Pleistocene and Holocene Human Remains from Equus Cave, South Africa

Frederick E. Grine
State University of New York at Stony Brook
and
Richard G. Klein
University of Chicago

INTRODUCTION

SETTING

Equus Cave (approximately 27° 37' S, 24° 38' E) is situated in one of a series of tufa (freshwater limestone) fans that mantle the Gaap Escarpment at Buxton, near Taung in the northern Cape Province of South Africa (Fig. 1). The escarpment is a 275 km long *cuesta* composed of Precambrian dolomitic limestone interbedded with shales along the southeastern margin of the Kalahari Desert. Several generations of tufa are present at Buxton and, because the holotype of *Australopithecus africanus* was recovered from a cave filling within the Thabaseek carapace (Peabody 1954; Butzer 1974), these fans have been extensively studied. The Thabaseek represents the oldest limestone body, followed by the Norlim, Oxland, Channel and Blue Pool tufas. Equus Cave, which developed as a result of progressive fissure enlargement, opens on the western face of the Oxland tufa. Some 250 cm of sandy deposit, containing an abundance of faunal remains and coprolites as well as some lithic artifacts, has accumulated within the cave, which lies at the contact of units Bx-5B and Bx-6 (Butzer *et al.* 1978).

STRATIGRAPHY

Systematic excavations of Equus Cave were undertaken by P. Beaumont and M. Shackley in March and April 1978 and again by Beaumont in 1982. The site, as encountered by them, had been considerably altered by limestone quarrying activity, and rubble

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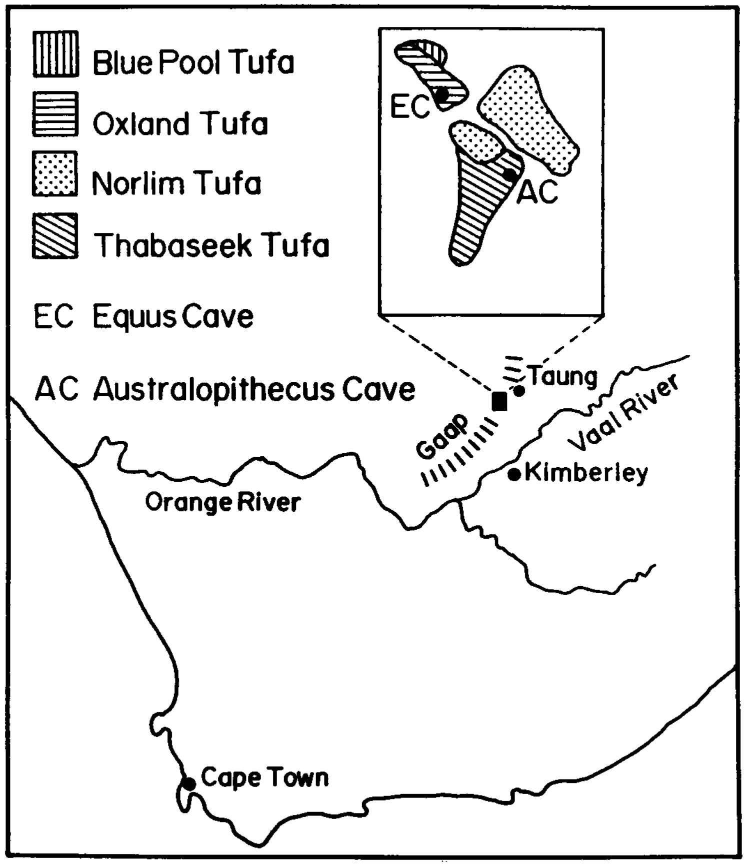

Fig. 1. Location of Equus Cave and distribution of principal tufa bodies at Buxton.

from the collapsed roof had to be removed before excavation could begin. A grid of squares measuring 2 m per side was laid out over the exposed deposit, and excavation proceeded according to arbitrary (7.5 cm deep) levels or "spits," grouped into four stratigraphic units (1A, 1B, 2A, and 2B).

The uppermost unit (1A) consists of some 40-50 cm of brown sandy loam and a grayish organic wash, and contains faunal remains and some lithic material attributable to the Later Stone Age (Beaumont *et al.* 1984). A Holocene age of Unit 1A has been determined by radiocarbon dates of 2,390 ± 55 yrs BP (Pta-2452) at mid-level and 7,480 ± 80 yrs BP (Pta-2495) from near the base of the unit (Beaumont *et al.* 1984). Unit 1B comprises some 30-60 cm of well-stratified, locally crossbedded, reddish-brown sandy loam with lenses of tufa grit. Unit 2A consists of about 60-70 cm of reddish-brown, coarsely-stratified sandy loam and sandy clay loam, with large roof block inclusions, while between 60 and 150 cm of similar sediment mainly without roof blocks comprises the basal unit, 2B. Unit 2B is notably the most fossiliferous, and provides the bulk of the faunal sample discussed below. Sporadic occurrences of Middle Stone Age artifacts have been recorded for the three lower units (Beaumont *et al.* 1984).

At present, absolute geochronological dates are not available for units 1B-2B. It is clear, nevertheless, that these sediments postdate the formation of the outer Oxland carapace, dated to between 230,000 and 256,000 yrs BP by uranium-series disequilibrium (Pta-2741) (Vogel and Partridge 1984). These units also certainly antedate the origination of a manganiferous patina that covers the Blue Pool Tufa I and that has been radiocarbon dated to greater than 32,700 BP (Butzer *et al.* 1978). Moreover, the dissolution and initial filling of Equus Cave is most likely associated with the accelerated spring discharge that accompanied the formation of Blue Pool Tufa I (Butzer 1984). Uranium-series dates of between 103,000 and 86,000 yrs BP (Pta-3265) have been recorded from the base of this tufa by Vogel and Partridge (1984). Thus, units 1B through 2B would appear to be older than 32,700 yrs and younger than about 94,000 yrs BP.

PALYNOLOGY

Together with abundant faunal remains, hyena coprolites occur throughout the sedimentary sequence, although these are less common in 1A than in the underlying units. Palynomorphs extracted from the unit 1A coprolites constitute assemblages that are similar to the modern spectrum of the surrounding Kalahari Thornveld vegetation, with the dominant arboreal pollens being those of *Tarchonanthus, Celtis,* and *Rhus* (Scott 1984).

The coprolite-derived pollen spectra from units 1B through 2B are indicative of a relatively more open vegetation. Unit 1B contains decreased arboreal percentages and a higher incidence of *Acacia,* while 2A and 2B possess even higher proportions of Gramineae and Compositae, suggestive of a Karroid grassland with few trees (Scott 1984). In addition, Scott's palaeobotanical analysis has led him to conclude that unit 2B probably represents the coldest phase of this depositional sequence, with annual temperatures perhaps 4°C lower than those of today.

FAUNAL REMAINS

The Equus Cave faunal sample comprises more than 32,000 identifiable elements from some 50 taxa of "large" mammals (hyrax-size and larger) (Table 1). The vast majority derive from units 1B-2B; thus, this is one of the world's largest Pleistocene

Table 1

Large mammal taxa of Equus Cave and the number of identified remains/minimum number of individuals by which each taxon is represented in the four lithostratigraphic units.

	STRATIGRAPHIC UNITS			
	1A	1B	2A	2B
Lagomorpha				
Leporidae				
gen. et sp. indet.	27/3	43/5	52/4	110/9
Rodentia				
Pedetidae				
Pedetes capensis	5/1	17/3	9/1	2/1
Hystricidae				
Hystrix africaeaustralis	9/2	13/2	19/2	68/6
Primates				
Cercopithecidae				
Papio ursinus	62/6	39/3	47/4	12/2
Carnivora				
Canidae				
Canis mesomelas	262/15	497/15	1122/41	4214/165
Vulpes chama	44/5	55/8	88/13	408/58
Otocyon megalotis	3/2	8/2	16/2	75/9
*Vulpes/Otocyon**	161/5	225/8	419/13	1512/52
Lycaon pictus	- - -	13/2	25/4	88/11
Mustelidae				
Mellivora capensis	1/1	1/1	8/3	18/4
Aonyx capensis	- - -	4/2	6/2	35/5

Table 1 continued

	STRATIGRAPHIC UNITS			
	1A	1B	2A	2B
Viverridae				
Genetta sp.	- - -	1/1	2/1	4/1
Atilax paludinosis	- - -	- - -	- - -	5/1
Herpestes ichneumon	5/2	- - -	- - -	- - -
Cynictis penicillata	2/1	12/2	19/2	52/3
Suricata suricatta	- - -	- - -	- - -	1/1
Hyaenidae				
Crocuta crocuta	2/1	11/2	29/4	128/13
Hyaena brunnea	35/5	58/8	151/11	492/41
Crocuta/Hyaena	41/6	83/9	214/13	737/45
Felidae				
Felis libyca	4/4	9/3	18/4	60/10
Felis nigripes	1/1	1/1	- - -	1/1
F. libyca/nigripes	15/4	42/3	47/4	106/10
Felis caracal/F.serval	4/1	16/1	86/4	278/8
Panthera leo	- - -	8/1	15/2	62/4
Panthera pardus	3/2	6/2	14/2	45/7
Acinonyx jubatus	- - -	1/1	1/1	1/1
P.pardus/A. jubatus	3/2	14/3	27/2	65/7
Tubulidentata				
Orycteropodidae				
Orycteropus afer	1/1	10/3	3/1	5/1
Hyracoidea				
Procavidae				
Procavia capensis	121/8	44/6	65/11	120/17

Table 1 continued

	STRATIGRAPHIC UNITS			
	1A	1B	2A	2B
Perissodactyla				
Equidae				
Equus burchelli	37/3	163/12	389/14	1341/44
† *Equus capensis*	- - -	16/2	41/4	169/9
Rhinocerotidae				
Diceros bicornis	- - -	2/1	5/2	14/3
Artiodactyla				
Hippopotamidae				
Hippopotamus amphibius	- - -	- - -	1/1	4/1
Suidae				
Phacochoerus aethiopicus	21/5	31/5	37/5	115/14
Giraffidae				
Giraffa camelopardalis	- - -	- - -	- - -	1/1
Bovidae				
Taurotragus oryx	3/2	2/2	6/1	20/2
Tragelaphus strepsiceros	2/1	9/3	8/3	26/5
Syncerus caffer	1/1	6/1	4/1	23/5
Hippotragus sp.	3/1	22/7	36/5	51/7
Kobus leche	- - -	10/2	29/4	90/9
Redunca fulvorufula	29/6	57/9	109/13	402/44
Pelea capreolus	14/3	17/3	73/10	221/20
Alcelaphus buselaphus / *Connochaetes gnou*	21/4	101/12	209/16	690/64

Table 1 continued

	STRATIGRAPHIC UNITS			
	1A	1B	2A	2B
† *Megalotragus priscus*	- - -	1/1	9/2	18/6
Damaliscus dorcas	7/2	50/6	240/18	824/69
Connochaetes taurinus	4/2	11/3	44/7	125/16
Antidorcus marsupialis	36/6	209/25	489/59	1606/163
† *Antidorcus bondi*	- - -	242/21	754/72	2512/201
Raphicerus campestris	44/5	97/12	180/21	372/38
Sylvicapra grimmia	22/4	15/4	10/2	9/2
Ovis aries/Capra hircus	11/4	- - -	- - -	- - -
Bovidae general				
small	98/5	191/12	294/21	680/38
small-medium	216/15	840/55	2144/151	7669/412
large-medium	75/6	388/24	978/40	3622/137
large	7/2	20/3	65/4	272/10
GRAND TOTALS	1179/97	- - - - - -	31149/1527	- - - - - -

*Note that the composite categories include bones assigned to the separate taxa and bones that could belong to either. The numbers for bovid species are based exclusively on dentitions and horncores. The numbers for bovid size categories include all bones. In the context of the taxonomic list, small bovids include only *Raphicerus*; small-medium bovids include *Antidorcus, Sylvicapra, Redunca, Pelea* and *Ovis/Capra;* large-medium bovids include *Damaliscus, Alcelaphus, Connochaetes, Kobus, Hippotragus* and *Tragelaphus;* large bovids include *Taurotragus, Syncerus* and *Megalotragus.*

macrofaunal samples. Although large mammals are overwhelmingly dominant, small mammals, birds, reptiles, and fish are variously present throughout the sequence. Only the large mammals are discussed here, but the other taxa do not contradict the inferences drawn from this sample.

The faunal assemblages clearly reflect the stratigraphic hiatus between 1A and the underlying three units. All of the species represented in unit 1A occurred in the area historically, and domestic animals (*Ovis* and/or *Capra*) are known only from this uppermost unit. Current evidence suggests that domestic stock was introduced to this region of southern Africa only within the last 2,000 to 3,000 years (Deacon *et al.* 1978).

Units 1B through 2B, on the other hand, preserve the remains of three extinct species (*Megalotragus priscus, Equus capensis* and *Antidorcus bondi*). The occurrence of the swamp-dwelling antelope, *Kobus leche,* in these strata is also noteworthy, inasmuch as it is not suited to the historic environment of this region. In historic times, *K. leche* has occurred no closer than northern Botswana (some 800 km to the north, across the Kalahari Desert), although it is represented in other late Middle-early Upper Pleistocene sites in the northwestern part of South Africa (Klein 1980). The presence of the lechwe suggests a relatively moister regional climate during the deposition of units 1B-2B.

Mean individual sizes in several of the carnivore species (*e.g., Canis mesomelas, Vulpes chama, Felis libyca*) of units 1B-2B significantly exceed the average sizes of modern individuals at the same latitude. Since mean body sizes of modern representatives of most of the species involved tend to increase with distance from the Equator (Klein 1985), this implies cooler temperatures during the deposition of the 1B-2B sediments. This implication is consistent with the palynological evidence and with an early Upper Pleistocene age.

The paucity of artifacts and obvious porcupine-gnawed bones, together with the abundance of hyena coprolites and hyena-damaged elements, suggests that hyenas were primarily responsible for the faunal accumulations in these units. With regard to the two hyena species represented (*Hyaena brunnea* and *Crocuta crocuta*), observations on recent animals (*e.g.*, by Kruuk 1972, 1976; Bearder 1977; Mills and Mills 1977; Mills 1978a, 1978b; Owens and Owens 1978, 1979) would seem to indicate the brown hyena (*H. brunnea*) to have been more important. Perhaps most significant is the comparative abundance of carnivores, especially jackals and foxes, in the faunal sample. Modern observations in the Kalahari have shown that jackal and other small carnivore bones are common in brown hyena lairs, but not in those of spotted hyenas. Also probably meaningful are the differences in the mortality profiles of the two hyena species in the Equus Cave sample. While *H. brunnea* is represented by a range of adults and numerous juveniles, *C. crocuta* remains are almost exclusively those of old adults. This difference would be predicted if the brown hyena bones derived mainly from normal attritional mortality in or near a nursery den, and if the spotted hyena elements were accumulated primarily through scavenging activity. Finally, the small modal size of the herbivore individuals in this sample, and perhaps even the sheer quantity of bone, may implicate the brown hyena. Spotted hyenas tend to feed on somewhat larger animals, and because they do not actively provision their young in communal nursery dens, spotted hyenas do not accumulate as much bone as do brown hyenas.

No detailed studies have been made of the extent to which species representation in hyena bone assemblages reflects species representation in the surrounding environment. Certainly the observations cited above clearly indicate that hyenas, like virtually all other agents responsible for bone accumulation, do not collect the remains of different species in direct proportion to their live abundance. The fact that species representation in a fossiliferous assemblage does not necessarily reflect species representation in the environment, and that the nature and degree of representational bias may be understood only in general terms, indicates that caution must be exercised when employing fossil assemblages to reconstruct palaeoenvironments.

Nevertheless, it is significant that grazing ungulates and mixed feeders are notably better represented than browsers, as was the case in historic times. This prevalence is especially clear in the category of small- to medium-sized bovids, which are the most abundant animals in the fauna as a whole. In terms of size, small- to medium-sized bovids would be expected to be common in a brown hyena accumulation, but there is no *a priori* reason to suppose that browsers of this size range would be far less common than grazers, unless the latter had been much more abundant in the immediate environment. Indeed, the three extinct species represented in the Equus Cave assemblage are all grazers. It therefore seems reasonable to conclude that the grasses favored by grazers played a prominent role in the regional vegetation, where areas of thicket or bush would have been correspondingly relatively restricted. The palaeoenvironmental parameters adduced from the faunal remains in Units 1B, 2A and 2B of Equus Cave correspond closely to the vegetational indications derived from palynological analysis.

HOMINID REMAINS

A total of thirteen hominid specimens are known from Equus Cave. Four were extracted in 1978 by Beaumont and Shackley, while another eight were recovered during Beaumont's 1982 excavation. Each one of these twelve specimens comprises a single, isolated tooth. Another specimen, consisting of a fragmentary left mandibular corpus with two molars, was found by C.K. Brain when he and K.W. Butzer visited the site in 1971. At that time the road in the quarry had cut through the deposit, and fossiliferous sediments were being eroded down the cutting. The mandibular fragment was among the bones recovered by them from the scree, and Brain (*in Litt.* 1984) has stated that he had no doubt at the time that these bones had come from the Equus Cave deposit.

The excavated specimens derive from each of the four sedimentary units (Table 2). One tooth (a maxillary central incisor) was recovered from a spit in square 15G in which Unit 1A could not be distinguished from Unit 1B. On the basis of its state of preservation, this tooth is considered to have been derived from Unit 1A. Similarly, while the stratigraphic provenance of the mandibular fragment is uncertain, its state of preservation strongly suggests that it derived from one of the three lower units (1B, 2A or 2B).

Table 2

Hominid Remains from Equus Cave

Stratigraphic Unit	Specimen		Grid Square
Unit 1A	EQ-H1	LM^1	K25
	EQ-H2	LM^3	J23
	EQ-H3	RM_3	K23
	EQ-44	LI^1	G15
Unit 1B	EQ45	RM_1	I19
Unit 2A	EQ-H6	LI^2	I22
	EQ-H7	LP^3	K20
	EQ-H8	$LM_?$ germ	J25
Unit 2B	EQ-H9	L^C	I2
	EQ-H10	LM^3	H19
	EQ-H11	RM^3	K26
	EQ-H12	RM3	K25
?Unit1B-2B	EQ-H 71/33	mand. frag	?

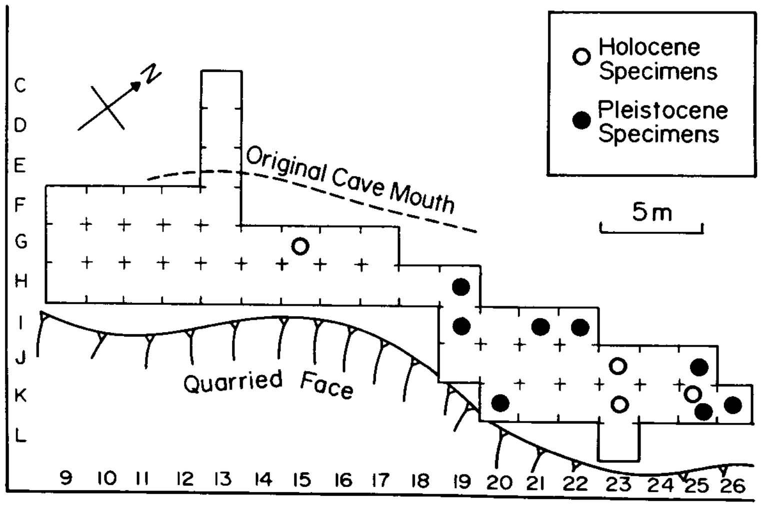

Fig. 2. Horizontal plan of Equus Cave showing spatial distribution of hominid specimens EQ-H1—EQ-H12. Open circles denote specimens from Unit 1A. Closed circles denote specimens from Units 1B-2B.

The spatial distribution of the excavated human remains is shown in Fig. 2. For the most part, these specimens are concentrated in the eastern moiety of the deposit. The eastern face of the cave is closest to the cutting from which the mandibular fragment was recovered, and it would, therefore, seem likely that this specimen also derived from within the eastern portion of the deposit.

DESCRIPTION

Remains from Unit 1A

EQ-H1 (Fig. 3a) comprises an incomplete left maxillary molar, adjudged to be a LM^1. The buccal moiety of the crown is missing, having been fractured along a line through the paracone and metacone, and both buccal roots have broken off, with only short remnants remaining above the level of the radicular trifurcation.

Viewed occlusally, the mesiolingual and distolingual corners are well-angled. The protocone is well-developed, while the hypocone is represented by a swelling at the lingual end of the distal marginal ridge. The paracone appears to have been somewhat better developed than the metacone. The distal marginal ridge is

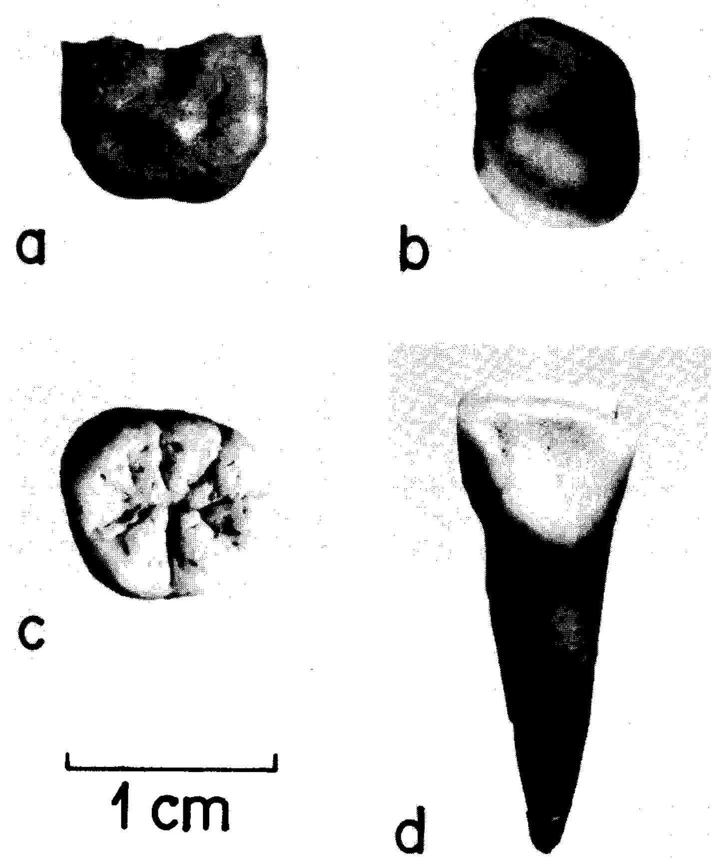

Fig. 3. Hominid remains from Unit 1A. a) occlusal view of EQ-H1; b) occlusal view of EQ-H2; c) occlusal view of EQ-H3; d) lingual view of EQ-H4. Mesial to left. Scale bar = 1 cm.

complete and thick, albeit relatively low, and the *crista obliqua* is constricted and partially incised at the base of the protocone.

The crown exhibits moderate occlusal wear, which has reduced the lingual cusps to approximately equivalent height. A moderately large, concave island of dentine is exposed on the protocone, while the hypocone evinces a tiny dentine exposure. It would appear, from the internal detail exposed buccally, that some dentine was exposed on the paracone. Occlusal wear is such that the presence or absence of the Carabelli trait cannot be ascertained, although it is almost certain that a large Carabelli cusp was not present. Facets on the mesial and distal crown faces attest to a slight to moderate degree of interproximal attrition.

The root neck is of moderate height (*circa* 4.5 mm), and has a mesiodistal (MD) diameter at the cervix of 7.4 mm. The exposed pulp chamber is of cynodont proportions (see below). The robust lingual root courses vertically with a slight lingualward flare.

The specimen reveals no apparent pathology.

The principal dimensions of the crown are as follows:

MD as measured: 10.3 mm
MD corrected: 10.7 mm
BL diameter: ------

EQ-H2 (Fig. 3b) comprises a complete, heavily worn LM^3. The crown presents a buccolingually elongate, ovo-rectangular outline. Wear has obliterated all occlusal detail, save for traces of the floor of the triradiate fissure of the trigon basin. The disposition of these remnants suggests that the protocone was the largest cusp. The strong angle assumed by the distolingual corner of the crown attests to the presence of a hypocone, but its size cannot be determined. Details of buccal and lingual surface morphology have been obliterated also by attritional reduction.

Occlusal wear has produced a broad, U-shaped dentine exposure that is open mesially. This surface is strongly bevelled distobucally. The buccal rim of enamel, which is somewhat higher than the adjacent dentine surface, evinces a relatively sharp margin. The slightly concave mesial contact facet attests to a moderate to strong degree of interproximal attrition.

The neck of the root extends upward for some 6.5 mm from the level of the distal cervical margin to the level of the trifurcation, and it measures 6.4 mm mesiodistally and 9.4 mm buccolingually at the cervix. The two buccal roots are approximately equivalent in size, and both slope distalward to become contiguous apically. The lingual root, which is somewhat better developed, follows a straight course with a slight distal inclination.

The crown exhibits a 1.5 to 2.0 mm wide band of hypoplastic enamel near the cervical margin along the lingual and mesiolingual faces. Mesially, a shallow carious lesion affects the enamel and dentine along the cervical margin and a second, small lesion is located in the middle of the interproximal facet.

The principal dimensions of the crown are as follows:

MD as measured: 8.8 mm
MD corrected: (9.3 mm)
BL diameter: 10.7 mm

EQ-H3 (Fig. 3c) consists of the complete crown and nearly complete root of an RM_3. The apical ends of the roots have been sheared off along a steep oblique plane that slopes cervicolingually-apicobuccally.

The crown presents a distally tapering, ovoid occlusal outline. All five principal cusps are represented; the protoconid being the largest, followed by the metaconid and entoconid in decreasing order of size. The slightly smaller hypoconid and hypoconulid are equivalent in size. While there is no development of a *tuberculum intermedium,* the crown evinces a large *tuberculum sextum,* which is equal in size to the hypoconid and hypoconulid. The occlusal surface is somewhat crenulate in appearance, with all cusps exhibiting secondary or tertiary fissures. The protoconid, metaconid, hypoconid, and entoconid meet at a central point, and therefore the primary occlusal fissures assume a cruciform (+) configuration. The crown lacks a distinct fovea anterior, and the distal trigonid ridge is deeply incised.

Buccally, the grooves on either side of the hypoconid are shallow and very short, and neither is associated with a terminal pit. The protoconidal surface presents a moderately deep, oblique fissure close to the occlusomesial corner that represents an expression of protostylid development. This feature is separated from the principal buccal groove by nearly 3.0 mm of enamel.

Occlusal wear is very slight, and while all six cusps reveal facet development, this is poorly developed on the metaconid and especially the entoconid. A flattened mesial contact facet attests to slight interproximal attrition.

A 1.0 to 2.0 mm wide band of discolored enamel rings the entire crown at the cervical margin, and there is further discoloring of the enamel near the occlusal margin along the buccal and distal faces. The buccal, distal, and lingual faces of the crown also exhibit hypoplastic mottling.

The root neck measures some 8.1 mm mesiodistally and 7.9 mm buccolingually at the cervix, and extends nearly 6.0 mm from the cervical margin to the level of the bifurcation of the mesial and distal plates. The bifurcation remains incomplete, however, as the plates are connected buccally by a thin sheet of cementum along their entire lengths. The root curves distalward, and the apical two-fifths curves buccally as well.

The principal dimensions of the crown are as follows:

MD as measured: 10.5 mm
MD corrected: 10.6 mm
BL trigonid: 9.7 mm
BL talonid: 9.4 mm
BL maximum: 9.8 mm

EQ-H4 (Fig. 3d) comprises a very nearly complete LI^1. Notwithstanding the loss of a rectangular sliver of enamel from its

Fig. 4. Hominid molar (EQ-H5) from Unit 1B. Mesial to left. Scale bar = 1 cm.

distobuccal corner, the crown is complete, and the root is preserved intact.

The buccal (= labial) face of the crown is moderately convex incisocervically, and it presents a rectangular outline. Lingually, the cervical eminence is moderately swollen and symmetrically disposed, and there is no tubular development. The lingual surface is moderately shovelled, with a prominent mesial and less well-developed distal marginal ridge.

Incisal wear is moderate, having produced a broad, lingually bevelled facet on which a narrow, long band of dentine is exposed. On the distal surface, the lingual portion of a flattened contact facet is present. The flat mesial interproximal facet is located on the mesiolingual aspect of the mesial marginal ridge. The disposition of this facet attests to central incisor winging, with the mesiodistal (MD) axis of the crown aligned at approximately 45° to the coronal plane.

The root, which measures 6.2 mm mesiodistally and 5.5 mm buccolingually at the cervix, courses vertically some 14.0 mm, gradually tapering to the apex.

The specimen presents no apparent pathology.

The principal dimensions of the crown are as follows:

MD as measured: 9.0 mm
MD corrected: 9.1 mm
BL diameter: 6.6 mm

Remains from Unit 1B

EQ-H5 (Fig. 4) consists of the nearly complete crown of an RM_1, which has suffered slight enamel loss from the lingual cervical margin and the apex of the protoconid. The root is missing save for a short buccal segment of the mesial radicular plate.

The crown presents an ovo-rectangular occlusal outline, and all five principal cusps are well developed. The protoconid is but exiguously larger than the metaconid, and the hypoconid, entoconid, and hypoconulid are approximately equivalent in size. The crown lacks a *tuberculum sextum*, while a moderately large *tuberculum intermedium* (= postmetaconulid) arises from the distal ridge of the metaconid. The metaconid contacts the hypoconid (producing a Y occlusal pattern) by means of a strong central ridge that is deflected distally (a "deflecting wrinkle"). A distinct fovea anterior is present, and this is completely enclosed mesially by a thick marginal ridge. The distal trigonid crest is large and is incised by a deep, albeit narrow, fissure. The fovea posterior is represented by an incompletely enclosed basin.

On the buccal face the groove between the protoconid and hypoconid is elongate and broad, but shallow, and there is a tiny pit at the cervical terminus of this depression. The distobuccal groove is shorter and narrower than the mesiobuccal. The upper half of the buccal protoconidal surface exhibits several faint, oblique furrows, that may represent some form of "protostylid" development.

Wear is limited to a very small, faint facet on the buccal side of the protoconid apex, adjacent to the area of enamel damage.

The specimen displays no apparent pathology.

The principal dimensions of the crown are as follows:

MD as measured: 13.5 mm
BL trigonid: 10.7 mm
BL talonid: 10.9 mm
BL maximum: 11.1 mm

Remains from Unit 2A

EQ-H6 (Fig. 5a) comprises a complete LI^2. The crown is almost peg-shaped, with a noticeably reduced mesiodistal diameter.

Buccally, the crown presents an incisocervically elongate, rectangular outline. The mesioincisal corner is sharp, approaching a 90° angle, whereas the distoincisal corner is rounded and obtusely angled, with the distal half of the incisal edge sloping cervically. Lingually, the cervical eminence is slightly swollen and symmetrically disposed; there is no tubercular development.

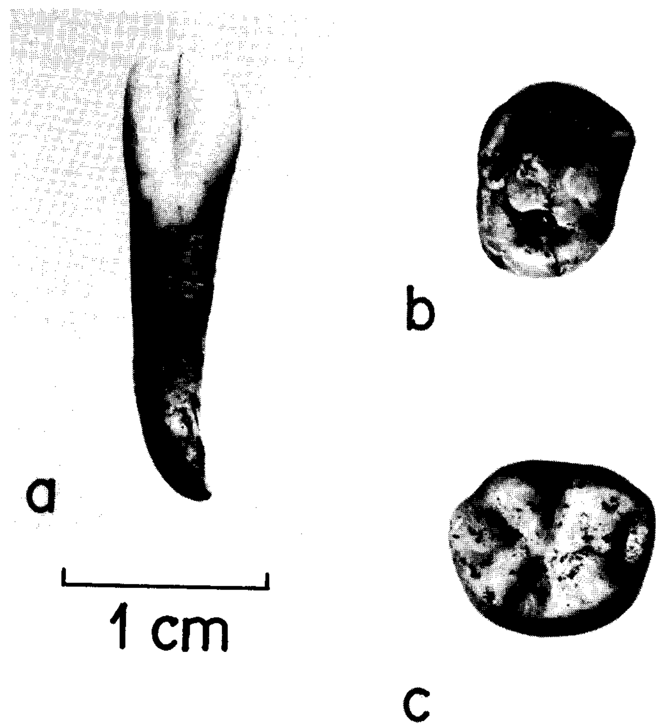

Fig. 5. Hominid remains from Unit 2A. a) lingual view of EQ-H6; b) occlusal view of EQ-H7; c) occlusal view of EQ-H8. Mesial to left except for c. Scale bar = 1 cm.

Moderately prominent mesial and distal marginal ridges, together with the absence of a median ridge, impart a moderate degree of shovelling to the lingual surface.

Neither a mesial nor a distal interproximal contact facet is present: wear is limited to light polishing over the distal half of the incisal edge.

The root, which measures 4.7 mm mesiodistally and 5.6 mm buccolingually at the cervix, follows a straight, vertical course for approximately two-thirds of its length (which is some 12.5 mm), while the apical third is curved distally.

The specimen presents a deep hypoplastic pit in the center of the distal half of the incisal edge, and the buccal face of the crown evinces a depression, the floor of which shows hypoplastic mottling near the cervical margin.

The principal dimensions of the crown are as follows:

MD as measured: 6.0 mm
BL diameter: 6.1 mm
Buccal height: 10.2 mm

EQ-H7 (Fig. 5b) consists of an incomplete LP^3. The crown is complete, although worn, while the root has been broken off some 7 to 8 mm above the cervical margin.

The crown possesses an ovo-rectangular occlusal outline; the buccal half shows slight mesiodistal dominance over the lingual moiety. The buccal margin is moderately convex mesiodistally, and the lingual margin presents a rounded, strongly convex profile.

Wear has reduced the occlusal aspect of the crown to a nearly planar surface. The only occlusal morphology that remains is a short fissure and pit that represent remnants of the central fovea between the buccal and lingual cusps. The buccal cusp is worn to a horizontal surface, while the lingual facet exhibits a slight lingualward bevel. Large dentine islands that taper mesially and distally are exposed on both cusps. A flattened mesial and concave distal contact facet attest to a moderate degree of interproximal attrition.

The root, which measures 5.5 mm mesiodistally and 9.3 mm buccolingually at the cervix, is undivided insofar as it is preserved, although two separate radicular canals are present at its broken end. The distal face of the root is flat, while the mesial surface presents a broad vertical groove that appears to deepen apically.

The specimen reveals no apparent pathology.

The principal dimensions of the crown are as follows:

MD as measured: 7.8 mm
MD corrected: 8.1 mm
BL diameter: 10.0 mm

EQ-H8 (Fig. 5c) comprises a complete, immature enamel cap and dentine filling of a left mandibular molar. It almost certainly represents a developing permanent tooth, and while its immaturity precludes certain assignation, the presence and sizes of the five principal cusps suggest it to be a first, or perhaps second, rather than a third molar.

As developed and preserved, the metaconid is slightly larger than the protoconid; the hypoconid, entoconid, and hypoconulid are of equivalent size. The metaconid contacts the hypoconid, and the latter is situated opposite the lingual groove such that the primary occlusal fissures form a symmetrical Y pattern. The crown shows no development of a *tuberculum sextum,* whereas a moderately protuberant postmetaconulid (= *tuberculum intermedium*) arises from the distal ridge of the metaconid. The fovea anterior is represented by a broad basin, while there is no development of a fovea posterior.

Meaningful measurement of the principal crown dimensions is not possible because of the immature nature of the enamel cap.

Remains from Unit 2B

EQ-H9 (Fig. 6a) represents a complete, albeit worn, LC. Apical wear has considerably reduced the height of the crown, with the result that almost all morphological detail has been lost.

The remaining part of the buccal surface is slightly convex apicocervically, and moderately convex mesiodistally; the mesial moiety of this face is somewhat more inflated than the distal. Lingually, the cervical eminence is moderately swollen and symmetrically disposed and, notwithstanding the degree of wear, there is no evidence of tubercular development. The only remnants of lingual surface morphology comprise a short, narrow, oblique fissure and a barely perceptible distal depression; these appear to have delimited a broad mesial and narrower distal marginal ridge.

Apical wear has produced a large facet that is bevelled distally and slightly lingually. A large, distally tapered dentine island is exposed on this facet, and the whole of the lingual surface evinces enamel wear. Slightly concave mesial and distal contact facets attest to a moderate degree of interproximal attrition.

The robust root measures 9.2 mm buccolingually and 6.1 mm mesiodistally at the cervix, and it follows a straight course with a slight distalward inclination for 18.7 mm from the buccal cervical margin to its apex. The mesial face is flat, while a shallow, longitudinal furrow incises the distal face. The root displays slight mesiodistal and strong buccolingual tapering to the apex.

The specimen reveals no apparent pathology.

The principal dimensions of the crown are as follows:

MD as measured: 8.7 mm
MD corrected: 9.1 mm
BL diameter: 9.8 mm

EQ-H10 (Fig. 6b) comprises the nearly complete crown and incomplete root of what is adjudged to be an LM^3. Damage to the crown is restricted to loss of enamel from the cervical margin along all but the distal aspect. The roots have been broken away such that 4 to 6 mm of the neck remains.

Viewed occlusally, the crown possesses a somewhat trapezoidal outline, with a mesially and buccally protuberant paracone. All four principal cusps are present; the protocone is but slightly larger than the paracone, while the metacone is notably smaller,

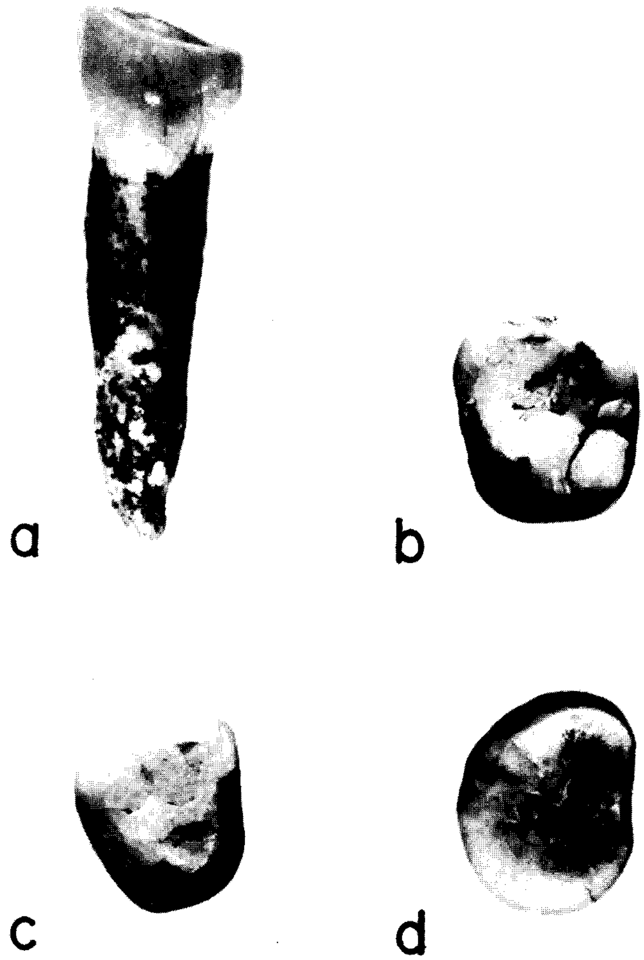

Fig. 6. Hominid remains from Unit 2B. a) lingual view of EQ-H9; b) occlusal view of EQ-H10; c) occlusal view of EQ-H11; d) occlusal view of EQ-H12. Mesial to left for a and b, mesial to right for c and d. Scale bar = 1 cm.

followed by the hypocone. The *crista obliqua* is constricted and incised at the base of the protocone. The distal marginal ridge is constricted by short, shallow fissures on its mesial and distal aspects, which serve to define an incipient distoconule.

There is no evidence of paramolar tubercle development, and while occlusal wear is such that the presence or absence of the Carabelli trait cannot be ascertained, the crown almost certainly lacked a well-developed Carabelli cusp.

Occlusal wear has blunted the distal cusps and reduced the protocone to a nearly flat horizontal plane. A very small, circular island of dentine is exposed on the protocone. The mesial contact facet is slightly concave, attesting to a slight to moderate degree of interproximal attrition.

The root neck, which measures 7.1 mm mesiodistally and 10.8 mm buccolingually at the level of the cervix, remains undivided over the 4 to 6 mm which is preserved.

The specimen reveals no apparent pathology.

The principal dimensions of the crown are as follows:

MD as measured: 9.5 mm
MD corrected: 9.7 mm
BL diameter: 11.0 mm

EQ-H11 (Fig. 6c) comprises a complete RM^3. The crown presents a trapezoidal occlusal outline, with the buccal half being mesiodistally dominant over the lingual. Considerable morphological detail has been lost through occlusal attrition, but it is readily apparent that the crown possessed at least three principal cusps. The protocone is the largest cusp, and the paracone is only slightly larger that the metacone. The hypocone, if present, would have been greatly reduced.

On the buccal face, only a faint remnant of the groove between the paracone and metacone remains visible. There is no evidence of paramolar tubercle development. The presence or absence of the Carabelli trait cannot be determined because of wear, although it is apparent that this crown lacked a well-developed Carabelli cusp.

Wear has reduced the occlusal surface to a rather flat plane with a lingual bevel. A large, triangular patch of dentine is exposed on the protocone, while the paracone has a small, circular exposure. A small, flattened facet on the mesial face of the crown suggests interproximal contact.

The neck of the root, which measures 9.4 mm mesiodistally and 13.8 mm buccolingually at the cervix, is relatively high, being some 8.5 mm from the level of the cervix to the radicular trifurcation. The dominant lingual root slopes lingually, while its apical portion turns vertically and distally. The distobuccal root courses almost straight vertically, whereas the mesiobuccal sweeps distalward.

Isolated patches of hypoplastic mottling are evident on the buccal and distal surfaces of the crown. The mesial face of the root presents a horizontal, buccolingually elongate (*circa* 5.9 mm) furrow immediately above the cervical enamel margin. The groove broadens slightly and deepens from buccal to lingual, attaining a maximum diameter of about 1.8 mm and a depth of approximately 0.7 mm. The floor of this furrow is scored by numerous fine striae of horizontal, buccolingual orientation.

The principal dimensions of the crown are as follows:

MD as measured: 8.8 mm
MD corrected: 8.8 mm
BL diameter: 10.0 mm

EQ-H12 (Fig. 6d) comprises a nearly complete RM^3. The crown is preserved intact, save for some slight loss to the cervical enamel margin, and the root system is very nearly complete, although it is rather heavily eroded.

The crown presents an irregular ovoid outline with a prominent mesiobuccal corner. Wear has obliterated almost all occlusal detail; only traces of the buccal and mesial limbs of the trigon basin remain discernible. It is evident that at least three principal cusps were present. The protocone and paracone appear to have been nearly equal in size and larger than the metacone. The hypocone, if present, would have been considerably reduced.

Buccally, the groove between the paracone and metacone is represented by a tiny depression; there is no pit associated with it, nor is there any development of a paramolar tubercle. Wear has reduced the protocone such that the presence or absence of the Carabelli trait cannot be determined, although the crown almost certainly lacked a well-developed Carabelli cusp.

The crown evinces moderate occlusal attrition, which has reduced the lingual moiety to a nearly flat plane, and has produced an elongate, crescent-shaped island of dentine on the protocone. Concave facets are present on the metacone and especially the paracone, and the buccal occlusal margin remains comparatively salient. A slightly concave mesial contact facet attests to a moderate degree of interproximal attrition.

The root neck, which measures 7.0 mm mesiodistally and about 10.4 buccolingually at the cervix, extends upward from this margin for between 6.0 and 7.0 mm to the level of the radicular trifurcation. The stout lingual root is vertically disposed, and the mesiobuccal root, which appears to have been better developed that the distobuccal, flares buccalward before curving distally over its apical portion.

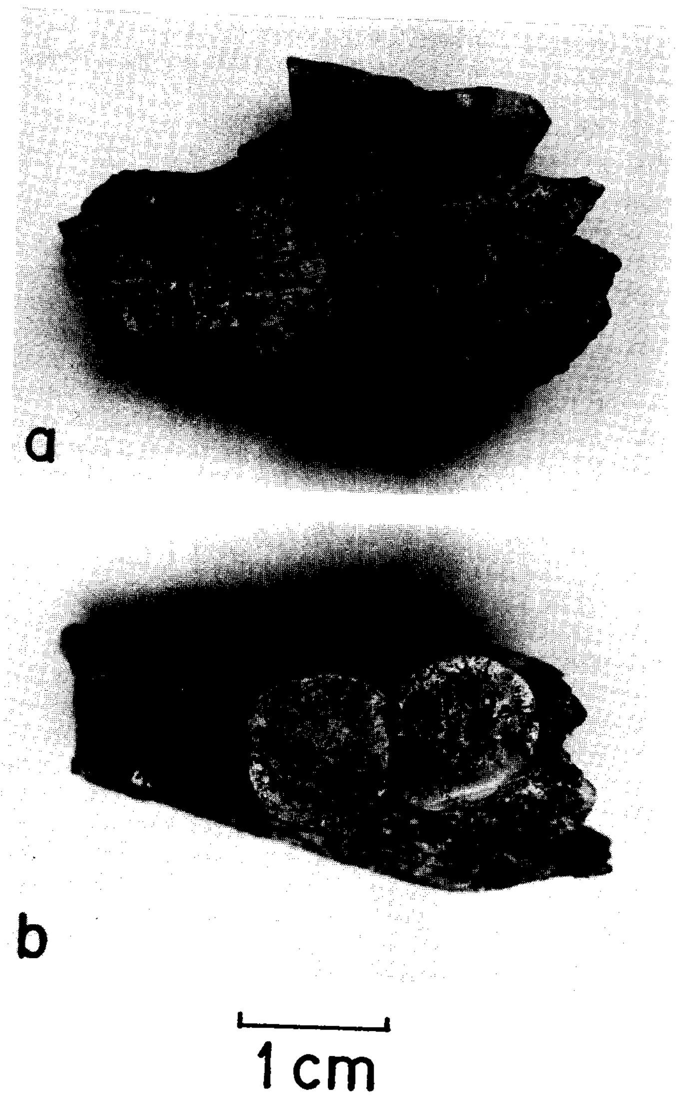

Fig. 7. Unprovenanced left mandibular fragment EQ-H71/33. a) lateral view; b) occlusal view. Mesial to left. Scale bar = 1 cm.

Several small, isolated hypoplastic pits are present on the buccal and distal surfaces of the crown.

The principal dimensions of the crown are as follows:

MD as measured: 9.2 mm
MD corrected: 9.4 mm
BL diameter: 11.0 mm

Remains of Uncertain Provenance

EQ-H 71/33 (Figs. 7 and 8) consists of a fragmentary left mandibular corpus containing intact, albeit heavily worn, second and third permanent molars. The corpus is fractured anteriorly at the level of the alveolar septum between the P_3 and P_4, and posteriorly some 5.0 mm behind the distal margin of the M_3. The base of the corpus is missing, with the most substantial loss being below the premolars and first molar. The alveolar margin is damaged anterior to the M_2; incomplete alveoli for the M_1 roots and a barely perceptible socket margin for the P_4 are preserved. A section of alveolar bone is missing from the lateral aspect opposite the M_2, and the anterior margin of the ramus is broken away opposite the M_3.

Laterally, the inferior origin of the rameal process is marked by a palpable bulge at the level of the mesial face of the M_1. The rameal surface forms an angle of about 20° with the corporeal surface anterior to it. The anterior margin of the ramus follows an oblique upward course, separated by some 5.0 mm from the lateral alveolar margin of the M_3. Although the free anterior border of the ramus has been lost, it is clear that it would have arisen opposite the M_3. Thus, in lateral view, the distal moiety of the M_3 would have been obscured by the anterior rameal margin.

Internally, the mylohyoid line is prominent and rather sharply angled below the M_3. Its prominence and angularity decrease anteriorly, however, such that below the M_2 the mylohyoid line is represented by only a gently rounded eminence.

Projected corporeal breadths, recorded by placing the fragment in approximate anatomical position, are as follows:

Diameter at M_1: 14.5 mm (est.)
Diameter at M_2: 16.5 mm
Diameter at M_3: 19.8 mm

The crowns of both molars, especially the M_2, are heavily worn. The occlusal aspect of the M_2 has been reduced to a nearly planar, mesiobuccally bevelled dentine surface. Buccally and lingually the M_2 preserves a very thin enamel rim, and while some enamel is present along the cervical margins mesially and distally, enamel has been obliterated from the occlusal margins of these faces by interproximal attrition. Whereas the M_2 is bevelled mesiobuccally, occlusal wear on the M_3 is strongest mesially,

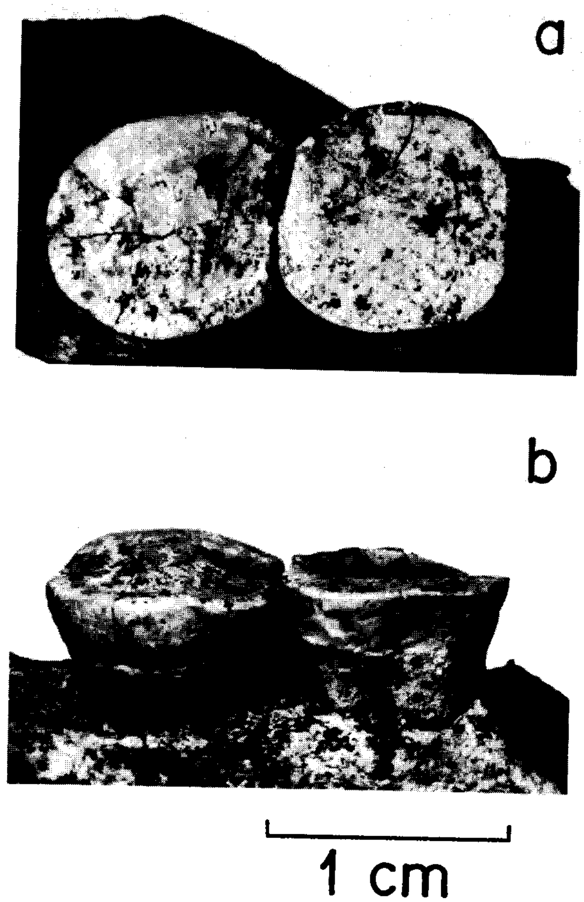

Fig. 8. Hominid specimen EQ-H71/33. a) occlusal view of M_2 and M_3; b) oblique lingual view showing helicoidal twist to occlusal plane. Mesial to right. Scale bar = 1 cm.

lingually, and distobuccally, with large dentine islands exposed on all cusps save the flattened hypoconid and the distolingual cusp. Thus, this specimen displays a rather pronounced helicoidal twist from the M_2 across the M_3.

The M_3 preserves the barely perceptible floors of some of the principal occlusal fissures, and from these remnants it is possible to discern the presence of all five principal cusps, together with the presence of a large accessory cusp. It is not possible, however, to determine whether this accessory feature comprised a large *tuberculum sextum* or a large *tuberculum intermedium.*

The root of the M_2 measures 10.2 mm mesiodistally and some 10.0 mm buccolingually at the level of the cervical margin, and it extends downward for some 5.7 mm from the buccal cervical margin to the level of the radicular bifurcation. Radiological examination reveals that the mesial and distal roots are well-developed and course vertically.

The root of the M_3 measures 9.5 mm mesiodistally and 9.8 mm buccolingually at the level of the cervical margin. Radiological examination reveals a vertically elongate neck and strong mesial and distal roots that slope distalward.

As preserved, the crown of the LM_2 measures 11.5 mm mesiodistally and 11.4 mm buccolingually. These values, however, represent minimum diameters; it is not possible to estimate the pristine dimensions with any degree of accuracy.

The principal dimensions of the LM_3 are as follows:

MD as measured: 12.4 mm
MD corrected: 12.8 mm
BL trigonid: 10.8 mm
BL talonid: 11.0 mm
BL maximum: 11.0 mm

Table 3

Mesiodistal and buccolingual diameters of Equus Cave hominid teeth

Tooth	Specimen	Unit	MD	BL
I^1	EQ-H4	1A	9.1	6.6
I^2	EQ-H6	2A	6.0*	6.1
$\underline{C}$	EQ-H9	2B	9.1	9.8
P^3	EQ-H7	2A	8.1	10.0
M^1	EQ-H1	1A	10.7	- - -
M^3	EQ-H2	1A	(9.3)	10.7
	EQ-H10	2B	9.7	11.0
	EQ-H11	2B	8.8	10.0
	EQ-H12	2B	9.4	11.0
M_1	EQ-H5	1B	13.5	11.1
M_1	EQ-H3	1A	10.6	9.8
	EQ-H71/33	?1B-2B	12.8	11.0

*EQ-H6 approaches a peg-shaped condition, with concomitant noticeable reduction in its MD diameter.

ODONTOMETRIC COMPARISONS

The corrected mesiodistal and maximum buccolingual diameters of the hominid tooth crowns from Equus Cave are recorded in Table 3. Comparative mensurational data obtained by Jacobson (1982) for a large sample of modern southern African, Bantu-speaking blacks are set out in Table 4. In most instances, the individual values for the Equus Cave specimens fall within 1 or 2 SDs of the means of the modern human sample, and in all but one case (the MD diameter of the EQ-H5 M_1), these values fall within 3 SDs of the means for southern African blacks (Fig. 9).

Table 4

Permanent tooth crown diameters of southern African blacks (after Jacobson 1982)

			N	$\overline{X}$	SD	SE
I^1	MD	male	144	8.82	0.66	0.055
		female	47	8.60	0.58	0.085
	BL	male	144	7.31	0.45	0.038
		female	47	7.14	0.50	0.073
I^2	MD	male	195	7.14	0.68	0.048
		female	71	6.85	0.66	0.079
	BL	male	195	6.73	0.54	0.039
		female	71	6.42	0.51	0.061
$\underline{C}$	MD	male	270	7.91	0.43	0.026
		female	93	7.50	0.38	0.040
	BL	male	270	8.72	0.59	0.036
		female	93	8.10	0.57	0.059
P^3	MD	male	295	7.27	0.43	0.025
		female	94	7.15	0.40	0.041
	BL	male	295	9.69	0.44	0.026
		female	94	9.34	0.52	0.054
M^1	MD	male	292	10.64	0.53	0.031
		female	92	10.43	0.51	0.053
M^3	MD	male	265	9.24	0.73	0.045
		female	81	8.79	0.96	0.107
	BL	male	265	11.64	0.78	0.048
		female	81	10.84	1.13	0.126
M_1	MD	male	277	11.39	0.60	0.036
		female	84	11.10	0.64	0.070
	BL	male	277	10.86	0.53	0.032
		female	84	10.65	0.53	0.058
M_3	MD	male	278	11.20	0.87	0.052
		female	73	10.86	0.87	0.102
	BL	male	278	10.59	0.71	0.043
		female	73	10.27	0.72	0.084

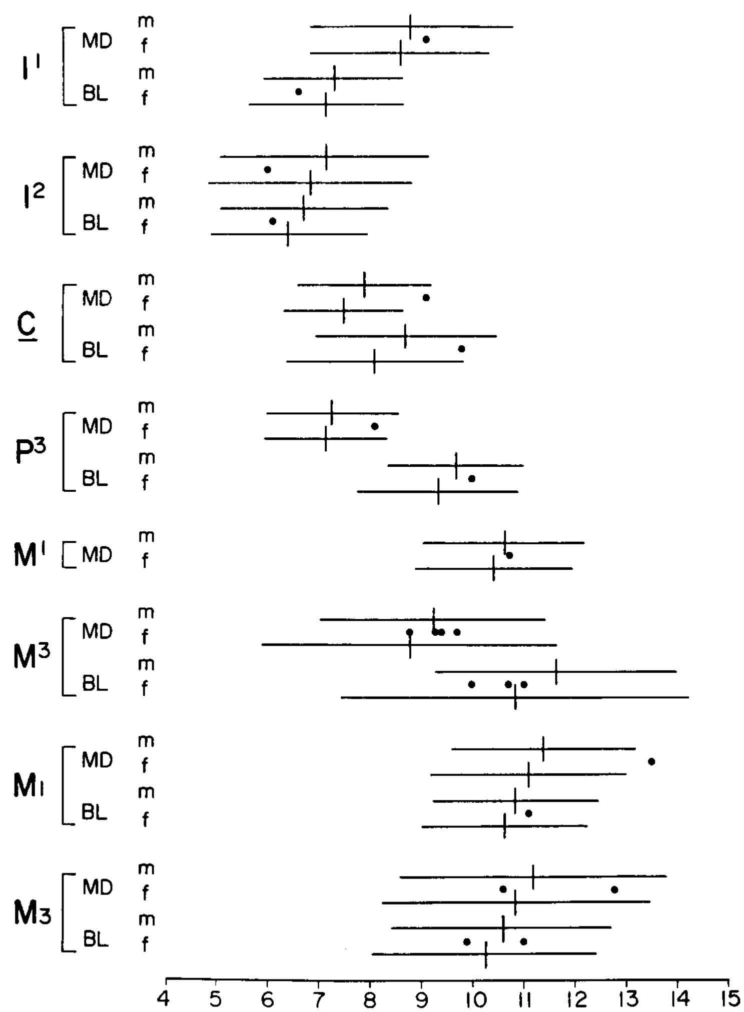

Fig. 9. Graphic companion of mesiodistal (MD) and buccolingual (BL) diameters of Equus Cave hominid tooth crowns (closed circles), with dimensions recorded for modern southern African blacks. Vertical bar, sample mean. Horizontal bar, sample mean ± 3 SD.

The diameters recorded for these Holocene specimens fall within 1 SD of the comparable modern sample means. As would be expected, none of these values have a low probability of being encountered among the present, indigenous inhabitants of South Africa (Table 5).

Similarly, most of the diameters of the crowns from Units 1B through 2B of Equus Cave fall within 1 or 2 SDs of the corresponding means of recent southern African blacks (Table 5). The only notable exceptions to this pattern of mensurational similitude pertain to the M_1 (EQ-H5) and the $\underline{C}$ (EQ-H9) from Units 1B and 2B (Fig. 9).

The MD diameter of EQ-H5 (13.5 mm) is comparatively large, falling outside the ranges established by 3 SDs of the modern male and female means (Fig. 9), and there is a significantly low probability that an M_1 with this MD diameter would be encountered in a sample of modern southern African blacks (Table 5). On the other hand, the BL diameter of this specimen (11.1 mm) falls within 1 SD of the comparative means for both males and females.

Table 5

Comparison of Equus Cave tooth crown diameters with those recorded for modern southern African blacks ('t' values)

Tooth	Specimen	Mesodistal		Buccolingual	
		Male	Female	Male	Female
HOLOCENE SPECIMENS					
I^1	EQ-H4	0.42	0.85	1.57	1.07
M^1	EQ-H1	0.11	0.53		
M^3	EQ-H2	0.08	0.53	1.20	0.12
M_3	EQ-H3	0.69	0.30	1.11	0.65
PLEISTOCENE SPECIMENS					
I^2	EQ-H6	1.67	1.28	1.16	0.62
$\underline{C}$	EQ-H9	2.76*	4.19***	1.83	2.97**
P^3	EQ-H7	1.93	1.65	0.70	1.26
M^3	EQ-H10	0.63	0.94	0.82	0.14
	EQ-H11	0.60	0.01	2.10	0.74
	EQ-H12	0.22	0.63	0.82	0.14
M_1	EQ-H5	3.51***	3.73***	0.45	0.84
M_3	EQ-H71/33	1.84	2.21	0.58	1.01

*$p < 0.01$; **$p < 0.005$; ***$p < 0.001$

The MD diameter of EQ-H9 (9.1 mm) falls just within the upper limit of the range established by 3 SDs of the modern black male sample mean, and above this limit for the black female average (Fig. 9), and there is a significantly low level of probability that a C with this MD diameter would be evinced in a sample of modern southern African blacks (Table 5). The BL diameter of EQ-H9 (9.8 mm) falls within 2 SDs of the modern black male sample mean, and just within the upper limit set by 3 SDs of the black female average recorded in Table 4. This value accordingly differs significantly from the female mean, but it does not differ significantly from the male values obtained by Jacobson (Table 5).

The MD diameters recorded for the EQ-H7 P^3 and the M_3 of EQ-H 71/33 are also comparatively large (Fig. 9), although both fall within 3 SDs of, and do not differ significantly from, the respective modern sample means (Table 5). The BL diameters of these two crowns fall within 1 or 2 SDs of the sample means for modern male and female southern African blacks (Table 3).

By comparison to a modern southern African standard, some of the Pleistocene specimens from Equus Cave evince sizeable crowns, but in most instances the diameters of these teeth, like those of the Holocene specimens, fall comfortably within the modern population limits (Fig. 9; Table 5). The overall similarity in size among these and modern crowns stands in contrast to the dimensional changes that have been demonstrated elsewhere for early Upper Pleistocene and recent human samples (Wolpoff 1979).

ODONTOSCOPIC COMPARISONS

With regard to the I^1 (EQ-H4), the lack of median lingual ridge and lingual tubercle development displayed by this crown finds correspondence among modern South African blacks, where approximately 51% of individuals present a lingually smooth I^1, and some 93% of homologues lack lingual tubercle development (Jacobson 1982). On the other hand, only about 3% of males and 9% of females examined by Jacobson (1982) evince a degree of I^1 shovelling comparable to or stronger than that shown by EQ-H4. I^1 winging in the individual represented by EQ-H4 may have been unilateral or bilateral, corresponding to categories 4 or 5 of Dahlberg (1963). Such unilateral or bilateral winging was not observed in a sample of 127 modern Kalahari San examined, and only about 2.0% of modern southern African blacks display these forms of I^1 rotation (Grine, unpubl.).

The I^2 (EQ-H6) from Unit 2A of Equus Cave is reduced, approaching a peg-shaped appearance. An incidence of only about 0.1% for this trait in modern South African blacks has been noted by de Villiers (1968), but inasmuch as only extreme examples were recorded by her, the frequency of the kind of crown reduction exhibited by EQ-H6 may be higher in this population. The lack of median lingual ridge and lingual tubercle development on the Equus Cave I^2 also characterizes the majority of recent black South Africans, where some 64% of individuals possess lingually smooth I^2s, and approximately 87% of these crowns lack a lingual tubercle (Jacobson 1982). About 11% of modern black I^2s show a degree of shovelling comparable to or stronger than that exhibited by the EQ-H6 crown.

Neither the $\underline{C}$ (EQ-H9) nor the P^3 (EQ-H7) preserve enough morphological detail to permit a comparative analysis.

The M^1 (EQ-H1) from Unit 1A finds correspondence with some 99.7% of modern black South Africans (Jacobson 1982) and fully 100% of recent San (Drennan 1929) homologues in its degree of hypocone development. Although the protocone is worn on EQ-H1, it is certain that this crown lacked a well-developed Carabelli cusp. Only 5.7% of modern black South Africans possess a Carabelli cusp on the M^1, and just under 17% of these crowns display either a well-developed cuspoid or "lobular" Carabelli trait (Jacobson 1984). Similarly, only about 7% of modern Kalahari San possess a well-formed "tubercle" of Carabelli on the M^1 (van Reenen 1964).

Four M^3s are present in the Equus Cave sample: one (EQ-H2) derives from Unit 1A, while the others (EQ-H10, 11, and 12) come from the underlying Pleistocene strata. EQ-H10 possesses all four principal cusps, and while the other three crowns are worn, EQ-H2 would appear to have been four-cusped, judging from its occlusal outline, whereas the other two crowns seem to have shown a reduced hypocone. According to Jacobson (1982), some 29% of modern South African black M^3s are four-cusped, while approximately 32% of these crowns possess a reduced hypocone. The corresponding percentage incidences recorded by Drennan (1929) for San M^3s are 12% and 38% respectively. Thus, a total of about 61% of black South African and 50% of San individuals possess M^3s with a hypocone, be it full or reduced. Although the four Equus Cave crowns are worn, it is almost certain that they did not possess a well-developed Carabelli cusp. Only about 0.2% of modern black South Africans evince a Carabelli cusp on the M^3, and only about 2% of these individuals possess either a well-developed cuspoid or "lobular" Carabelli feature (Jacobson 1982). That is, the lack of a large Carabelli trait on the four Equus Cave M^3s finds correspondence with some 98% of the modern indigenous inhabitants of southern Africa. Finally, although EQ-H2 is too worn to ascertain the absence or presence of a paramolar tubercle, this buccal style is absent from the three Pleistocene homologues. Fully 99.5% of modern southern African blacks lack any manifestation of this feature on the M^3 (Jacobson 1982).

The single M_1 from Unit 1B (EQ-H5) has five well-developed principal cusps; some 99% of modern San and South African blacks possess five-cusped first lower molars (Grine 1981). The Y occlusal configuration shown by EQ-H5 is also displayed by approximately 81% of black and 89% of San homologues (Grine 1981). The metaconid deflecting wrinkle exhibited by EQ-H5 is also shown by 19.0% of modern black and 21.5% of modern San M_1s (Grine 1981). Some 95% of black and 84% of San M_1s lack a *tuberculum sextum*, as does the EQ-H5 crown, while the noticeable *tuberculum intermedium* shown by this Equus Cave specimen finds correspondence among some 15% of black and 20% of San homologues (Grine 1981). The moderately deep buccal grooves exhibited by EQ-H5 are evinced also by approximately 60% of recent southern African black homologues, while only some 7% of these crowns possess a terminal pit, as shown by the Equus Cave molar (Jacobson 1982). The buccal protoconidal surface of the EQ-H5 crown reveals several faint depressions that may represent incipient expression of a protostylid; only about 0.4% of recent black M_1s show any trace of this trait (Jacobson 1982).

The only M_2 represented in the Equus Cave sample, which is preserved in the EQ-H 71/33 mandibular fragment, is worn so as to preclude any morphological comparisons.

Two M_3s are preserved in the Equus Cave collection; one (EQ-H3) derives from Unit 1A, while the other is contained in the mandibular fragment, and is worn such that little morphological detail is preserved. Both specimens are five-cusped, as are 79% of black and 81% of San M_3s (Grine 1981). EQ-H3 possesses a well-developed *tuberculum sextum*, and the presence of an additional cusp is indicated on the EQ-H 71/33 M_3, although it is not possible to ascertain whether it comprised a *tuberculum sextum* or *tuberculum intermedium*. The former cuspulid is present on some 20% of black and 31% of San M_3s, while some 11% of black and 6% of San individuals evince a *tuberculum intermedium* on the third molar. As with the EQ-H3 crown, the occlusal fissures form a + pattern on approximately 39% of modern South African black and San homologues (Grine 1981). Approximately 53% of modern southern African, Bantu-speaking blacks, and nearly 75% of modern Kalahari San, possess M_3s with metaconid crest morphology comparable to that on the EQ-H3 crown (Grine 1981). The EQ-H3 specimen possesses a short, narrow buccal groove without a terminal pit; negligibly developed buccal furrows are evinced by about 62% of black M_3s, while just over 97% of their crowns lack a pit associated with the buccal groove (Jacobson 1982). A noticeable protostylidal furrow is present on the EQ-H3 M_3, whereas only 3.7% of modern black homologues possess any development of this feature (Jacobson 1982).

Morphologically, the Equus Cave tooth crowns are comparable to those of the present-day, indigenous inhabitants of southern Africa. That is, almost all of the non-metrical traits evinced by the Equus Cave specimens occur in high frequencies among the southern African, Bantu-speaking blacks and (for those features for which relevant observations have been made) among the San. The only noteworthy exceptions to this pertain to the presence of protostylidal furrows on EQ-H3 and EQ-H5, this trait being exceedingly rare, albeit not unknown, among recent southern African blacks. The degree of lingual shovelling exhibited by EQ-H4 and EQ-H6 is also relatively uncommon within the recent black population, but comparable and even stronger degrees of lingual excavation of the I^1 and I^2 are certainly represented.

PULP CAVITY DIMENSIONS

Interest in the relative size of the molar pulp chamber was initiated by Gorjanović-Kramberger's (1907, 1908) description of an unusual root form in nearly half of the Neanderthal specimens from the Husnjakovo rock shelter, Krapina. In these teeth, the root was largely unbifurcated and of a cylindrical or "prismatic" appearance. Concomitantly, the pulp cavity was apically enlarged, a condition referred to by Keith (1913) as taurodontism. Taurodont molars have been recorded in a number of other European Neanderthal specimens, where its apparent commonality has come to be regarded as one of the characteristics of that group (Stringer *et al.* 1984).

Shaw (1928) defined three categories of expression of taurodontism (*i.e.*, hypotaurodont, mesotaurodont, and hypertaurodont) which have been employed in several qualitative and quantitative analyses of this condition in modern human populations (Shaw 1928; Pederson 1949; Moorrees 1957; Brabant and Kovacs 1961; Keene 1966; Shifman and Chanannel 1978).

Lateral radiographs of five specimens from Equus Cave (EQ-H1, 3, 11, 12, and 71/33) were obtained at 90 KV, 10 milli-amp and 38 impulses using Kodak Ultra-Speed D film. Four variables

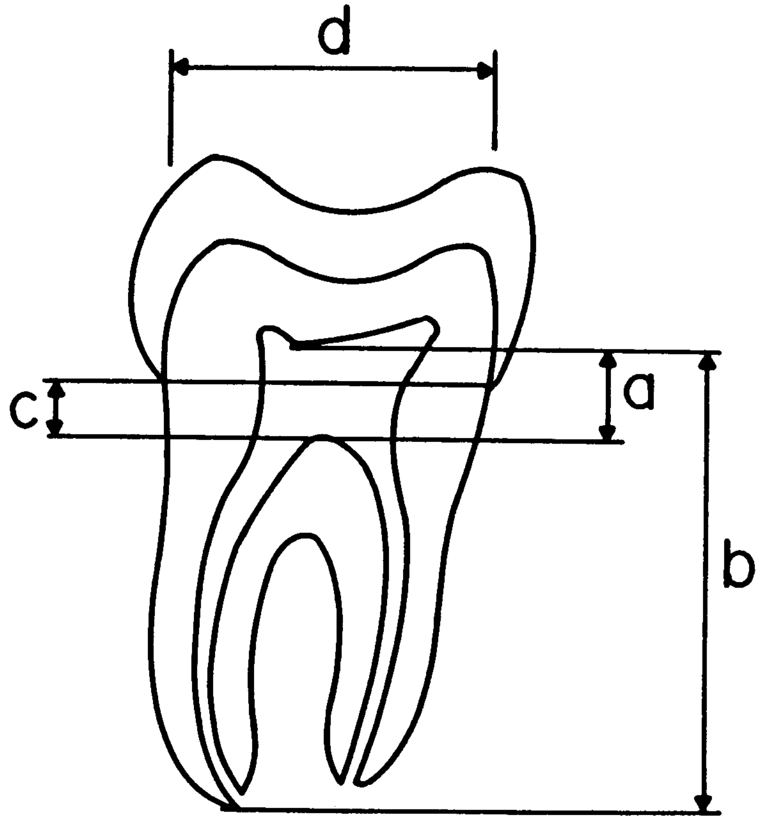

Fig. 10. Mesiodistal cross-section of molar tooth indicating the three variables measured. Line between mesial and distal cervical margins forms horizontal base. Variable *a:* perpendicular distance from lowest point on pulp chamber roof to highest point on pulp chamber floor. Variable *b:* perpendicular distance from lowest point on pulp chamber roof to apex of longest root. Variable *c:* perpendicular distance from cervical base line to highest point on pulp chamber floor. Variable *d:* mesiodistal diameter of the root neck at the level of the cervical margin.

Variable *a* corresponds to variables "Y" of Keene (1966) and "1" of Shifman and Chanannel (1978); variable *b* corresponds to variables "Z" of Keene (1966) and "2" of Shifman and Chanannel (1978); variable *c* corresponds to variable "3" of Blumberg *et al.* (1971) and Shifman and Chanannel (1978); variable *d* corresponds to variable 2 of Blumberg *et al.* (1971).

(Fig. 10) were measured on the radiographs of these five specimens, while these diameters were recorded directly on the sectioned EQ-H1 tooth (Table 6). Visual inspection led to the intuitive classification of these specimens as being "cynodont" (EQ-H1, 11, 12 and 71/33) or, at most, "hypotaurodont" (EQ-H2 and 3).

According to Keene's (1966) classification, which is based solely upon the value of the "taurodontism index" (TI), specimens EQ-H1 and EQ-H 71/33 are "cynodont," specimens EQ-H11 and 12 are barely "hypotaurodont," while specimens EQ-H2 and 3 are "hypotaurodont." The classification scheme devised by Shifman and Chanannel (1978), which employs the absolute value of variable C together with different category delineations of the TI, finds EQ-H1 and the M_3 of EQ-H 71/33 to be "cynodont," and EQ-H2, 3, and 11 to be "hypotaurodont" (EQ-H12 presents an apparent anomaly, inasmuch as the value for variable C is less than the "taurodont" minimum of 2.5 mm, while its TI value falls within the range of "hypotaurodontism" set by these authors).

As noted by Blumberg *et al.* (1971), the deposition of secondary dentine on the roof of the pulp chamber with increasing ontogenetic age (and, presumably, a concomitant increase in the amount of occlusal wear) will have an appreciable effect upon the use of the TI as an indicator of this phenomenon. They found that variable C (Fig. 10) and the MD diameter of the root at the level of the cervical margin were the major discriminating factors

Table 6
Root and pulp chamber diameters of Equus Cave molar teeth

Tooth	Spec.	Unit	a	b	c	d	TI
M^1	EQ-H1	1A	1.8	11.5	2.8	7.4	15.65
M^3	EQ-H2	1A	3.8	13.2	3.0	6.4	28.79
	EQ-H11	2B	3.4	13.6	3.4	9.4	25.00
	EQ-H12	2B	3.0	11.6	2.0	7.0	25.86
M_2	EQ-H71/33	1B-2B	1.4	13.5	- -	10.2	10.37
M_3	EQ-H3	1A	3.8	12.7	3.9	8.1	29.92
	EQ-H71/33	1B-2B	1.5	13.0	1.9	9.5	11.54

Variables a-d are as defined in Figure 10.
TI = variable a/variable b x 100.

between taurodont and non-taurodont teeth. Comparisons of these two variables for the EQ-H3 and EQ-H 71/33 M_3s with the lower molar data for American whites and blacks published by Blumberg *et al.* (1971) reveal these two specimens to be non-taurodont.

While the incidences of taurodontism that have been recorded for modern human populations vary according to the criteria used to define this phenomenon (Shaw 1928; Keene 1966; Blumberg *et al.* 1971; Shifman and Chananel 1978), in none of these studies would the Equus Cave molars be considered as being more than hypotaurodont (*i.e.*, marginally taurodont). Certainly, none of the specimens from the Pleistocene sediments of this site displays the degree of pulp chamber enlargement that appears to be so prevalent among similarly aged human remains from Europe (Kallay 1963; Stringer *et al.* 1984).

MANDIBULAR CORPUS DIMENSIONS

As noted above, the projected breadths of the EQ-H 71/33 mandibular corpus are 14.5 mm (est.) at the level of the M_1, 16.5 mm at the level of M_2, and 19.8 at the level of M_3. Corporeal diameters at the level of the M_1 and M_2 for southern African black adults are recorded in Table 7. The data presented in this table are derived from measurements kindly supplied by Professor H. de Villiers.

While the values for the Equus Cave specimen are slightly larger than the respective male and female means recorded in Table 7, the EQ-H 71/33 diameters fall comfortably within the observed sample ranges, and within 1 SD of the means obtained for modern male and female samples. The mediolateral diameters of the corpus of EQ-H 71/33, like the dimensions of the teeth it contains, do not differ in any way from those of the modern indigenous inhabitants of South Africa.

DISCUSSION

The origin of anatomically modern *Homo sapiens* continues to be one of the more perplexing problems in hominid palaeontology. The central question is whether anatomically modern *Homo sapiens* arose from a common source population and then spread through migration and replacement, or whether the modern autapomorphic morphologies evolved in parallel in different regions from local archaic populations (Howells 1976; Wolpoff 1980; Thorne and Wolpoff 1981; Stringer *et al.* 1984; Wolpoff *et al.* 1984; Pilbeam 1985). In this context, attention has recently become increasingly focused upon sub-Saharan Africa as

Table 7

Mandibular corpus diameters at the level of the first and second permanent molars for southern African blacks

Level	Sex	N	$\overline{X}$	SD	SE	Obs. Range
M_1	male	50	13.58	1.77	0.25	9.8-17.6
	female	49	13.30	1.55	0.22	10.0-16.3
M_2	male	50	15.16	1.77	0.25	11.4-19.1
	female	50	14.95	1.53	0.22	12.1-17.9

the source of the earliest anatomically modern fossils (Leakey *et al.* 1969; Beaumont *et al.* 1978; Rightmire 1979, 1981, 1984; Bräuer 1984a,b; Stringer 1984; Stringer *et al.* 1984). Of particular pertinence to this problem are the southern African sites of Klasies River Mouth and Border Cave.

Klasies River Mouth has yielded, among a small number of human remains from the Middle Stone Age layers, several incomplete mandibles (KR 13400, 14695, 16424, 21776, and 41815) and a frontal (KR 16425), dated by geological inference to between about 120,000 and 95,000 yrs. B.P., that are metrically and morphologically within the range of modern anatomical variation (Singer and Wymer 1982).

The skeletal remains of four individuals from Border Cave (BC-1, 2, 3, and 5) that have been attributed to Middle Stone Age context are completely modern in appearance (de Villiers 1973, 1976; Rightmire 1979, 1984; Bräuer 1984a, b). Although it has been argued at length that these remains are in a Middle Stone Age context and therefore between about 85,000 and 110,000 yrs. B.P. (Beaumont *et al.* 1978; Butzer *et al.* 1978; Beaumont 1980), Klein (1983) has cited factors regarding the "excavation" of BC-1 and BC-2 and the state of preservation of BC-3 and BC-5 which indicate that the purported stratigraphic associations and concomitant geochronologic ages of these specimens should be treated with some circumspection. Nevertheless, as noted by Klein (1983), the Border Cave evidence for anatomically modern humans in the late Middle-early Upper Pleistocene gains some support from the securely provenanced fossils from Klasies River Mouth.

The Equus Cave human remains described here comprise four isolated teeth from the Holocene levels, eight isolated teeth from the early Upper Pleistocene (Units 1B through 2B), and a fragmentary mandibular corpus containing two teeth that most probably derives also from these Pleistocene sediments. As might be expected, the Holocene remains, which have a maximum age of some 7,500 yrs. B.P., are morphologically and metrically indistinguishable from the teeth of modern indigenous peoples of Southern Africa. In only two instances are the metrical values of the teeth from the Pleistocene units of Equus Cave comparatively large for modern homologues, and in both cases (EQ-H9 and especially EQ-H5) only the mesiodistal diameters are enlarged. Apart from the mesiodistal diameters of these two teeth, all other metrical values for the Pleistocene specimens fall comfortably within the range of modern variation. The overall similarity in size among the Pleistocene crowns from Equus Cave and the teeth of modern southern African populations stands in contrast to the temporal dimensional changes that have been demonstrated over the corresponding timespan in other geographic regions. Moreover, the pulp chambers of the Equus Cave molars resemble those of modern homologues in their dimensions, and none displays the taurodontic enlargement that appears to be so prevalent among similarly-aged hominid remains from Europe. In addition, most all of the non-metrical morphological traits evinced by the Equus Cave teeth occur in high frequencies among the modern indigenous populations of southern Africa. While the protostylidal furrows on the EQ-H3 and EQ-H5 molars and the degree of lingual shovelling shown by the EQ-H4 and EQ-H6 incisors are relatively uncommon, these features are not unknown among recent populations. Finally, the corporeal diameters of the mandibular fragment from Equus Cave (EQ-H 71/33) fall well within modern South African population ranges and, insofar as it is preserved, the morphology of this rather gracile jaw is of modern aspect.

Notwithstanding the fact that the human remains from Equus Cave are even more incomplete than those from Border Cave and Klasies River Mouth, these isolated teeth and the mandibular fragment appear to provide some additional evidence for the morphological similarity of early Upper Pleistocene and recent human populations in southern Africa. Clearly, the southern African fossil evidence suggesting anatomical modernity for Middle Stone Age peoples by the late Middle-early Upper Pleistocene would be more compelling if the remains were more complete and more numerous. Nevertheless, interpretation of genetic evidence has suggested that modern humans originated on the order of 100,000 yrs. B.P. (Jones 1981, 1985), an order of antiquity that would be in keeping with the inferred ages of the Border

Cave, Klasies River Mouth, and Equus Cave hominid fossils. Certainly there appears to be some evidence for morphological continuity in southern Africa over the last 100,000 years or so. The genetic evidence, together with the fossil evidence, may well lend support to proposals that modern human populations are descended from the late Middle-early Upper Pleistocene peoples of sub-Saharan Africa.

SUMMARY AND CONCLUSIONS

Equus Cave opens on the western face of the Oxland tufa, one of a series of freshwater limestone fans that mantle the Gaap Encarpment near Taung, in the northern Cape Province of South Africa. The sandy deposits filling Equus Cave comprise four lithostratigraphic units (1A, 1B, 2A, and 2B), which contain a rich abundance of faunal remains as well as some lithic artifacts. Systematic excavations undertaken in 1978 and 1982 resulted in the recovery of four isolated human teeth attributable to the uppermost unit (1A), a single human molar from Unit 1B, three isolated teeth from Unit 2A, and four isolated human teeth from Unit 2B. An unprovenanced fragmentary mandibular corpus containing two molars found in 1971 most likely derived from one of the three lowermost units (1B, 2A, or 2B).

The uppermost unit (1A) is Holocene in age, with a maximum age of some 7,500 yrs B.P. by radiocarbon determination. Unit 1A contains a number of lithic artifacts attributable to the Later Stone Age, a modern fauna, including domestic stock in the topmost spits, and a pollen assemblage that is closely comparable to the modern Kalahari Thornveld spectrum.

The lower sandy units (1B through 2B), which unconformably underlay Unit 1A, have been dated by geological inference to between about 94,000 and 33,000 yrs. B.P. The fauna from Units 1B through 2B is homogeneous and strikingly different from that of Unit 1A, and these remains appear to have been accumulated primarily by the brown hyena, *Hyaena brunnea*. Three extinct species (*Equus capensis, Megalotragus priscus, Antidorcus bondi*) are represented in the lower three units, which contain a notably better representation of grazers and mixed feeders than browsers. The corresponding pollen assemblages comprise small numbers of arboreal palynomorphs, and higher proportions of Gramineae and Compositae, suggestive of a Karroid grassland with few trees. Faunal and palynological analyses suggest, moreover, that the lower units were deposited under somewhat cooler conditions than prevail today.

The fragmentary human remains from Equus Cave are described in detail here. Analysis of the four teeth from the Holocene deposits reveals them to be indistinguishable, both morphologically and metrically, from the teeth of the modern indigenous inhabitants of southern Africa. The early Upper Pleistocene remains from Equus Cave also fall comfortably within the range of variation for recent southern African humans in terms of tooth crown morphology, tooth crown size, the dimensions of molar pulp chambers, and in mandibular corpus morphology and breadth. The only exceptions to this pattern of overall similitude are the comparatively large mesiodistal diameters of the M_1 from Unit 1B and the $\underline{C}$ from Unit 2B, but in both cases the buccolingual diameters of these crowns fall comfortably within recent population limits.

The overall similarity in size among the Pleistocene specimens from Equus Cave and homologues of recent southern African peoples stands in contrast to the temporal changes that have been demonstrated in other geographic regions. Also, none of the Equus Cave molars evinces the sort of taurodontic enlargement that appears to be so prevalent among comparably aged hominid specimens from Europe.

Despite being incomplete and fragmentary, the human remains from Equus Cave provide some evidence, in addition to that from sites such as Border Cave and Klasies River Mouth, for the morphological modernity of the late Middle-early Upper Pleistocene inhabitants of southern Africa. The Equus Cave specimens, like those from Border Cave and Klasies River Mouth, suggest that there has been some degree of morphological continuity in southern Africa over the last hundred millennia or so, and, together with genetic evidence, these fossils may suggest that modern human populations are descended from the Middle Stone Age peoples of sub-Saharan Africa.

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