely on simpler, but cruder, metrical descriptions (e.g. Wolpoff, 1971; Johanson & White, 1979; Blumenberg & Lloyd, 1983). Thus, we have sacrificed a reduction in sample size for better quality data. Others may take a different view of the balance of this equation, but doubtless the two strategies both have contributions to make to the pool of knowledge about early hominids. Non-metric traits have been included in this analysis, and others in the series, but always in the context of a carefully validated numerical assessment scheme which allows the degree of expression of traits to be compared between samples. This study is limited to the crowns of mandibular premolars; their root morphology, together with that of the molars, will be considered in a separate publication.

The methods used to describe and quantify the crown morphology of the mandibular premolars are broadly similar to those employed for the study of the molars (Wood & Abbott, 1983; Wood *et al.* 1983). When the list of measurements and observations was being prepared, particular attention was paid to previous assessments of the occlusal morphology of modern human mandibular premolars (e.g. Kraus & Furr, 1953; Ludwig, 1957; Biggerstaff, 1969) as well as to relevant odontographic studies of early hominids (Robinson, 1956; Sperber, 1974). This study is based on the same informal taxonomic categories that were used for the analyses of mandibular molar crown morphology. Details of the fossil hypodigms subsumed within each category are given elsewhere (Wood & Abbott, 1983) and extra information is only included in this paper if the allocations deviate from the principles set out in the earlier publication. The absence, in this series of publications, of any detailed consideration of the extensive fossil hominid collection from the Omo demands some explanation. The remains from the Omo were collected from strata whose nature suggests that the predominant sedimentary environment was a relatively high energy fluviatile one (de Heinzelin, Haesaerts & Howell, 1976). Such a depositional environment has influenced the taphonomic processes operating on the Omo hominid remains so that, compared to other East African hominid sites, there are relatively few mandibles, even fewer crania, and therefore a high proportion of isolated teeth (Bishop, 1976). Thus, the hominid evidence from the Omo, because of the lack of non-dental morphological evidence, can provide little information which can help towards defining the dental characteristics of early hominid taxa. Instead, it represents *par excellence* the sort of collection for which the dental characteristics of taxa, derived as described in this and earlier papers, could be used to help sort the preserved teeth into taxonomic categories, and such a study of the isolated teeth from the Omo is planned (Pank, Uytterschaut & Wood, in preparation).

MATERIALS AND METHODS

Fossil sample

This analysis was based on a sample of 91 hominid mandibular premolar teeth (43 P_3s and P_4s), from at least 71 individuals. These figures represent the cumulative total of teeth, but the effects of wear and damage have meant that the specimens on which it was possible to record individual measurements and observations usually made up a smaller subset of the total. Premolar crowns are included only if sufficient of the fissure pattern is preserved to identify the boundaries of the three main elements of the crown. Thus heavily worn and excessively weathered tooth crowns were excluded from this study. Specimens were placed in one of six informal taxonomic categories, or were classed as 'unknown'; details of the categories are given in an earlier publication (Wood & Abbott, 1983). Teeth were assigned to a category only if there was sufficient independent morphological evidence from the cranium and jaws to sustain such an allocation. It should be noted that specimens which were classed as 'unknown' in the two earlier studies were similarly classified in this analysis. In this way the premolar crown evidence can serve as a check on the earlier allocations to see if they corroborate, or run counter to, the affinities suggested by mandibular molar crown size and morphology. Any specimen whose taxonomic attribution is contentious (e.g. KNM-ER 1802) was treated as 'unknown', as were all isolated teeth. Where specimens are common to this study and the previous ones on the mandibular molars their taxonomic allocation is as in the earlier study.

Teeth from East African sites that are included in any part of the present study are listed in Table 1 and those from sites in southern Africa are set out in Table 2; both tables list the taxonomic categories to which they have been assigned. Some specimens have the same tooth preserved on both the right and the left side; in such cases both sets of measurements are recorded. While this has the disadvantage that it apparently duplicates similar data, the presence in the multivariate plots of antimeres provides a useful perspective on the variation which exists between the different taxonomic categories.

Linear measurements

Linear measurements of the crown were made using Vernier calipers with tips specially machined to allow them to be inserted between teeth which remain *in situ* in the mandible. Measurements were recorded to the nearest 0·1 mm and were made on at least two occasions by each of two observers; mean values of the measurements were used for subsequent computations. The average genuine measurement discrepancy was of the order of 1 %. Definitions of the three linear measurements are given in Table 3 and the measurements are illustrated for a P_3 and a P_4 in Figure 1 (A) and (B).

Table 1. *List of Plio-Pleistocene hominid premolar teeth from East African sites, together with their taxonomic category*

Specimen no.	P_3	P_4	Taxonomic category	Specimen no.	P_3	P_4	Taxonomic category
Site: Koobi Fora							
KNM-ER 729 R	—	1	EAFROB	KNM-ER 1802 R	1	1	Unknown
KNM-ER 729 L	1	1	EAFROB	KNM-ER 1802 L	—	1	Unknown
KNM-ER 802 R	—	1	EAFROB	KNM-ER 1808 L	1	—	EAFHER
KNM-ER 802 L	—	1	EAFROB	KNM-ER 1816 R	—	1	EAFROB
KNM-ER 806 R	1	—	EAFHOM	KNM-ER 1816 L	1	1	EAFROB
KNM-ER 806 L	1	—	EAFHOM	KNM-ER 2599 L	1	—	Unknown
KNM-ER 818 L	—	1	EAFROB	KNM-ER 3229 R	—	1	EAFROB
KNM-ER 992 R	1	1	EAFHOM	KNM-ER 3229 L	—	1	EAFROB
KNM-ER 992 L	1	1	EAFHOM	KNM-ER 3230 R	1	1	EAFROB
KNM-ER 1171 L	—	1	EAFROB	KNM-ER 3230 L	1	1	EAFROB
KNM-ER 1477 L	1	—	EAFROB	KNM-ER 3734 L	1	1	EAFHOM
KNM-ER 1482 R	—	1	Unknown	KNM-ER 3885 R	—	1	EAFROB
KNM-ER 1482 L	—	1	Unknown	KNM-ER 5431 R	1	—	Unknown
KNM-ER 1801 L	—	1	Unknown	KNM-ER 5431 L	1	1	Unknown
Site: Olduvai Gorge							
O.H. 6 L	1	—	EAFHOM	O.H. 13 L	1	1	EAFHOM
O.H. 7 R	1	1	EAFHOM	O.H. 16 R	1	1	EAFHOM
O.H. 7 L	1	1	EAFHOM	O.H. 16 L	—	1	EAFHOM
O.H. 13 R	1	1	EAFHOM	O.H. 22 R	1	1	EAFHER
Site: Peninj							
Peninj R	1	1	EAFROB	Peninj L	—	1	EAFROB

Table 2. *List of Plio-Pleistocene hominid premolar teeth from sites in southern Africa, together with their taxonomic category*

Specimen no.	P_3	P_4	Taxonomic category	Specimen no.	P_3	P_4	Taxonomic category
Site: Swartkrans							
SK 6 L	1	—	SAFROB	SK 74 R	1	1	SAFROB
SK 7 R	—	1	SAFROB	SK 88 L	—	1	SAFROB
SK 9 L	—	1	SAFROB	SK 96 L	1	—	SAFROB
SK 18 L	1	—	SAFHER	SK 100 R	1	—	SAFROB
SK 23 R	1	1	SAFROB	SK 826 L	—	1	SAFROB
SK 23 L	1	—	SAFROB	SK 827 L	—	1	SAFROB
SK 30 L	1	—	SAFROB	SK 831 R	1	—	SAFROB
SK 34 R	1	—	SAFROB	SK 857 R	1	—	SAFROB
SK 34 L	—	1	SAFROB	SK 1587 L	—	1	Unknown
SK 55 L	1	—	SAFROB	SK 1588 R	—	1	Unknown
SK 72 L	1	—	SAFROB				
Site: Sterkfontein							
Sts 24 L	1	—	SAFGRA	Stw/H 14 L	—	1	SAFGRA
Sts 51 R	1	—	SAFGRA	Stw/H 56 L	—	1	SAFGRA
Sts 52b R	1	1	SAFGRA	TM 1523 L	—	1	SAFGRA
Site: Makapansgat							
MLD 2 L	1	—	SAFGRA				
Site: Kromdraai							
TM 1517 R	—	1	SAFROB	TM 1600 L	1	—	SAFROB
TM 1517 L	1	1	SAFROB	TM 1601 L	1	1	SAFROB

Table 3. *Definitions of linear measurements of hominid mandibular premolar crowns*

(1) Mesiodistal diameter (uncorrected)
Distance between parallel lines erected at right angles to the mesiodistal axis of the crown and arranged so as to be tangential to the most mesial and distal points on the crown. This measurement takes no account of interproximal wear.
(2) Mesiodistal diameter (corrected)
In those specimens in which interproximal wear is present the original outline of the distal and mesial crown border was estimated by reference to the overall crown outline and the buccolingual extent of the wear facet(s) (Fig. 1A and B).
(3) Buccolingual diameter (maximum)
The maximum distance between the buccal and lingual crown borders taken at right angles to the longitudinal axis of the crown.

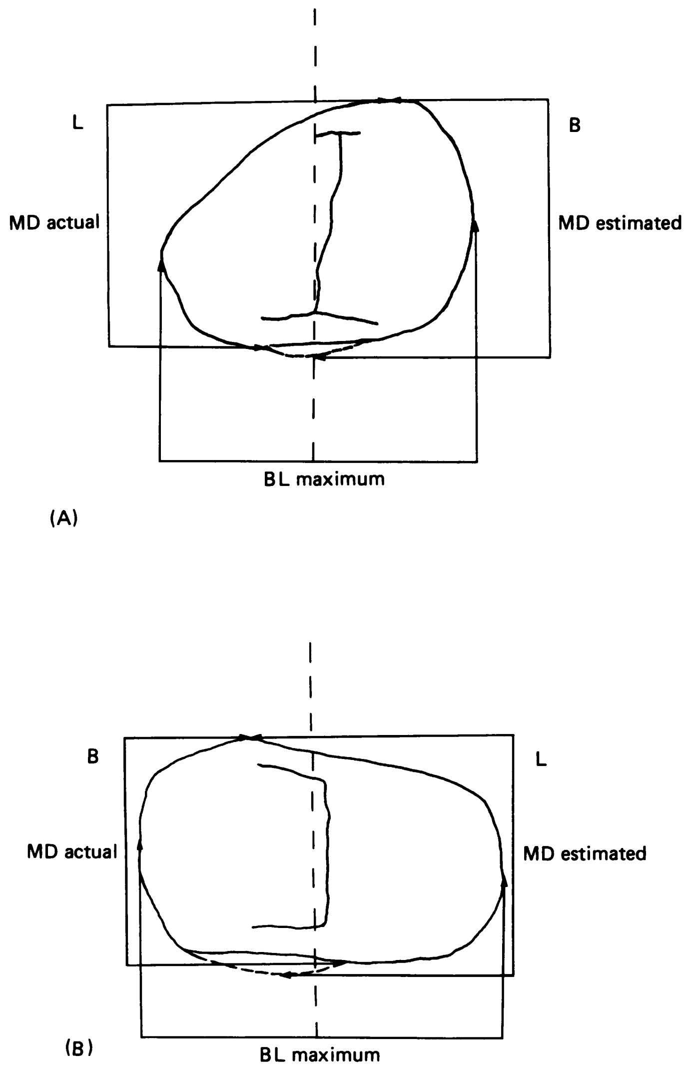


Fig. 1 (A–B). Diagrams showing the linear measurements used in the study as they would be taken on (A) a typical right P_3, and (B) a typical left P_4.

The linear dimensions were used to compute two measures of crown base area: (i) computed crown base area (uncorrected) = mesiodistal diameter (uncorrected) × maximum buccolingual diameter, and (ii) computed crown base area (corrected) = mesiodistal diameter (corrected) × maximum buccolingual diameter. In addition, the crown shape index was computed for each tooth crown. This expresses the maximum buccolingual diameter as a percentage of the mesiodistal diameter (corrected) i.e. BL/MD(C) × 100. The mean value, coefficient of variation, standard deviation and range were computed for the estimates of crown base area and the crown shape index; statistical summaries are given for each of the major taxonomic categories (Tables 6, 9).

Morphological traits

The presence and expression of four morphological traits were scored for each mandibular premolar tooth crown in which sufficient detail was preserved. The traits recorded in this sample are defined in Table 4 and were based on a larger number of features described for modern human premolars by Kraus & Furr (1953) and Ludwig (1957); some of the definitions have their origins in even earlier papers, but these are cited and reviewed in the two references given above.

Crown, cusp and talonid areas

The projected surface area of the crown, and the areas of the major cusp components, were measured from specially prepared occlusal photographs. Detail of the orientation of the teeth for photography, the photographic system used and the technique for preparing the enlarged prints are given in Wood & Abbott (1983). The boundaries of the main cusps and the talonid were defined by selected reference points (see below), and the areas so demarcated are shown in Figure 2. Cusp and talonid areas were measured on the photographic prints, using a fixed-arm planimeter. The average of three readings was taken for each measurement, and then this was scaled to original size by dividing by the square of the enlargement factor for each occlusal photograph. Tests showed that measurement error represented approximately 1% of the total variance. The areas of the main cusps and the talonid, their sum and the total occlusal area (for some teeth it was possible to measure the area of the whole tooth despite the fact that damage, or wear, had obliterated the fissures defining one, or more, component enamel areas) were then recorded. Simple descriptive statistics of the absolute areas were computed for the whole sample, and for the separate taxonomic categories, to check for measurement and transcription errors. However, interest lay not just in the absolute size of the crown elements (for the sum of these is simply the overall size of the crown) but in any differences in relative cusp size. The data were, therefore, also analysed in terms of relative cusp and talonid size, the area of each being expressed as a percentage of the total occlusal area. The mean, standard deviation and range of the relative areas were calculated for each of the four major taxonomic categories, and the significance of any differences between categories was assessed using Student's *t*-test. The patterns of variation of the absolute and relative cusp areas of teeth in the taxonomic categories, and in the 'unknown' group, were then analysed separately by computing the principal components of the covariance matrix (PCm) and by studying the pattern of Mahalanobis distances between the sample means.

Fissure pattern

The patterns of the primary fissures were compared by analysing the X/Y coordinates of defined points on the fissure system and crown margin. In view of the

Table 4. *Definition of morphological traits of hominid mandibular premolar crowns*

Cusp number

The number of cusps was recorded as 2, 3, etc. A cusp is defined as an enamel feature which has an independent apex and which is defined by fissures; in worn teeth a cusp is scored on the basis of the remaining fissure pattern. The two 'main' cusps, the buccal (or protoconid) and the lingual (or deuteroconid), are included within the score. Additional cusps are either extra lingual cusps, or cusp features elsewhere on the talonid.

Relative position of the main lingual cusp

The buccal cusp (or protoconid) usually has a ridge running lingualwards from it, the central protoconid ridge. The numerical score relates to the position of the main lingual cusp (or deuteroconid) relative to this ridge.

(1) The bulk of the deuteroconid is mesial to the long axis of the central protoconid ridge.
(2) The bulk of the deuteroconid is distal to the long axis of the ridge.
(3) The deuteroconid is centred on the long axis of the ridge.

Median longitudinal fissure

The median longitudinal fissure (or sagittal sulcus) runs mesiodistally between the buccal and main lingual cusps. The numerical scores relate to the expression of the fissure.

(1) The fissure is deep and uninterrupted.
(2) The fissure is evident, but interrupted by enamel ridges leading from the main cusps.
(3) A fissure is not evident.

Grooves

The lingual and buccal surfaces of the teeth can be incised by grooves. The presence or absence of a groove has been scored for four positions on the tooth, mesio- and distobuccal and mesio- and distolingual.

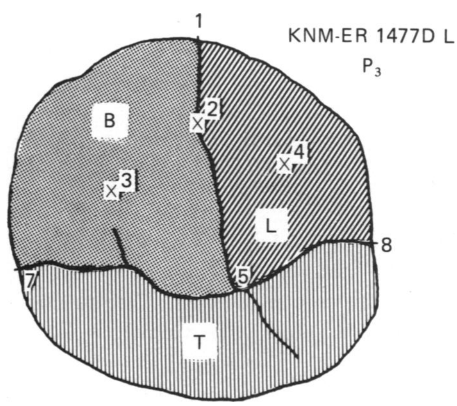


Fig. 2. Diagram showing the measured areas of the main cusps and talonid of a typical left P_3.

variations in the incidence of additional cusps, this analysis did not include information about the secondary fissures associated with these cusps. Tracings of the fissure system and the crown outline were made from the occlusal photographs and the positions of points 1–16 were clearly marked on the tracings (Fig. 3; Table 5). These reference points have been chosen for their particular utility at reflecting variation within this hominid sample and are based on those defined for modern human mandibular first and second premolars by Biggerstaff (1969).

To simplify the data analysis, the differences between left and right teeth were eliminated by mirror imaging teeth from the right side. A co-ordinate reference frame and an origin for each tracing were defined in the following way. Each tooth tracing was orientated with its mesiodistal axis perpendicular to the X axis, and positioned so that the most distal point on the crown was touching the X axis. The Y axis was then

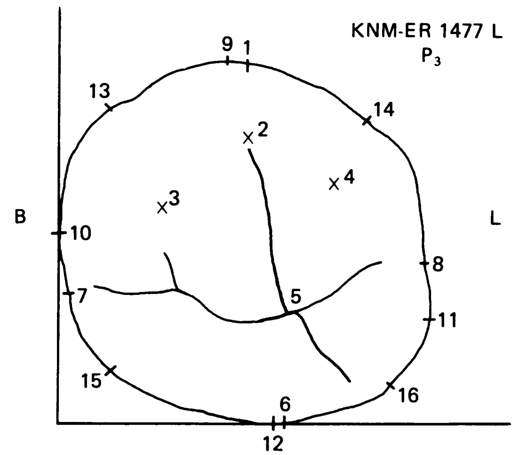


Fig. 3. Diagram to illustrate the location of the reference frame and the reference points used to record the fissure pattern. The points are defined in Table 5.

Table 5. *Definitions of the reference points located on the crown margin, cusp tips and primary fissures of hominid mandibular premolars*

(1) The point on the border of the crown directly opposite (i.e. mesial to) (A) the mesial fovea, or (B) the intersection of the median longitudinal fissure with the mesial foveal fissures/transverse fissures.
(2) The mesial fovea, or the intersection of the median longitudinal fissure with the mesial foveal fissures/ transverse fissures.
(3) The tip of the buccal cusp (or protoconid) determined by inspection. In the case of worn teeth the centre of the dentinal facet was taken to represent this point.
(4) The tip of the lingual cusp determined by inspection. In the case of worn teeth, in which minimal dentine exposure was present, the centre of the dentinal facet was taken to represent this point.
(5) The distal fovea, or the intersection of the median longitudinal fissure with the distal foveal fissure/ transverse fissures.
(6) The point on the distal border of the crown located directly opposite (i.e. distal to) point 5.
(7) The point on the buccal border of the crown which marks either (A) the intersection of the disto-buccal foveal/transverse fissure with the buccal border, or (B) which is located directly opposite (i.e. buccal to) the termination of the distobuccal foveal/transverse fissure.
(8) The point on the lingual border of the crown which marks either (A) the intersection of the distolingual foveal/transverse fissure with the lingual border, or (B) which is located buccolingually opposite the termination of the distolingual foveal/transverse fissure.
(9) The most mesial point on the crown.
(10) The most buccal point on the crown.
(11) The most lingual point on the crown.
(12) The most distal point on the crown.
(13) The point which represents the intersection of the mesiobuccal/distolingual diagonal with the mesiobuccal border of the crown.
(14) The point which represents the intersection of the mesiolingual/distobuccal diagonal with the mesio-lingual border of the crown.
(15) The point which represents the intersection of the mesiolingual/distobuccal diagonal with the distobuccal border of the crown.
(16) The intersection of the mesiobuccal diagonal with the distolingual border of the crown.

arranged so that it passed through the most buccal point on the crown. The intersection of the axes served as the origin (0, 0) for the co-ordinate analysis, and, for purposes of calibration, marks were made on both axes 7 cm from the origin (Fig. 3).

The tracings were analysed on a PCD-Type 1B digitizer. In order to compensate for minor differences in magnification of the occlusal photographs, the digitizer was calibrated using the 7 cm marks. The X/Y co-ordinates of each reference point were then recorded. All tracings were made by the same observer, but the interpretations of the fissure pattern were always checked with a second person. Checks on the measurement technique have established that errors in the co-ordinate plotting are minimal.

The co-ordinates used to define the fissure pattern and crown outline were analysed by 'Procrustes' analysis (Gower, 1975). This technique undertakes a pairwise comparison of the patterns of reference points. The patterns are enlarged translated and rotated so that the sum of the squared distances between homologous points is minimised. The algorithm defines the centroid (or 'centre of gravity') of each crown pattern as the mean of the X and Y co-ordinates of all the points. Differences in size are eliminated by expanding or contracting the image ('enlargement') so that the sum of the squared distances between each point and the centroid is equal to unity. The centroids of each pair are then lined up ('translation') and finally the pattern of points is rotated around the axis of the centroid ('rotation') until the sum of the squared distances between landmarks is minimised. In this case, because all the points are in two dimensions, the 'rotation' is simply a matter of finding a single angle. 'Procrustes' analysis can also 'reflect' the image, but this was unnecessary in this study because the tracings of the right teeth had been mirror-imaged at an earlier stage of an analysis.

The sum of the squared distances is an expression of 'likeness' between each pair of tooth crowns, and these pairwise comparisons are combined to form a similarity matrix. In this study, the complex relationships between teeth expressed in the matrix have been portrayed in two ways. In the first, the tooth crowns were represented by points which were plotted using axes which preserve the maximum amount of information about relationships, the so-called Principal Coordinates (PCd) (Gower, 1966). In the second method, the distance of each tooth from the centroids of the taxonomic categories was expressed as a distance measure, and these were assembled into a matrix for each tooth type.

RESULTS

Crown size

The results of the computed and directly measured estimates of crown size, the latter determined as the crown base area, are presented in two Tables. The first of these, Table 6, gives a statistical summary of the data for the four main taxonomic groups and compares the two values for computed crown area with the area measured by planimetry (MCBA); Table 7 provides the same data for individual teeth in the 'unknown' category. Adjustments of the mesiodistal diameter for interproximal wear result in insignificant differences between the uncorrected and corrected computed crown area, and there are no systematic differences in the effect of wear on the size of the P_3s and P_4s.

The measured crown base area of each tooth crown is less than the computed area and the extent to which computed crown base area over-estimates the measured area is presented as a percentage difference in Table 8. The mean values and the range of discrepancies for each taxonomic category given in that Table show that, with the exception of EAFROB, the discrepancies between the two measures, and therefore the degree of deviation from a rectangular outline, are greater for P_3 than for P_4.

Crown shape

The shape of the crown outline has been compared using the crown shape index; approximately square crowns have values of 100 and crowns which are relatively

Table 6. *Crown base areas of the four major taxonomic categories of Plio-Pleistocene hominid mandibular premolars (all areas are given in mm²).*

	P_3						P_4					
	X	*N*	S.D.	C.V.	Min.	Max.	*X*	*N*	S.D.	C.V.	Min.	Max.
EAFROB												
Computed (U)	142	6	13·9	9·8	126	158	205	14	23·6	11·5	169	240
Computed (C)	144	6	15·5	10·8	126	165	208	13	25·5	12·3	172	240
Measured (C)	116	5	16·2	14·0	90	131	159	13	24·3	15·3	123	191
SAFROB												
Computed (U)	114	15	12·1	10·6	95	130	148	10	16·3	11·0	126	178
Computed (C)	117	15	12·0	10·3	95	132	151	10	15·8	10·5	132	178
Measured (C)	88	15	9·0	10·3	69	104	118	11	14·2	12·0	98	136
SAFGRA												
Computed (U)	113	3	12·1	10·7	106	127	125	4	10·6	8·5	119	141
Computed (C)	113	3	12·1	10·7	106	127	127	4	12·2	9·6	119	145
Measured (C)	80	4	13·2	16·5	66	96	102	4	9·3	9·1	92	114
EAFHOM												
Computed (U)	90	8	16·2	18·0	70	117	98	9	15·0	15·3	70	113
Computed (C)	92	11	13·6	15·4	71	118	99	9	13·9	14·0	74	113
Measured (C)	69	8	10·4	15·1	53	86	77	9	11·1	14·4	55	89

(U) = uncorrected. (C) = corrected.

Table 7. *Crown base areas of Plio-Pleistocene hominid mandibular premolars other than those in the main taxonomic categories (all areas in mm²)*

	Computed (uncorrected)	Computed (corrected)	Measured (corrected)
P_3			
KNM-ER 1802 R	123	123	94
KNM-ER 1808 L	88	88	—
KNM-ER 5431 R	129	129	86
KNM-ER 5431 L	129	129	87
O.H. 22 R	93	93	65
SK 18 L	87	90	70
P_4			
KNM-ER 1482 L	116	118	—
KNM-ER 1802 R	137	137	110
KNM-ER 1802 L	143	143	115
KNM-ER 5431 L	154	154	106
O.H. 22 R	86	90	70
SK 1587 L	123	126	103
SK 1588 R	126	126	105

elongated mesiodistally have lower values. The mean values and a statistical summary of the four major taxonomic categories are given in Table 9. There is considerable overlap between the crown shape of the taxonomic categories for both tooth types, but trends and statistically significant differences are to be found among both the P_3 and P_4 values. The narrowest P_3 crowns are seen in EAFHOM and the broadest (i.e. most buccolingually expanded) in SAFGRA. Thus, P_3 crown shape does offer a useful discriminator for determining the taxonomic affinities of the smaller-toothed East African remains, a proposal that was first made more than two decades ago (Leakey, Tobias & Napier, 1964). Among the P_4 crowns it is the two East African taxonomic

Table 8. *Comparisons of the percentage difference between computed and measured corrected crown base areas for the four major taxonomic categories of early hominid mandibular premolars (computed − measured/measured* × 100).

	X	*N*	S.D.	Min.	Max.
P_3					
EAFROB	28·3	5	10·1	20·6	45·3
SAFROB	33·0	15	5·3	23·0	40·0
SAFGRA	33·8	3	9·4	25·3	48·8
EAFHOM	33·5	8	3·9	28·1	38·6
P_4					
EAFROB	30·6	12	7·1	21·0	39·6
SAFROB	26·8	10	6·5	18·1	36·0
SAFGRA	25·3	4	5·3	18·0	30·6
EAFHOM	28·2	9	4·5	21·1	34·0

Table 9. *Crown shape indices (BL/MD(C)* × 100) *of hominid mandibular premolar teeth*

	X	*N*	S.D.	Min.	Max.
P_3					
EAFROB	117	6	10·2	103	133
SAFROB	116	15	8·2	95	127
SAFGRA	124	3	10·4	113	134
EAFHOM*	105	11	12·1	90	128
P_4					
EAFROB†	107	13	6·2	97	116
SAFROB	117	10	5·5	110	123
SAFGRA	116	4	6·1	111	124
EAFHOM	109	9	11·6	89	128

	X		*X*
KNM-ER 1482 P_4 L	126	KNM-ER 5431 P_4 L	103
KNM-ER 1802 P_3 R	107	O.H. 22 P_3 R	91
KNM-ER 1802 P_4 R	105	O.H. 22 P_4 R	111
KNM-ER 1802 P_4 L	97	SK 18 P_3 L	113
KNM-ER 1808 P_3 L	116	SK 1587 P_4 L	108
KNM-ER 5431 P_3 R	131	SK 1588 P_4 R	110
KNM-ER 5431 P_3 L	123		

* EAFHOM and SAFGRA mean values are significantly different at $P < 0{\cdot}05$ (2-tailed). EAFHOM and EAFROB mean values are significantly different at $P < 0{\cdot}05$ (2-tailed).

† EAFROB and SAFGRA mean values are significantly diffferent at $P < 0{\cdot}05$ (2-tailed). EAFROB and SAFROB mean values are significantly different at $P < 0{\cdot}001$ (2-tailed).

categories that have relatively narrow P_4 crowns. Thus, crown shape independent of crown size apparently does not separate EAFROB from EAFHOM, but interestingly there is a notable difference between the shape of the P_4 crowns of the EAFROB and SAFROB samples.

Morphological traits

The expression of the four morphological variates of the tooth crown has been recorded for each of the mandibular premolar taxonomic groups (Table 10). With only a few exceptions, the sample sizes are too small for statistical tests of frequency

Table 10. *Incidence of morphological traits in the four major taxonomic groups of Plio-Pleistocene hominid mandibular premolars*

	Cusp no.				Relative position lingual cusp*			Median longitudinal fissure*			Marginal grooves			
											MB†	DB	DL	ML
	2	3	4	5	1	2	3	1	2	3	P A‡	P A	P A	P A
P_3														
EAFROB	1	2	0	0	3	0	1	3	0	0	2–0	2–1	0–2	0–2
SAFROB	5	2	1	0	9	5	0	7	3	0	5–8	11–2	0–8	2–7
SAFGRA	4	0	0	0	2	2	0	0	4	0	7–1	8–0	2–3	1–4
EAFHOM	10	0	0	0	0	5	3	0	1	9	7–2	6–3	0–8	4–3
P_4														
EAFROB	0	2	2	3	8	2	0	13	0	0	7–4	11–0	1–7	0–9
SAFROB	0	5	1	1	4	5	0	6	1	0	2–7	9–0	4–4	0–9
SAFGRA	3	0	0	0	1	2	0	1	1	0	2–2	3–1	0–4	0–4
EAFHOM	6	2	0	0	0	8	0	3	4	1	2–5	4–3	2–5	0–7

* for explanation of the code, see Table 4.
† MB = mesiobuccal; DB = distobuccal; DL = distolingual; ML = mesiolingual.
‡ P = present; A = absent.

to be reliable, and the results will therefore be discussed in terms of the distributions given in Table 10 and summarised in Table 11.

Cusp number

There are differences in the incidence of additional cusps both between taxonomic categories and between tooth types within those categories. Only 'robust' australopithecine P_3s have more than two cusps, but an additional cusp (or cusps) is apparently not a *sine qua non* of the relatively small 'gracile' australopithecine sample. For P_4s, the distribution is somewhat clearer. No 'robust' australopithecine P_4 has just the two main cusps, whereas only two out of 11 'non-robust' hominid P_4s have more than two cusps. Posterior premolar teeth with four or more cusps are only found within the two 'robust' australopithecine taxonomic categories.

Relative positions of the lingual cusp

The degree of symmetry of the trigonid part of early hominid mandibular premolar crowns varies more between taxa than between tooth type. With only one exception in both P_3 and P_4, the lingual cusp is either mesial to, or aligned with, the main buccal cusp in the two 'robust' australopithecine categories. This is also the pattern for the small sample of teeth in the SAFGRA category, but in EAFHOM none of the 16 premolar crowns has a lingual cusp which is mesial to the main buccal cusp.

Median longitudinal fissure

The two 'robust' taxonomic categories are consistent in that for both P_3 and P_4 (a total of 33 teeth), all but four are scored as having a deeply incised median fissure, and even the four exceptions are classed as having a moderately incised fissure. The pattern for the two 'non-robust' taxonomic categories, and for EAFHOM in particular, is inconsistent between tooth types. For P_3, all but one of ten teeth are scored as having no evidence of a median longitudinal fissure, whereas for P_4 the sample is split nearly equally between the deeply and moderately incised states for the fissure.

Table 11. *Summary of morphological trait distribution between taxonomic categories*

Cusp no.	Relative position of lingual cusp		Median longitudinal fissure		Marginal grooves	
P_3						
EAFROB 2 >	EAFROB	Mesial	EAFROB	Deep		
SAFROB	SAFROB	or	SAFROB		SAFROB –	Shallow MB
	SAFGRA	central				
			SAFGRA –	Shallow	SAFGRA –	Deeper MB and DB
SAFGRA	EAFHOM –	Distal				
			EAFHOM –	Absent	EAFHOM –	Absent DB
EAFHOM < 2						
P_4						
EAFHOM 3 >	EAFROB	Mesial	EAFROB	Deep	EAFROB	Deep
SAFROB	SAFROB	or	SAFROB		SAFROB	DB
SAFGRA		central				
SAFGRA	EAFHOM –	central, none	SAFGRA	Variable	SAFGRA	Variable
EAFHOM < 3		mesial	EAFHOM		EAFHOM	DB

Grooves

In general, all taxonomic categories tend to have a higher incidence of buccal than of lingual grooves. There is more concordance between groove incidence lingually or buccally than there is between the possible mesial or distal groove locations. The distribution of grooves in the P_4s shows more polarisation than for P_3 crowns. Distobuccal grooves are present in all 20 mandibular premolar crowns allocated to the two 'robust' categories, yet not one of the 18 teeth of the same two categories possesses a mesiolingual groove. Indeed, whereas seven out of 23 hominid P_3s have a mesiolingual groove, none of the 29 early homonid P_4s in this sample has such a feature.

Cusp and talonid areas

Univariate analysis

A statistical summary of the absolute areas of the three main cusp components of the four major taxonomic categories is presented in Table 12 and a summary of the corresponding relative areas is given in Table 13. The values of both absolute and relative cusp areas for teeth in the minor taxonomic categories and in the 'unknown' group are given in Table 14. The significance of the differences between the mean values of the taxonomic groups has been explored using pairwise Student's *t*-tests, and the results of these are presented in Table 15. A striking aspect of these results is the consistency in relative size of the main lingual cusp across both tooth type and taxonomic category (Figs. 4, 5); the major variations are between taxonomic categories. The P_3s and P_4s of EAFROB both have a relatively larger talonid than do the corresponding teeth of the two 'non-robust' categories. The 'robust' australopithecines from southern Africa sites also show evidence of relative expansion of the distal part of the premolar crown, but not to such an exaggerated degree as is seen in EAFROB. SAFGRA and EAFHOM are similar to each other with respect to the relative areas of the cusp components but differ from the two 'robust' groups. The talonid is relatively larger in the P_4s than the P_3s in all four taxonomic categories.

Table 12. *Absolute main cusp and talonid areas of early hominid mandibular premolars by taxonomic category*

	Buccal cusp					Lingual cusp					Talonid				
	X	*N*	S.D.	Min.	Max.	*X*	*N*	S.D.	Min.	Max.	*X*	*N*	S.D.	Min.	Max.
P_3															
EAFROM	40·4	3	5·0	35·3	45·2	31·4	3	4·3	26·6	35·0	41·7	3	12·9	28·7	54·6
SAFROB	39·3	14	5·2	28·6	48·7	24·2	13	3·6	16·8	28·7	25·1	13	4·8	17·9	31·9
SAFGRA	41·9	4	7·1	36·3	51·0	20·9	4	4·6	16·7	25·8	17·3	4	3·4	12·7	20·4
EAFHOM	36·2	8	8·1	21·0	44·3	17·6	8	3·8	12·9	23·0	15·2	8	3·0	10·0	19·9
P_4															
EAFROB	45·9	11	9·0	33·1	57·1	47·1	11	10·1	28·3	58·0	67·9	11	7·6	58·3	76·7
SAFROB	42·2	9	4·9	33·5	48·6	32·7	9	4·3	26·8	40·1	41·8	9	7·7	27·6	50·5
SAFGRA	41·2	4	5·1	36·3	48·0	29·2	4	2·7	25·5	31·5	30·8	4	3·6	27·2	35·6
EAFHOM	32·8	8	4·7	24·9	38·8	24·4	8	3·0	20·9	28·4	22·7	8	5·2	14·7	28·5

The sample sizes do not always accord with the numbers of specimens listed in the Materials and Methods section. The damaged teeth which have been excluded are listed below.

P_3: EAFROB–KNM-ER 1816, 729 and Peninj.
SAFROB–SK 30 and SK 6 (lingual cusp and talonid).
EAFHOM–KNM-ER 806 R and L.

P_4: EAFROB–KNM-ER 818, 1801,1816 (lingual cusp and talonid), and Peninj R and L.
SAFROB–SK 34 and 74.
EAFHOM–KNM-ER 3734.

Table 13. *Relative main cusp and talonid areas of early hominid mandibular premolars by taxonomic group*

	Buccal cusp					Lingual cusp					Talonid				
	X	*N*	S.D.	Min.	Max.	*X*	*N*	S.D.	Min.	Max.	*X*	*N*	S.D.	Min.	Max.
P_3															
EAFROB	36·1	3	2·7	34·4	39·1	28·0	3	2·9	24·7	29·8	36·3	3	4·9	31·8	41·6
SAFROB	44·4	14	4·2	36·2	51·4	27·4	13	2·8	23·1	30·7	28·5	13	4·6	21·4	34·9
SAFGRA	52·3	4	2·6	48·9	55·3	26·0	4	2·2	23·3	28·4	21·8	4	3·9	19·3	27·5
EAFHOM	52·1	8	6·9	39·6	60·4	25·8	8	6·4	19·4	39·6	22·0	8	3·2	17·6	27·5
P_4															
EAFROB	29·1	11	2·1	25·3	33·2	28·9	10	2·7	23·0	32·1	42·6	10	4·0	37·6	50·0
SAFROB	36·4	9	3·5	32·3	44·2	28·0	9	2·0	25·1	31·3	35·7	9	3·6	28·2	40·3
SAFGRA	40·5	4	1·8	38·4	42·1	28·9	4	2·7	25·6	31·5	30·3	4	2·1	27·2	31·9
EAFHOM	41·2	8	5·5	33·8	52·0	30·6	8	2·8	27·5	36·4	28·3	8	5·1	20·1	32·6

The damaged teeth which have been excluded are the same as in Table 12.

Table 14. *Absolute and relative cusp and talonid areas for hominid mandibular premolars other than those in the major taxonomic categories*

	Buccal cusp (absolute)	Lingual cusp (absolute)	Talonid (absolute)	Buccal cusp (relative)	Lingual cusp (relative)	Talonid (relative)
P_3						
KNM-ER 1802 R	43·0	23·0	27·3	45·9	24·5	29·1
KNM-ER 1808 L	—	—	—	—	—	—
KNM-ER 5431 R	53·8	18·3	13·7	62·9	21·4	16·0
KNM-ER 5431 L	61·0	13·8	12·2	70·4	15·9	14·1
O.H. 22 R	34·2	17·3	13·0	52·8	26·7	20·1
SK 18 L	33·3	21·0	15·3	47·8	30·2	22·0
P_4						
KNM-ER 1482 L	—	24·0	—	—	—	—
KNM-ER 1802 R	38·8	31·6	38·8	35·4	28·8	35·4
KNM-ER 1802 L	41·1	32·9	40·1	35·7	28·6	34·8
KNM-ER 5431 L	40·9	26·3	38·9	38·7	24·9	36·8
O.H. 22 R	31·6	19·6	19·2	45·1	28·0	27·4
SK 1587 L	37·9	24·8	41·4	36·8	24·1	40·2
SK 1588 R	40·8	29·6	34·4	38·9	28·2	32·8

Multivariate analysis

The retention of overall size (i.e. absolute cusp areas) has little effect on the distribution of P_3s, but the separation between the P_4s of EAFHOM and SAFGRA is better for the absolute (Fig. 8) than for the relative cusp area data (Figs. 7, 8).

The percentage variance and the eigen-vectors explained by, and generated from, the principal components analysis of the absolute and relative cusp area data for P_3s and P_4s are given in Table 16. The three elements of the first principal component (PFm I) computed from the absolute cusp area data are equal in size for both P_3 and P_4, but the patterns of weighting differ between the teeth. The weights are approximately equal for each of the three main crown components in the P_4s, suggesting that PCm I represents a true 'size axis' for this tooth. However, they are unequal for P_3, suggesting that both 'shape' and 'size' information are included in this axis (Jolicoeur & Mosimann, 1960; Wood, 1978). As one would expect, the sign and the weightings become more heterogeneous when size is deliberately removed as in the relative cusp area values. Thus, as was the case for the molar teeth (Wood *et al.* 1983), separation along PCm I of the absolute cusp area data is dominated by size and not shape and it is for this reason that further discussion will concentrate on the relative cusp area data. Inspection of the separate P_3 and P_4 plots (Figs. 6, 7) shows a relatively continuous distribution of specimens along PCm I. Individual members of the taxonomic categories are not distributed randomly, but are grouped as indicated by the symbols; the grouping is tighter for the P_4s than for the P_3 data. The greatest admixture of taxonomic groupings is between SAFGRA and EAFHOM; EAFROB and SAFROB are relatively distinct from each other and from the other two taxonomic categories. The factors responsible for the arrangement of the individual specimens along the pairs of orthogonal axes are given as annotations to the respective figures. Although the first two principal components account for the majority of the variance, they do not account for all of it. The distribution of the taxonomic categories within the total hyperspace can be best judged from the matrix of Mahalanobis D^2 distances; the distances between groups means are given in Table 17. The distribution of specimens

Table 15. *Between-group comparisons of relative cusp areas: significance values based on t-test, using pooled variances and two-tailed model*

	Buccal cusp				Lingual cusp				Talonid			
	EAFROB	SAFROB	SAFGRA	EAFHOM	EAFROB	SAFROB	SAFGRA	EAFHOM	EAFROB	SAFROB	SAFGRA	EAFHOM
P_3												
EAFROB	—				—				—			
SAFROB	< 0·01	—	—	—	N.S.	—	—	—	< 0·05	—	—	—
SAFGRA	< 0·001	< 0·01	—	—	N.S.	N.S.	—	—	< 0·01	< 0·05	—	—
EAFHOM	< 0·01	< 0·01	N.S.	—	N.S.	N.S.	N.S.	—	< 0·001	< 0·01	N.S.	—
P_4												
EAFROB	—				—				—			
SAFROB	< 0·001	—	—	—	N.S.	—	—	—	< 0·001	—	—	—
SAFGRA	< 0·001	< 0·05	—	—	N.S.	N.S.	—	—	< 0·001	< 0·05	—	—
EAFHOM	< 0·001	< 0·05	N.S.	—	N.S.	< 0·05	N.S.	—	< 0·001	< 0·01	N.S.	—

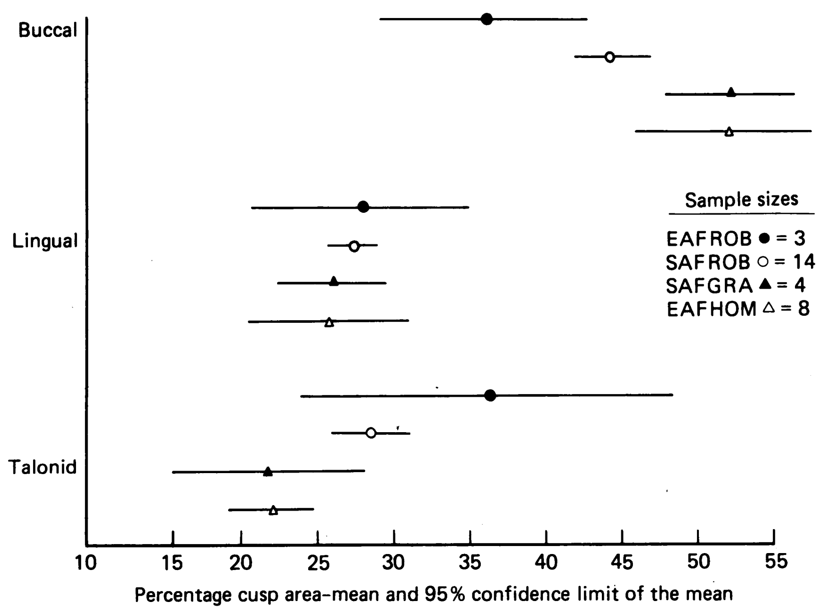


Fig. 4. Mean values and 95% confidence limits of the relative areas of the main cusps and talonid of the P_3s for the major taxonomic categories. The sample sizes of the taxa marked with an asterisk are one smaller than the number given in the Figure.

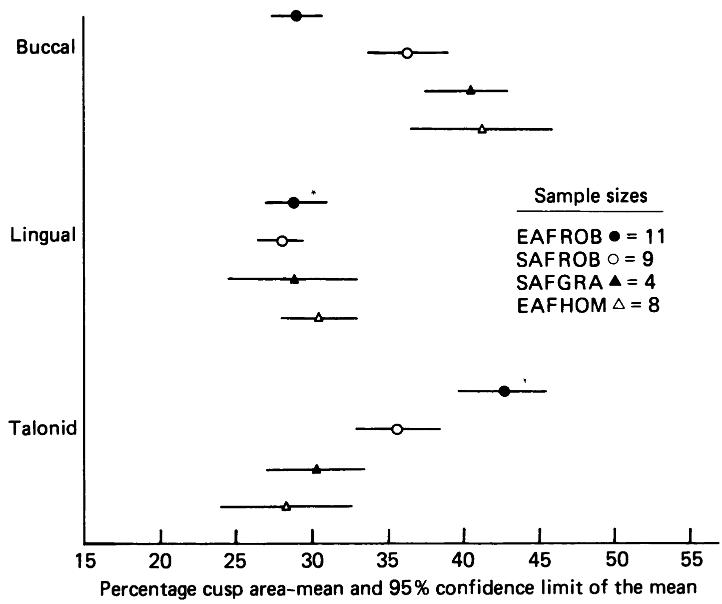


Fig. 5. Mean values and 95% confidence limits of the relative areas of the main cusps and talonid of the P_4s for the main taxonomic categories. The sample sizes of the taxa marked with an asterisk are one smaller than the number given in the Figure.

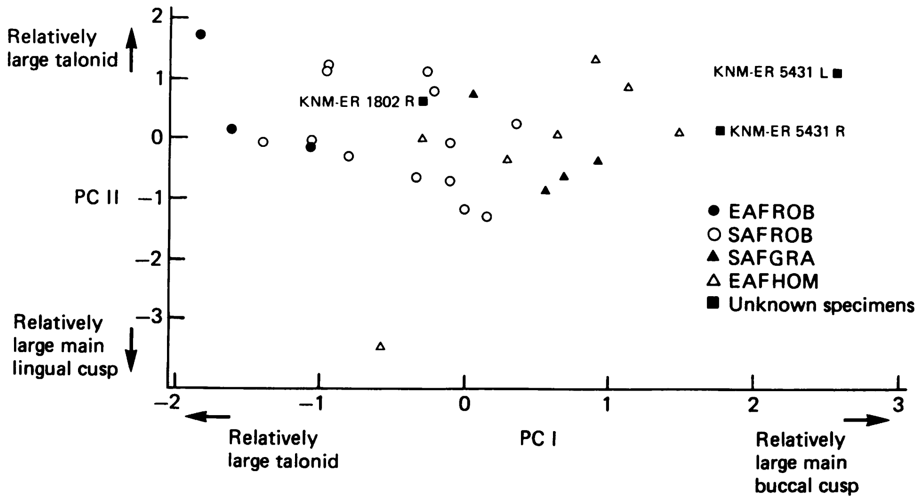


Fig. 6. Plot of the first (PC I) and second (PC II) principal components generated from the covariance matrix of the relative cusp area data for early hominid P_3s.

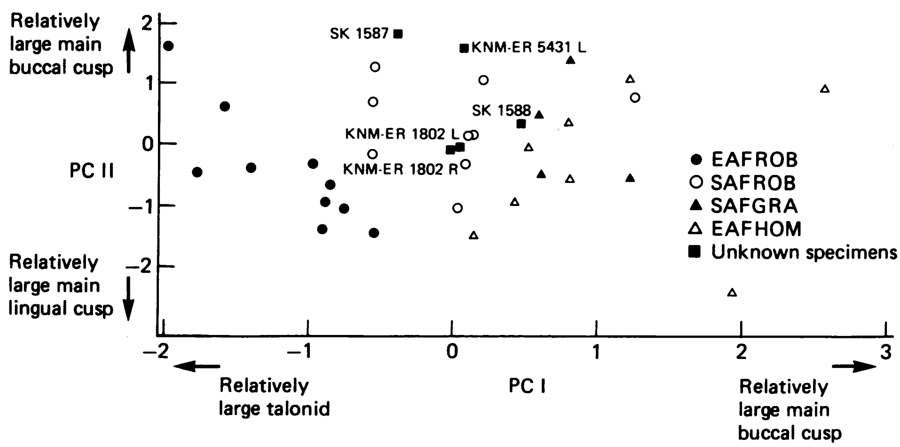


Fig. 7. Plot of the first (PC I) and second (PC II) principal components generated from the covariance matrix of the relative cusp area data for early hominid P_4s.

which have right and left teeth preserved provides a useful perspective on the differences between taxonomic categories and individual specimens and antimeres have been specially identified in Figures 6, 7 and 8.

Fissure pattern

The arrangement of the major fissures in the hominid mandibular premolars has been compared using the sum of the squared distances between homologous landmarks. A pair of teeth with little difference in fissure pattern would have similar values. Such pairwise comparisons result in a similarity matrix and the relationships between teeth determined from such a matrix have been pictured graphically using Principal Coordinate Axes (Gower, 1966). The relationships between the P_3s and P_4s in the sample are represented in Figures 9 and 10.

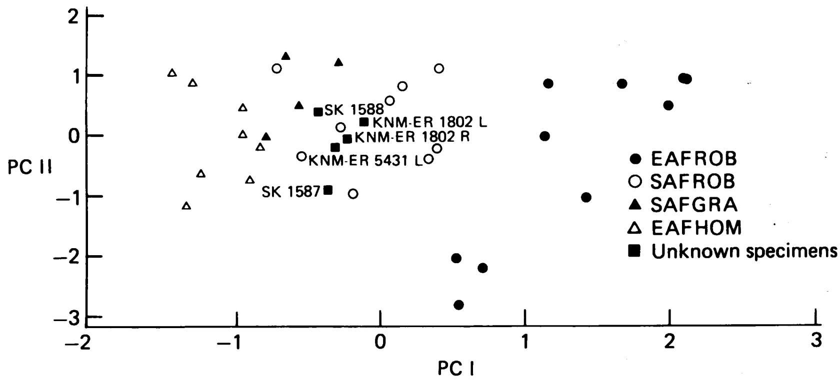


Fig. 8. Plot of the first (PC I) and second (PC II) principal components generated from the covariance matrix of the absolute cusp area data for early hominid P_4s.

Table 16. *Percentage contributions to the total variance and eigenvector scores of the first and second principal components derived from absolute and relative cusp area data for hominid mandibular premolars*

	Absolute cusp area				Relative cusp area			
	PCm I		PCm II		PCm I		PCm II	
	P_3	P_4	P_3	P_4	P_3	P_4	P_3	P_4
Eigen-values								
Percentage variance	0·60	0·90	0·33	0·07	0·83	0·88	0·17	0·12
Eigen-vectors								
Buccal cusp	0·10	0·77	0·99	0·59	0·99	0·96	0·11	0·28
Lingual cusp	0·84	0·94	−0·01	0·25	−0·57	0·33	−0·82	−0·94
Talonid	0·98	0·99	−0·07	−0·17	−0·89	−0·99	0·45	0·16

In the plots, the first (PCd I) and second (PCd II) principal co-ordinates explain rather more than (P_3 = 58 %) and slightly less than (P_4 = 48 %) half the variance, but for both teeth PCd I contains a little more than a third of the total variance (P_3 = 38 %; P_4 = 35 %). There is less overlap between taxonomic categories in the P_4s than for the P_3s. The nature of the reference points used in this study means that differences in the aggregate of the squared distances reflect not only fissure pattern, but also crown shape. This joint contribution to the pattern of distances is reflected in the fissure and crown outlines of teeth which illustrate the ends of the range of variation of respective P_3s (Fig. 11) and P_4s (Fig. 12). The fissure patterns of teeth within the 'unknown' category will be considered in the discussion section.

DISCUSSION

This analysis has provided precise metrical evidence of heteromorphy of early hominid P_3s and P_4s, both between tooth types and taxonomic categories. Comparisons between the traditional computed crown area measurements taken in this study, and those of an earlier study (White, Johanson & Kimbel, 1981) show there to be little discrepancy between comparable sample parameters. The maximum dis-

Table 17. *Mahalanobis D^2 distances between the means of the taxonomic categories derived from the covariance matrix of relative cusp area data for hominid P_3s and P_4s*

	EAFROB	SAFROB	EAFHOM	SAFGRA
P_3				
EAFROB	—	—	—	—
SAFROB	1·98	—	—	—
EAFHOM	3·87	1·91	—	—
SAFGRA	3·89	1·92	0·09	—
P_4				
EAFROB	—			
SAFROB	2·82	—	—	—
EAFHOM	4·45	1·92	—	—
SAFGRA	4·54	1·79	0·93	—

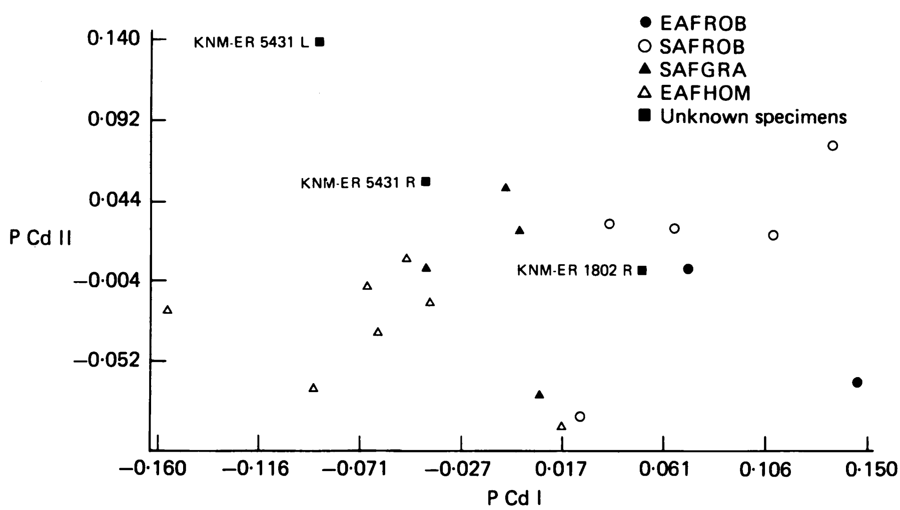


Fig. 9. Principal coordinate plot of early hominid P_3 fissure pattern data.

crepancy is 8% and the average is 3·5%; these are comparable levels of correspondence to those noted between studies for the the mandibular molar data (Wood & Abbott, 1983). However, these differences do not alter the high average discrepancy between computed crown areas, as computed in either study, and the more precise and accurate direct measurements of crown base area made in the present analysis.

The differences in overall crown base area between the major taxonomic categories are greater for P_4 than for P_3. The ranges of the anterior mandibular premolar crown areas of EAFROB and EAFHOM do not overlap, but there is considerable overlap between SAFGRA and, on the one hand, the larger-toothed SAFROB category, and on the other, the smaller-toothed EAFHOM specimens. The pattern of distribution of P_4 overall size is the same as that for the P_3s but, at least for the samples used in this study, the intertaxonomic differences are greater so that, for example, there is no range overlap in the P_4s between EAFHOM, SAFGRA and EAFROB (Fig. 13). As these are the three taxa which are most likely to be represented at East African hominid sites, this observation may help with the taxonomic assessment of specimens whose allocation is in doubt. In particular it may help to sort mandibles which have teeth

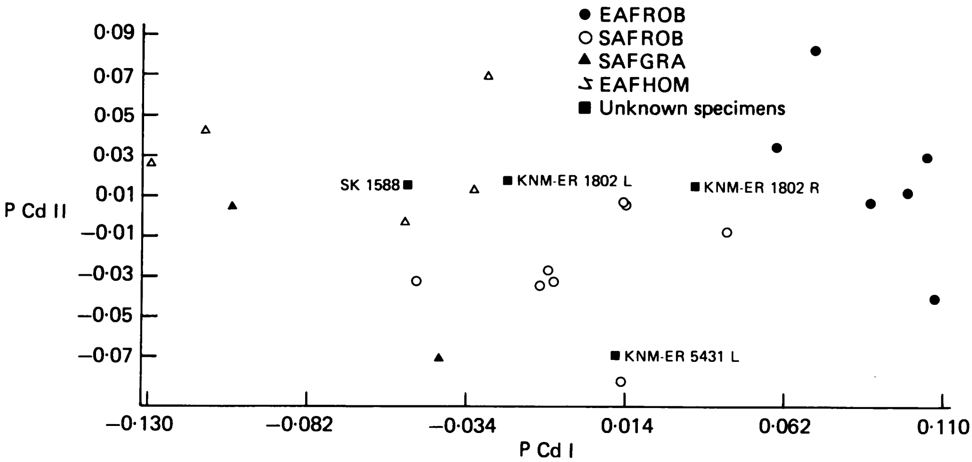


Fig. 10. Principal coordinate plot of early hominid P_4 fissure pattern data.

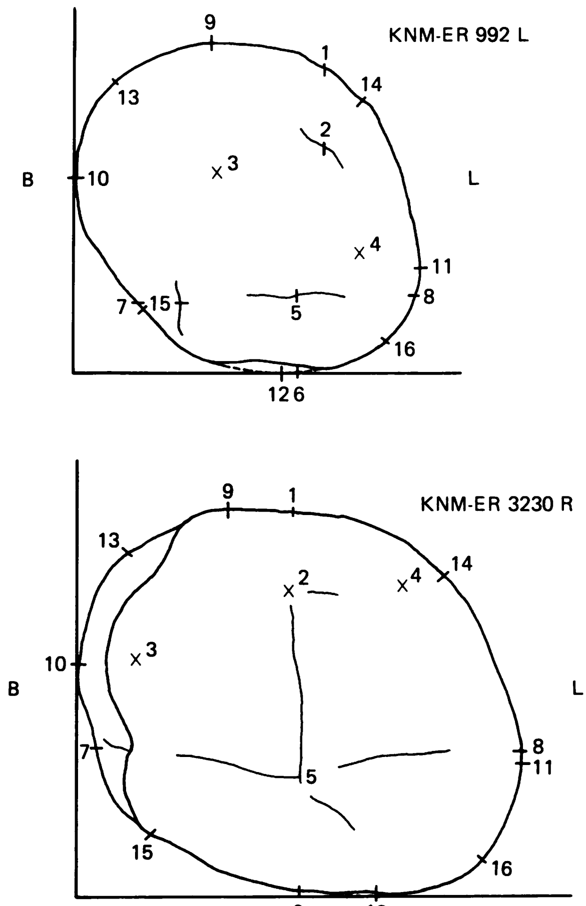
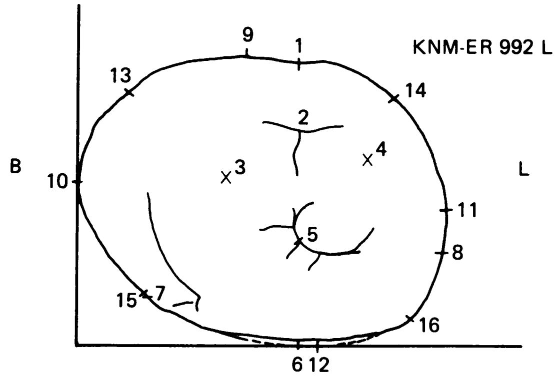


Fig. 11. Specimens illustrating the extremes of the range of variation of the fissure pattern of early hominid P_3s. Patterns have been mirror-imaged to facilitate comparison.



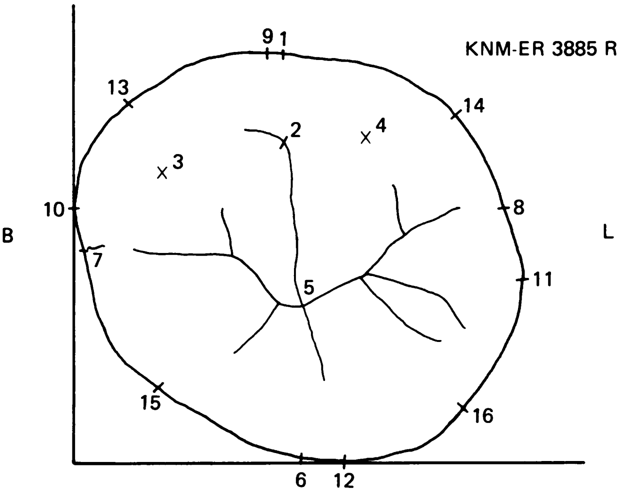


Fig. 12. Specimens illustrating the extremes of the range of variation of the fissure pattern of early hominid P_4s. Patterns have been mirror-imaged to facilitate comparison.

preserved *in situ* but whose taxonomic attribution is problematic (Wood & Van Noten, 1986).

Mandibular premolar crown shape was cited as one of the defining features of *Homo habilis* in the original description of that taxon (Leakey *et al.* 1964). Claims made in that paper formed the basis of a lively exchange of opinion (Robinson, 1965; Tobias, 1966). Sperber (1974) more recently included an assessment of crown shape in his analysis of australopithecine dental remains from sites in southern Africa. Tobias (1966) found that the shape contrasts between australopithecines and early hominines to be greater for P_4 than P_3. Sperber (1974) commented on the degree of individual variability in crown shape for both tooth types, but suggested that P_4 variation was the more systematic of that in the two tooth types.

The results of this recent study point to the contrary conclusion, i.e. that crown shape discriminates better between taxonomic categories for P_3 than for P_4. Although the range of crown shape index values of the EAFHOM sample overlaps with those of EAFROB and SAFGRA, the sample means are significantly different at the 5% level (Table 9). The average shape indices for the P_4s are smaller than those for the

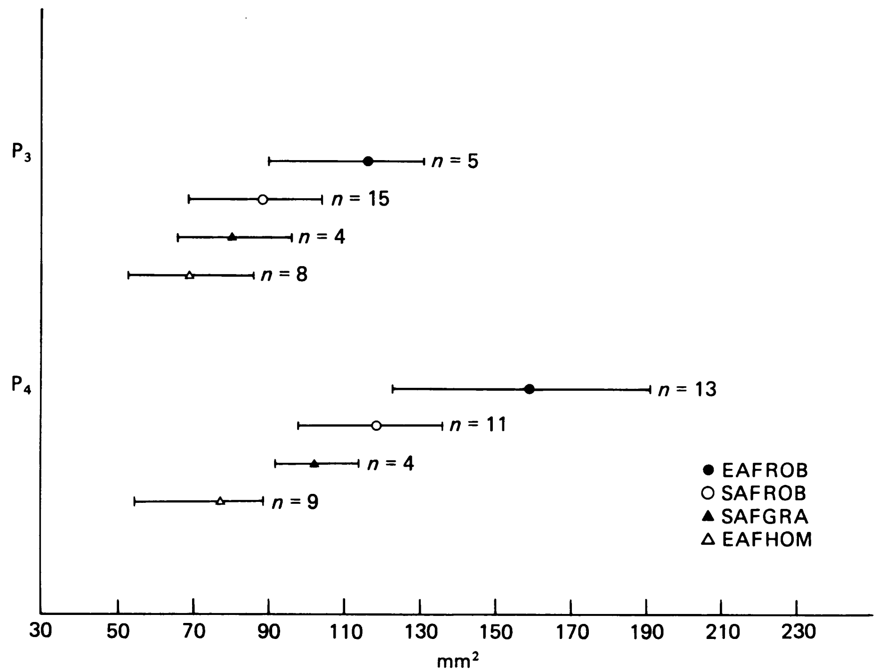


Fig. 13. Mean and range of P_3 and P_4 measured crown base area of the major taxonomic categories of early hominid mandibular premolars.

P_3s in EAFROB and SAFGRA. This is, however, not so much an expression of differences in buccolingual breadth, but more an indication of the degree to which the talonid is elongated in P_4 in these two taxonomic categories. The shape differences between the P_4s of EAFROB and SAFROB are statistically significant, but puzzling. When Jungers & Grine (1986) studied the shape trends within the mandibular molars, they found that EAFROB molars were relatively more elongated than those of SAFROB. For the P_4s, the relatively more elongated teeth are apparently in the SAFROB category.

Several workers have commented on the differences in crown morphology between the mandibular premolars attributed to *Australopithecus robustus* and *A. africanus*, but Robinson (1956) and Sperber (1974) have provided the most detailed analyses of this material. Robinson (1956) suggested that the P_3 crown of *A. africanus* was asymmetrical, with a well-defined lingual cusp, and that the buccal grooves of the teeth of that taxon were more marked than those in *A. robustus*. In *A. africanus* the mesial buccal groove was also deeper than the distal one and the median longitudinal fissure was also shallower. The P_4 crowns of *A. africanus* were also more asymmetrical and the buccal grooves were claimed to be equally well-developed, with any differences in depth being in *A. robustus*, in which the distal groove was the deeper. Sperber (1974) came to essentially similar conclusions about the groove systems and he also stated that in both the P_3s and P_4s of *A. africanus* the lingual cusp is consistently situated mesial to the buccal one. He claimed that in *A. robustus* the relationship of the main cusps is more variable. The two authors differ in their assessment of cusp number, with Robinson (1956) suggesting that *A. africanus* P_3s have just two cusps, whereas Sperber (1974) refers to all australopithecine mandibular premolars as tricuspid.

The results of the present survey support some of these conclusions, but not others

(Table 10). The P_3 crown scores for cusp number are decisive in suggesting that teeth with more than two cusps are confined to the two 'robust' australopithecine taxonomic categories. As far as the disposition of the two main P_3 cusps is concerned, all three australopithecine taxonomic categories have lingual cusps which are either mesial to, or alongside, the buccal cusps. In EAFHOM, the lingual cusp is either alongside, or distal to, the buccal cusp element. The form of the P_3 median longitudinal fissure also shows variation between taxonomic categories. It is scored as deeply incised in the two 'robust' australopithecine categories, intermediate in SAFGRA and is absent in the majority of EAFHOM teeth. The pattern of marginal grooves demonstrated in this study confirms the observations of Robinson (1956) and Sperber (1974), i.e. buccal grooves are more marked than lingual, with the mesiobuccal grooves in SAFGRA being deeper than those in SAFROB.

In the posterior premolars the trends for three of the observations, that is cusp number, cusp disposition and median longitudinal fissure development, are similar to those observed for the P_3s. Thus, 'robust' australopithecine P_4s have three, or more cusps, and EAFHOM is the taxonomic category in which none of the crowns is scored as having mesially situated lingual cusps. The two 'robust' australopithecine taxonomic categories, with the exception in each of a single individual, have marked median longitudinal fissures, with only EAFHOM showing evidence of significant enamel bridging between the two main cusps. As far as the marginal grooves are concerned, the distobuccal groove is consistently deeper in the two 'robust' taxonomic categories, whereas its expression in SAFGRA and EAFHOM is more variable. The distribution of morphological traits among the taxonomic categories is summarised in Table 11, and it is evident that all four traits can contribute to taxonomic diagnosis. Cusp number will distinguish 'robust' from 'non-robust' taxonomic categories, and the three other features have the potential to sort EAFHOM teeth from those of the SAFGRA category.

Much of the discussion about the morphology of australopithecine mandibular premolars has centred on the degree to which the crowns are 'molarised' or at least 'molariform' (Robinson, 1956; Sperber, 1974). The term 'molarised' is used, at least in relation to teeth of extant forms, to refer to modern *Homo* P_4s which have more than two cusps (Biggerstaff, 1969, p. 165). However, in the palaeontological literature, 'molarised' is the term used for premolars which have a relatively large talonid (viz. Robinson, 1956), and which may, or may not, have additional cusps. We shall retain this latter usage for the subsequent discussion. Hitherto, most attention has been paid to the different degrees of talonid development among the premolars of the 'robust' and 'gracile' australopithecines from southern African sites. The P_3s of the 'robust' australopithecines from Swartkrans and Kromdraai, while marginally larger crowned than those belonging to *A. africanus*, are assessed as being generally bicuspid, whereas most of the P_3s of the latter taxon are scored as having an additional small talonid (Robinson, 1956; Sperber, 1974). For P_4s, published observations suggest that the reverse is the case, with 'robust' australopithecine teeth having a more developed talonid than their 'gracile' counterparts (Sperber, 1974). The same author quotes the surface area of talonids as a percentage of the whole crown, but these areas are evidently computed from relatively crude linear length and breadth measurements of the mesial and distal parts of the crowns.

The techniques used in this study allow a more precise and accurate estimate of talonid size to be made, and the results disagree with previous estimates of talonid size within the southern African hominid samples. As it is defined in this study, the talonids of both SAFROB P_3s and P_4s are larger than those of the teeth within the SAFGRA category.

Indeed, despite the larger size of the talonids of the P_4, the differences in relative size of the talonid between SAFROB and SAFGRA are greater in the P_3s than for the P_4. Thus, by the definition given above, the P_3 crowns of SAFROB are relatively more molarised than those of the P_4s. However, the eigen-vector scores for the three main cusp components are similar for both P_3s and P_4s, suggesting that the pattern of covariation between the size of the main cusps and the talonid is similar for each tooth type. Inspection of Figures 4 and 13 establishes that the rank order of relative talonid size is similar to that of overall crown size, i.e. the larger the crown, the relatively larger the talonid, apparently at the expense of the buccal cusp.

The change of shape with size, so-called allometric shape change, is a widespread phenomenon in the natural world (Gould, 1966). The most economical hypothesis of these cusp relationships is that the large talonid of 'robust' australopithecine mandibular premolars is not a special adaptation, but a predictable consequence of the relative megadonty of this group of early hominids. For this to be the case, there must be (*a*) evidence of a statistically significant relationship between shape and size, and (*b*) evidence that such a relationship would predict a relatively larger talonid in a larger tooth, i.e. that there was a positively allometric relationship ($\alpha = > 1$) between crown size and talonid size. An allometric basis for the difference in relative talonid size between the P_3s of SAFGRA and SAFROB can be effectively discounted because there is no significant difference in measured crown base area between the two samples. However, statistically significant differences can be demonstrated between the sample means of SAFGRA and EAFROB for P_4 and between EAFROB and the remainder of the hominid sample for both P_3 and P_4. Ideally, the relationship, if any, between crown and talonid size should be investigated in a comparative sample, and not one derived from the fossil hominid record itself (Wood, 1979), but there is no extant higher primate with a comparable spectrum of mandibular premolar morphology, so that the relationship has to be investigated within the hominids themselves. If there is a generalised relationship between crown and talonid size in hominids, it should be operating within the two 'non-robust' hominid taxonomic categories. To investigate this, the teeth from these categories have been pooled and the nature of any relationship between crown and talonid size has been investigated (Table 18). These results confirm that there is more than a random relationship between crown and talonid size in the test group, but they also demonstrate that the allometry coefficients are not significantly different from unity. Thus, the relationship does not differ from isometry, so that large teeth will retain the same shape, i.e. the talonid should occupy the same proportion of the crown of a larger tooth as it does of a smaller tooth crown. Therefore, this evidence suggests that the larger-crowned P_4s of SAFROB and P_3s and P_4s of EAFROB would not be expected to have relatively larger talonids as a simple consequence of size. Allometry can thus be rejected as the reason for the shape change. It is, however, noteworthy that when the relationship between crown and talonid size is investigated within the three australopithecine taxonomic categories, there is not only a statistically significant relationship, but it is a positively allometric one (Table 18). Some workers have proposed that the taxa subsumed into these three categories are successive adaptations within the same lineage (White, Johanson & Kimbel, 1981). It would be tempting to conclude that relative talonid enlargement of the mandibular premolars must now be included as one of the special adaptive features of such a lineage, but this does not follow. Such a positive allometric trend also exists in P_3s when EAFHOM is substituted for SAFGRA (Table 18), yet no serious worker has suggested that EAFHOM/SAFROB/EAFROB is a plausible evolutionary sequence.

Table 18. *Relationship between overall crown area and talonid size of early hominid mandibular premolars as reflected in least squares regression*

	Slope	S.E.	95% intervals
P_3			
SAFGRA + EAFHOM	0·91	0·27	0·32–1·50
EAFROB + SAFROB + SAFGRA	1·65	0·28	1·06–2·24
EAFROB + SAFROB + EAFHOM	1·50	0·10	1·30–1·70
EAFHOM + SAFGRA + SAFROB	1·43	0·23	0·96–1·90
P_4			
SAFGRA + EAFHOM	1·37	0·34	0·63–2·11
EAFROB + SAFROB + SAFGRA	1·40	0·12	1·14–1·66
EAFROB + SAFROB + EAFHOM	0·51	0·05	0·41–0·61
EAFHOM + SAFGRA + SAFROB	1·58	0·16	1·25–1·91

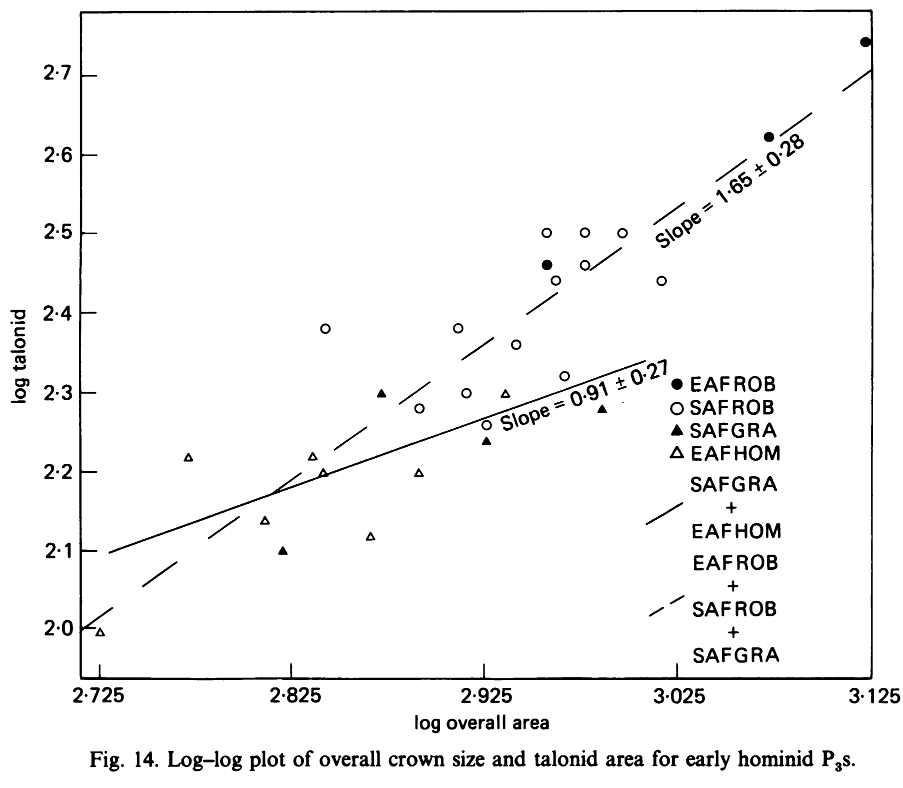


Fig. 14. Log–log plot of overall crown size and talonid area for early hominid P_3s.

These relative size relationships are more easily appreciated by reference to Figure 14, which is a log–log plot of P_3 overall crown and talonid areas upon which the pooled SAFGRA/EAFHOM regression line has been drawn, together with the interspecific slope calculated for the three pooled australopithecine taxonomic categories.

Table 19. *Observations of the reference categories which can provide a guide to the affinities of unknown specimens*

(1)	Crown base area
(2)	Crown shape
(3)	Absolute cusp and talonid area
(4)	Relative cusp and talonid area
(5)	Morphological traits
	(A) Cusp number
	(B) Relative position of lingual cusp
	(C) Median longitudinal fissure
	(D) Marginal grooves
(6)	Fissure pattern

Affinities of 'unknown' specimens

The results which have been reviewed in the foregoing sections suggest that all the variables which have been examined have some utility for taxonomic diagnosis. The present study included ten tooth crowns (Tables 1, 2) belonging to teeth which are either isolated (e.g. KNM-ER 5431), or which are associated with mandibles whose affinity is problematic (e.g. KNM-ER 1482 and 1802). The left P_4 in the mandible KNM-ER 1801 is too fragmentary to offer any useful evidence about the affinities of that mandible; the remaining specimens will be considered in turn.

The six measurements, or categories of observations, which have the potential to provide information on affinities are listed in Table 19. The attributions that are indicated by overall crown area, crown shape and the absolute and relative size of the cusp components have been deduced as follows. The raw data for each variable, or category of variables, have been assembled into a covariance matrix from which canonical variates have been extracted using Canonical Variates Analysis (CVA). The CVA statistical package that was used for this analysis (SPSSX) includes the facility to compute posterior probabilities. The result is expressed as a series of percentages, which are the likelihood that an individual specimen would be assigned to a particular taxonomic category. If the affinity of the specimen is unambiguous (i.e. a 100% value), then that category alone is given. When any ambiguity exists (i.e. values of < 100%), then the taxonomic categories scoring the two largest percentages are cited.

Two designs have been used for these assessments of affinities. In the first, unknown specimens from Koobi Fora and Swartkrans were each offered the 'choice' of three taxonomic categories. The Koobi Fora remains were offered EAFROB, EAFHOM and SAFGRA; the three comparators used for the smaller number of Swartkrans tooth crowns were EAFHOM, SAFGRA and SAFROB. In the second experimental design, posterior probabilities were computed for just two taxa; EAFHOM and EAFROB for East African remains, and SAFROB and SAFGRA for the Swartkrans specimens. The affinities suggested by the three, and two, taxon designs are given in, respectively, Tables 20 and 21. As assessment of the utility of each of the four 'tests' can be obtained from their ability to correctly classify 'known' teeth from Koobi Fora and Swartkrans. According to this criterion, absolute cusp area is a more reliable indicator of affinity than relative cusp area; this is perhaps not surprising for it contains both size and shape information. The low percentages associated with crown shape for P_4 for both designs, and for P_3 for the three taxon designs suggest that any allocations given to isolated teeth on the basis of crown shape must be regarded with some scepticism.

Table 20. *Taxonomic affinities of teeth in the unknown category (by canonical analysis)*

Specimen	Type	Crown area	Absolute cusp area	Relative cusp area	Crown shape
Design group for Koobi Fora		P_3: 71 % correctly classified P_4: 92 % correctly classified	P_3: 73 % correctly classified P_4: 95 % correctly classified	P_3: 67 % correctly classified P_4: 77 % correctly classified	P_3: 55 % correctly classified P_4: 38 % correctly classified
Koobi Fora					
KNM-ER 1802	P_3 R	SAFGRA (59 %)/ EAFROB (26 %)	SAFGRA (70 %)/ EAFHOM (29 %)	SAFGRA (58 %)/ EAFHOM (42 %)	EAFHOM (50 %)/ EAFROB (41 %)
	P_4 R	SAFGRA (73 %)/ EAFHOM (23 %)	SAFGRA (84 %)/ EAFHOM (16 %)	SAFGRA (61 %)/ EAFHOM (38 %)	EAFROB (45 %)/ EAFHOM (35 %)
	P_4 L	SAFGRA (75 %)/ EAFHOM (17 %)	SAFGRA (89 %)/ EAFHOM (11 %)	SAFGRA (72 %)/ EAFHOM (28 %)	EAFROB (61 %)/ EAFHOM (29 %)
KNM-ER 5431	P_3 R	SAFGRA (61 %)/ EAFHOM (31 %)	SAFGRA (70 %)/ EAFHOM (30 %)	SAFGRA (53 %)/ EAFHOM (47 %)	SAFGRA (80 %)/ EAFROB (20 %)
	P_3 L	SAFGRA (62 %)/ EAFHOM (29 %)	SAFGRA (63 %)/ EAFHOM (37 %)	SAFGRA (57 %)/ EAFHOM (43 %)	SAFGRA (60 %)/ EAFROB (38 %)
	P_4 L	SAFGRA (70 %)/ EAFHOM (28 %)	SAFGRA (95 %)/ EAFHOM (1 %)	SAFGRA (70 %)/ EAFHOM (29 %)	EAFROB (50 %)/ EAFHOM (34 %)
Design group for Swartkrans		P_4: 75 % correctly classified	P_4: 90 % correctly classified	P_4: 67 % correctly classified	P_4: 52 % correctly classified
Swartkrans					
SK 1587	P_4 L	SAFGRA (71 %)/ SAFROB (23 %)	SAFROB (81 %)/ SAFGRA (18 %)	SAFROB (98 %) SAFGRA (1 %)	EAFHOM (47 %)/ SAFGRA (30 %)
SK 1588	P_4 R	SAFGRA (67 %)/ SAFROB (29 %)	SAFGRA (77 %)/ SAFROB (18 %)	SAFGRA (43 %)/ SAFROB (30 %)	EAFHOM (43 %)/ SAFGRA (32 %)

Design group for Koobi Fora: EAFROB/EAFHOM/SAFGRA. Antimeres were included.
Design group for Swartkrans: EAFHOM/SAFGRA/SAFROB.
NA indicates cases where damage, poor preservation, wear or lack of access has prevented the observations of measurements being made.
Value in (%) is the probability that the specimen belongs to that taxon.

Table 21. *Taxonomic affinities of teeth in the unknown category (by canonical analysis)*

Specimen	Type	Crown area	Absolute cusp area	Relative cusp area	Crown shape
Design group for Koobi Fora		P_3:92% correctly classified P_4: 100% correctly classified	P_3: 100% correctly classified P_4: 100% correctly classified	P_3: 100% correctly classified P_4: 100% correctly classified	P_3: 71% correctly classified P_4: 45% correctly classified
Koobi Fora					
KNM-ER 1802	P_3 R	EAFROB (63%)	EAFHOM (93%)	EAFHOM (100%)	EAFHOM (56%)
	P_4 R	EAFHOM (84%)	EAFHOM (100%)	EAFHOM (100%)	EAFROB (56%)
	P_4 L	EAFHOM (66%)	EAFHOM(100%)	EAFHOM (100%)	EAFROB (66%)
KNM-ER 5431	P_3 R	EAFHOM (77%)	EAFHOM (100%)	EAFHOM (100%)	EAFROB (99%)
	P_3 L	EAFHOM (73%)	EAFHOM (100%)	EAFHOM (100%)	EAFROB (96%)
	P_4 L	EAFHOM (92%)	EAFHOM (100%)	EAFHOM (100%)	EAFROB (59%)
Design group for Swartkrans		P_4: 60% correctly classified	P_4: 92% correctly classified	P_4: 92% correctly classified	P_4: 50% correctly classified
Swartkrans					
SK 1587	P_4 L	SAFGRA (70%)	SAFROB (93%)	SAFROB (100%)	SAFGRA (64%)
SK 1588	P_4 R	SAFGRA (66%)	SAFGRA (87%)	SAFGRA (80%)	SAFGRA (61%)

Design group for Koobi Fora: EAFROB/EAFHOM.
Design group for Swartkrans: SAFGRA/SAFROB.
NA, indicates cases where damage, poor preservation, wear or lack of access has prevented the observations or measurements being made.
Value in (%) is the probability that the specimen belongs to that taxon.

Table 22. *Morphological traits, and their taxonomic affinities, for unknown specimens*

Specimen no.	Cusp no.	Relative position of lingual cusp	Median longitudinal fissure	Marginal grooves
P_3				
KNM-ER 1802 R	3 (EAFROB)	Distal (EAFHOM)	Shallow (SAFGRA)	DB deep (SAFGRA or EAFROB)
KNM-ER 5431 R	2 (?)	Distal (EAFHOM)	Deep (EAFROB)	DB deep (SAFGRA or EAFROB)
KNM-ER 5431 L	2 (?)	Distal (EAFHOM)	Deep EAFROB)	DB deep (SAFGRA or EAFROB)
P_4				
KNM-ER 1482 L	2 (SAFGRA or SAFROB)	—	Absent (EAFHOM)	—
KNM-ER 1802 R	3 (?)	Distal (?)	Deep (EAFROB)	DB present (EAFROB)
KNM-ER 1802 L	3 (?)	Distal (?)	Deep (EAFROB)	DB present (EAFROB)
SK 1587 L	3 (?)	Mesial (SAFGRA or SAFROB)	Deep (SAFROB)	DB deep (SAFROB)
SK 1588 L	4 (SAFROB)	Distal (?)	Deep (SAFROB)	DB present (SAFROB)

Table 23. *Distances between 'unknown' teeth and the centroids of the main taxonomic categories based on the Procrustes analysis of P_3 fissure pattern*

	EAFROB	EAFHOM	SAFROB	SAFGRA	KNM-ER 1802 R	KNM-ER 5431 R	KNM-ER 5431 L
EAFROB	0						
EAFHOM	3·62 E-2	0					
SAFROB	1·11 E-2	2·41 E-2	0				
SAFGRA	2·17 E-2	5·60 E-2	1·03 E-2	0			
KNM-ER 1802 R	1·60 E-2	2·44 E-2	1·47 E-2	1·53 E-2	0		
KNM-ER 5431 R	4·25 E-2	1·80 E-2	2·78 E-2	1·28 E-2	3·75 E-2	0	
KNM-ER 5431 L	7·69 E-2	3·43 E-2	4·91 E-2	3·16 E-2	4·69 E-2	1·92 E-2	0
					(SAFROB/ SAFGRA and EAFROB)	(SAFGRA/ EAFHOM)	(SAFGRA/ EAFHOM)

Table 24. *Distances between 'unknown' teeth and the centroids of the main taxonomic categories based on the Procrustes analysis of P_4 fissure pattern.*

	EAFROB	EAFHOM	SAFROB	SAFGRA	KNM-ER 1802 R	KNM-ER 1802 L	KNM-ER 5431 L	SK 1588
EAFROB	0							
EAFHOM	2·69 E-2	0						
SAFROB	1·11 E-2	1·03 E-2	0					
SAFGRA	3·11 E-2	8·45 E-3	8·81 E-3	0				
KNM-ER 1802 R	1·36 E-2	1·86 E-2	1·17 E-2	3·00 E-2	0			
KNM-ER 1802 L	2·03 E-2	8·59 E-3	1·01 E-2	1·52 E-2	1·38 E-2	0		
KNM-ER 5431 L	2·62 E-2	2·35 E-2	1·21 E-2	2·58 E-2	1·70 E-2	2·54 E-2	0	
SK 1588	2·59 E-2	6·96 E-3	1·10 E-2	9·37 E-3	1·98 E-2	4·99 E-3	2·73 E-2	0
					(SAFROB/ EAFROB)	(EAFHOM/ SAFROB)	(SAFROB/ EAFHOM)	(EAFHOM/ SAFGRA)

The affinities suggested by the distribution of morphological traits cannot be assessed with the same degree of precision; the samples are small, and the scoring of the traits is inevitably more subjective than the measurement of crown area. However, when the results listed in detail in Table 10 (and summarised in Table 11) are compared with the trait scores for the unknown specimens given in Table 22, it is possible to suggest the tentative taxonomic allocations which are given in parentheses in Table 22.

The Procrustes technique was used to compute distances between the fissure patterns of the 'unknown' tooth crowns and those of teeth allocated to the taxonomic categories. The distance matrices are given for P_3s and P_4s in Tables 23 and 24 respectively. The group centroid(s) which are closest to each of the 'unknown' crowns is given in brackets at the foot of the two Tables.

The only metrical evidence available about the affinity of KNM-ER 1482 is the crown size of the left P_4. Its measured crown base area, 118, is closest to the ranges of values for SAFGRA and EAFHOM (Table 6). A similar pattern of affinity is indicated by the morphological traits, and this suggests that the specimen is closer to the morphology of more gracile homonids than to the two 'robust' australopithecine taxa. The right P_4 of KNM-ER 1482 only provides information about cusp number and the median longitudinal fissure. The combination of the presence of just the two main cusps, and the absence of a median longitudinal fissure, are strong evidence for affinities with EAFHOM and SAFGRA. There are no mandibular molar crown size data with which to compare this conclusion, but the enamel thickness values of the molar and premolar crowns are either beyond, or at the very lower end of, the range of EAFROB values (Beynon & Wood, 1986).

The mandible, KNM-ER 1802, provides evidence for both types of mandibular premolar teeth. The posterior probabilities computed from the metrical evidence, according to the three taxon design, suggest that the closest taxonomic category is SAFGRA. If the choice is narrowed to two taxa, it is assigned to EAFHOM, although P_3 crown area, and the more unreliable P_4 crown shape data, suggest that EAFROB is the closest category. The evidence from the morphological traits is confused, but the more reliable trait indicators, i.e. P_3 median longitudinal fissure expression and cusp position, are consistent with an assignment to EAFHOM. However, the fissure pattern evidence suggest affinities with the two 'robust' taxonomic categories, and it is also noteworthy that both the P_3s and P_4s of KNM-ER 1802 tend to cluster with SAFROB in the plots of the first two principal components (Figs. 6, 7, 8). The evidence from the relative size of the molar crown cusp components pointed to affinities with EAFHOM when using a two taxon design (Wood *et al.* 1983), but if the taxonomic 'choice' were widened to three taxa (Stringer, 1986), SAFGRA was the closest group. Crown size, the incidence of additional cusps and the fissure pattern likewise suggested links with EAFHOM or EAFROB. These results thus present a confusing picture of the dental affinities of KNM-ER 1802. While the dental evidence is, by and large, against its belonging to the East African 'robust' australopithecines, as defined by the dental reference samples used in this analysis, there is also sufficient evidence that, by the same criteria, it does not belong to EAFHOM either. If the jaw is hominine, then it belongs to an individual, and perhaps to a group, which in terms of its crown morphology, shares features in common with 'robust' australopithecine taxa.

The only metrical evidence available for KNM-ER 2599 is the area of the buccal cusp; this value is outside the range of EAFROB, but within that of SAFROB and EAFHOM. The evidence from cusp number is equivocal, but the presence of an uninterrupted median longitudinal fissure suggests affinities with the two 'robust' australopithecine taxa. The specimen KNM-ER 5431 was recovered from the Lower Member of the Koobi Fora Formation (Leakey & Walker, 1985), in deposits which may be around $3 \cdot 10^6$ B.P. years old (McDougall, 1985). The pattern of affinities which are suggested by its mandibular premolar crown morphology is similar to that of KNM-ER 1802. These results can do little more than confirm that this specimen does not belong to the East African 'robust' australopithecine category, but the same qualifications about any attribution to *Homo* that were suggested for KNM-ER 1802 also apply to KNM-ER 5431.

The two P_4s from Swartkrans, SK 1587 and 1588, belong to, respectively, a mandible and a mandibular fragment. Evidence from crown shape can be discounted; this variable discriminates too poorly between the reference samples. Absolute size, either of the whole crown, or of its elements, and the relative size of the crown components, point to SK 1587 having affinities with SAFROB and SK 1588 to SAFGRA, and the less reliable evidence of the morphological traits suggests both teeth have affinities with SAFROB. These conclusions almost exactly mirror those reached on the basis of the morphology of the first mandibular molars associated with each of these jaws (Wood *et al.* 1983). The combined results suggest that SK 1587, despite its small size, is properly attributed to *A. robustus*; the evidence for such an attribution for SK 1588 is less firm.

CONCLUSIONS

This study has demonstrated sufficient discontinuities between the form of mandibular premolar tooth crowns of early hominid taxa to suggest that details of the morphology of these teeth may be useful for taxonomic diagnosis. The design of the study, by insisting on unambiguous criteria for inclusion in the reference taxa, probably exaggerates the discontinuity, but its presence is not in doubt.

The major differences in crown morphology are between EAFROB and the remaining taxa (Tables 13, 17), with the differences in relative talonid size being most marked. Investigation of the allometric relationships between the size of cusp components and overall crown size in 'non-robust' australopithecines does not suggest that a relatively large talonid is a simple size-dependent phenomenon, resulting from the larger size of 'robust' australopithecine, and especially EAFROB, mandibular premolar crowns. Thus, relative talonid enlargement has to be added to the growing list of dental features of the 'robust' australopithecines, and more particularly the East African variant, *A. boisei*, which should be considered as functional adaptations, and not simply regarded as consequential on the larger overall size of these hominids (Wood & Stack, 1980; Wood *et al.* 1983; Beynon & Wood, 1986).

The potential of these results for the taxonomic identification of isolated tooth crowns, and for the attribution of more complete specimens whose affinities are in doubt, has been explored. Some of the specimens can be allocated to existing taxa, but the affinities of others is less clear. This points to the need for further work to determine the polarity of the differences of both the relative size of the crown components, and the distribution of morphological traits. These data would allow evidence about morphological differences to be translated into hypotheses of relationship, and thus help in the systematic analysis of material which does not apparently fit into the better established hominid taxa.

SUMMARY

Accurate measurements were made of the overall size of both the crown and its components of 91 mandibular premolar teeth of early hominids. The shape of the crown outline and the fissure pattern, and the expression of four morphological traits, were also recorded. Non-dental criteria were used to allocate the specimens into four major taxonomic categories (EAFROB, EAFHOM, SAFROB and SAFGRA), approximating to the hypodigms of, respectively, *A. boisei*, *H. habilis* and *Homo sp.*, *A. robustus* and *A. africanus*. Those specimens that could not be so allocated were regarded as 'unknown'.

Intertaxonomic overall size differences were established for both the P_3 and P_4, with the latter showing little overlap in crown size between the three taxonomic categories usually associated with East African sites (i.e. EAFROB, EAFHOM and SAFGRA). Crown shape is a better discriminator between taxonomic groups for P_3 than for P_4, with the P_3s of EAFHOM showing less buccolingual expansion than the other taxonomic categories. Cusp number, the location of the lingual cusp and the expression of the median longitudinal fissure, show systematic variation between the main taxonomic categories, with the 'robust' taxa being distinguished by additional distal cusps, and a more deeply incised median longitudinal fissure, and EAFHOM being peculiar in having a distally situated lingual cusp. Marginal grooves show more overlap in their incidence and expression between taxonomic categories.

Both the 'robust' australopithecine taxonomic categories have relatively large talonids, apparently at the expense of the size of the buccal cusp. The relative talonid enlargement was greater for P_3 than for P_4, a conclusion which is at variance with previous published assessments. Investigation of the allometric relationships between relative talonid size and overall crown size in the pooled 'non-robust' taxonomic categories did not suggest that talonid enlargement was a simple consequence of a larger-size crown.

The results of multivariate analysis demonstrate that the absolute areas of the main cusps and the talonid provide marginally the more effective discrimination between the main taxonomic categories than do the relative areas of the cusp components. The removal of the simpler effects of overall size reduces the differences between taxa, but does not eliminate them.

The data for the four taxonomic categories were used as a reference framework for the investigation of the affinities of those teeth in the unknown category for which detailed data were available. The sum total of the mandibular premolar morphology of KNM-ER 1482, 1802 and 5431 suggests that it is unlikely that these specimens should simply be allocated to EAFROB. Instead, they show varying degrees of affinity to EAFHOM and SAFGRA, but with the latter two specimens showing evidence of the retention, or development of, several characters associated with 'robust' australopithecines.

The two mandibles from Swartkrans show, in the case of SK 1587, affinities with *A. robustus*, and for SK 1588, a mixture of features, some of which align that specimen with *A. robustus*, and others of which suggest it is closer to SAFGRA.

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