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EXTINCT EQUIDS FROM LIMEWORKS CAVE AND CAVE OF HEARTHS, MAKAPANSGAT, NORTHERN PROVINCE, AND A CONSIDERATION OF VARIATION IN THE CHEEK TEETH OF *EQUUS CAPENSIS* BROOM

by

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ABSTRACT

Dental specimens of *Hipparion libycum* from Limeworks Cave, and *Equus capensis* from Cave of the Horse's Mandible in the Limeworks Cave entrance and from Cave of Hearths on the farm Makapansgat in the Makapansgat Valley are described. The concept of restricted local formations within each cave is discussed. Qualitative variation in the cheek teeth of *E. capensis*, based on a sample of 40 upper and 60 lower permanent premolars and molars from Cave of Hearths, demonstrates that there appears to be no correlation in the occurrence of one enamel feature with another between teeth of presumed different individuals. Teeth within a molar row show similar development of features between teeth, whether premolar or molar, as shown by plis, progressive migration of the protocone isthmus along the row, and penetration of the buccal valley to between the enamel loops of the metaconid and metastylid. Consequently, earlier descriptions of species of large Pleistocene *Equus* in Southern Africa founded on isolated teeth and, using such qualitative variation, are inept, unsuitable and inappropriate, and modern taxonomies synonymising them under *E. capensis* are supported. The Cave of Hearths 'loose breccia' (Beds 1-3 of Mason, 1988) containing earlier Stone Age/Later Acheulean artifacts, is circumstantially dated between 300 000 and 200 000 years BP.

KEY WORDS: Makapansgat Valley, Late Pleistocene, Cave of Hearths, Limeworks Cave, *Hipparion lybicum*, *Equus capensis*, dental variation.

HISTORICAL INTRODUCTION

The Makapan caves lie on the farms 'Makapansgat' and 'Swartkrans' in both south and north walls of the valley of the Mwaridzi stream (also known as the 'Makapan River' or'Makapanspruit'), about 16 km east of Potgietersrus, Northern Province (Figure 1). The Mwaridzi drains part of the Strydpoortberge and is a tributary of the Mogalakwena River ('Magalakwyn' on some maps), which it enters west of Potgietersrus. The caves are located at about latitude 24°08′ south, longitude 29°16′ east, and at an altitude of about 1500 masl. The caves formed from the combined effects of subsidence and solution in the Malmani Dolomite of the Transvaal Supergroup (Partridge, 1975) and have been refilled by stratified deposits of travertine, cave earth, soil, fragments of dolomite from the roof, and biological remains.

Seven named caves are located within the Makapansgat valley - Peppercorn Cave, Buffalo Cave, Swartkrans Prospects, Limeworks Cave (including Cave of the Horse's Mandible), Historic or Makapan's Cave, Cave of Hearths, and Rainbow Cave - respectively from west to east. Buffalo and Limeworks Cave and Cave of Hearths have yielded extinct equids, but only Limeworks Cave and Cave of Hearths will be considered here. Buffalo Cave has yielded both *Hipparion* cf. *lybicum* and *Equus* cf. *capensis* (Kuykendall *et al.*, 1995), with *E. capensis* first recorded by Broom (1937).

Limeworks Cave was first reported to be fossiliferous by W.I. Eitzman (Dart, 1925), a school teacher in Pietersburg, who began collecting fossils in the Makapansgat Valley. Some of these fossils were donated to the Department of Anatomy, University of the Witwatersrand by Dart (1925) who published a short note on the 'Limeworks' occurrence. After 1927 Dart was responsible for the collection of the many additional specimens from Limeworks Cave (Malan, 1988). Cooke (1952) and Oakley (1954a, 1954b) discussed the significance of the fossil faunas obtained by James W. Kitching in the 1940s and 1950s. Wells & Cooke (1956) first reported the three-toed equid *Stylohipparion* sp. from Limeworks Cave and Ewer (1958) referred it to '*Stylohipparion van Hoepeni* spp.' Boné & Singer (1965) recorded '?*Stylohipparion steytleri*' from Makapansgat and justified this taxonomic identity as 'after Cooke (1963).' Churcher (1970, Table 8) recognised *Hipparion steytleri* and ?*Equus capensis* from Limeworks Cave and *E. capensis, E. burchelli* and *E. plicatus* (since considered conspecific with *E. capensis*) from Cave of Hearths. Churcher & Richardson (1978, Table 20.1) revised the species to *H. libycum* and *E. (Dolichohippus) capensis*. Churcher & Watson (1993) recombine this hipparion's name as *H. l. steytleri*.

Cave of Hearths was recognised as containing fossils in 1925 when Eitzman collected fossils from it. Dart (1925) also noted it as fossiliferous and was

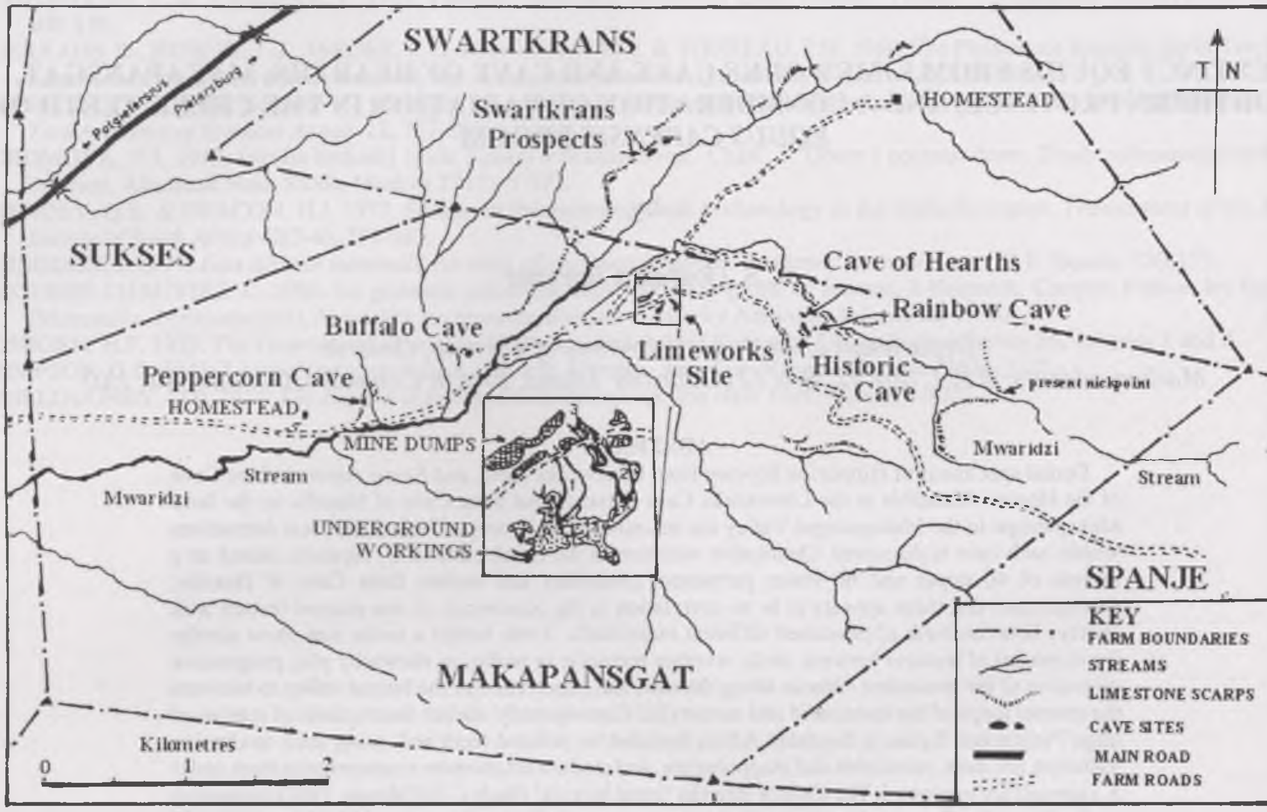

Figure 1. Map of the Makapansgat Valley and Makapansgat Farm with named cave sites.

responsible for the collection of additional fossils after 1927. Only *Equus burchelli* and *E. capensis* are reported from this cave (Churcher & Richardson, 1978; Cooke, 1988). Because of the cave's early history of exploration for mineral lime and the removal of most of the breccias by the miners, its stratigraphy and interpretation are unclear and its palaeontological importance less manifest than that revealed in Limeworks Cave.

GEOLOGY OF THE DEPOSITS AND CONTAINING STRATA

Breccias are recorded within Limeworks Quarry or Cave, the north side of Buffalo Cave, Rainbow Cave, Cave of Hearths and Swartkrans Prospects. Wells & Cooke (1956:4) discussed the basic history of cavern formation, infilling, sapping and thinning of the roof, and solution of the breccias, and conclude that 'similar lithological sequences of detrital cave deposits may vary widely in age.' As the nickpoint of the Mwaridzi Stream Makapan River in the Malmani Dolomite migrated eastwards, water tables would have progressively lowered within the dolomite and surface erosion increased on the downstream slopes below the nickpoint. Thus the caves might reflect a crude older to younger west to east sequence. Assuming that the caves formed at similar depths due to equivalent hydrological circumstances and with comparable thicknesses of overlying dolomite roofs, and that surface erosion progressed at similar rates above each cave, connection of the cavities to the surface may also have been sequential from west to east. Thus the basal faunas within the caves may be older in the western caves (Peppercorn and Buffalo caves) and younger in the eastern caves (Cave of Hearths and Rainbow Cave). Later stratigraphic units might therefore contain faunal elements that could be much later than the time of penetration of the roof and could be later than basal faunas in the younger eastern caves.

As the fillings of the different caves at Makapansgat are spatially disjunct and are probably temporally asynchronous, at least at the times that the cavities became connected with the surface, it is unwise to consider all the breccias and other deposits within Limeworks Cave, Cave of Hearths, Rainbow Cave, etc., as comprising a single formation. It is even less likely that Sterkfontein Cave or other Krugersdorp caves would also have developed in parallel synchronism. In effect, each cave's infilling constitutes a much restricted local formation and the term 'Makapansgat Formation' (of Partridge, 1975) is appropriate only for the fillings within Limeworks Cave to which Partridge applied it. The stratified deposits within each cave should logically be termed a formation named from the cave, with those within Makapansgat or Historic Cave the 'Makapan Cave Formation' and those within Limeworks Cave the Limeworks Cave Formation (=Makapansgat Formation), etc. The term 'Makapansgat Caves' Group' might be suitable to embrace all the deposits in the caves within the valley. Recently, McKee (1995) demonstrated a faunal seriation in selected southern

African caves that supports asynchronous fossiliferous deposits between the Makapansgat caves, specifically Makapansgat Members 3 and 4, and Cave of Hearths, as well as between the Krugersdorp caves.

MATERIALS

All specimens are housed in the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, Gauteng, South Africa and are accessioned with the prefix 'LM' for Limeworks Cave, Makapan, materials or 'COH' for Cave of Hearths specimens. The *Hipparion lybicum* remains mainly comprise isolated whole or partial cheek teeth lacking roots and from which most of the outer cementum has spalled. Only three specimens (LM 197, 181-488, and one unnumbered) comprise dental series within fragments of dentaries. Two milk teeth (M 2480 & 2481) may be associated on the evidence of occlusal wear and interdental facets and derive from an individual hipparion. A few additional hipparion specimens, including some metapodials, are also conserved in the Bernard Price Institute's collections (M.A. Raath, *pers. comm*., Feb., 1999), but they were unavailable to me when I carried out my examinations. These had evidently been included among unidentified bovid elements from the cave.

The specimens are stained in various hues of red, brown and yellow from iron oxides and black from manganese dioxide. Calcium carbonate crystals occur within some pulp cavities or within bones and over some enamel surfaces. The matrix preserved on the crowns of the teeth and in spaces between portions of the dentaries of LM 197 and the unnumbered specimen is coarse and red from haematite.

Identification of specimens to position in the jaw and tooth row may be difficult for isolated equid cheek teeth. Second premolars (P2s) are identified from their prolonged mesial areas (often broken), but the third and fourth premolars are considered indistinguishable because sizes and enamel patterns overlap. Similarly, only third molars are identifiable on their distal conformation and firsts and seconds are

MALMANI DOLOMITE (roof)	
MEMBER 5	Locally stratified brownish-red silty sand matrix with abundant chert and dolomite fragments: formerly Brain's (1958) 'Phase II Red Breccia'. Contains scattered bone; *Australopithecus* jaw, *Papio* skeletal and dental remains; two *Equus capensis* jaw fragments from Cave of the Horse's Mandible at the northwest entrance to the adit into the eastern quarry (Figure 1 and Wells & Cooke, 1956, fig. 2).
Erosional Unconformity	
MEMBER 4	Pink, thick, silty sand matrix with angular chert and dolomite fragments and some bone clusters: formerly Brain's (1958) 'Upper Phase I Pink Breccia'. *Oreotragus*, *Tragelaphus* (kudu), small *Parapapio*, *Gigantohyrax*, *Procavia transvaalensis*, *P. capensis/antiqua*.
Unconformity	
MEMBER 3	Thin layer of closely packed bone bed cemented by calcite: generally equivalent to Brain's (1958) 'Lower Phase I Grey Breccia.' Highly fossiliferous and has produced most of the Limeworks local fauna including Bovinae, rhinoceros, small *Hyaena*, bushpig, *Hipparion lybicum*.
MEMBER 2	Brownish-red, bedded, fossiliferous silt to fine sand, with angular chert and dolomite fragments, deposited subaqueously: formerly basal part of Brain's (1958) 'Lower Phase I' unit. Birds, pig and rhinoceros.
MEMBER 1	White travertine, frequently banded very pale brown, and brown laminated, crystalline calcite, frequently containing bones, either isolated or in articulation as full or partial skeletons.
MALMANI DOLOMITE (floor)	

Figure 2. Stratigraphic sequence of infilling deposits at Limeworks Cave, Makapansgat (Makapansgat Formation, Partridge, 1975; after Brock *et al.*,1977).

indistinguishable by patterns, There are no other qualitative distinguishing characters, and crown heights are similar and thus uninformative. Interdental facets and inclinations of the worn dental surfaces to the occlusal plane may assist in placing fourth premolars posterior to third, or second molars posterior to first molars. However, permanent lower molars are usually reliably distinguished from premolars because their buccal mesial valleys do not penetrate lingually between the bases of the enamel loops of the metaconids and metastylids (Figure 3). In newly erupted teeth these criteria are undeveloped because of immature stages of wear. Figure 3 illustrates the features in the enamel patterns of worn upper and lower cheekteeth. The named features are those referred to in the text. The terminology follows Churcher & Richardson (1978, 387, Figure 20.5).

Not all specimens were fit for line illustration and only those sufficiently complete and with clearly visible enamel patterns are depicted in Figures 4-7.

Specimens listed in Tables 1-10 (Appendix 1) are those that were sufficiently complete for measurement or recording of qualitative features. Not all specimens were recorded in both manners for various reasons including breakage, worn dimension points, worn surfaces, or form obscured by still adhering matrix, etc.

LIMEWORKS CAVE

Depositional History and Stratigraphy

The Limeworks Cave lies on the south side of the Makapansgat Valley (Figure 1), west of the Historic Cave and Cave of Hearths and east of Peppercorn and Buffalo caves on the north side of the valley. The cave originally formed as a solution cavity at a lower level than the present cave. The original roof collapsed to move the cavity upwards. The enlarged cavity then became filled by travertine and cave earth, brought in through seepage, solution and fluviatile transport and, after an opening to the surface was established, by windblown dust and water transported soil and rock fragments, and by additional dolomite blocks fallen from the roof (Brain, 1956; Partridge, 1975). Fossil bones, teeth and coprolites are incorporated in this complex later breccia.

Brain (1956) was the first to classify the sediments contained within Limeworks Cave based on a detailed analysis of their variations. He recognised five sedimentological units, numbered 1 to 5 from bottom to top. Butzer (1971) criticised Brain's palaeoenvironmental deductions, considered his basic premises ambiguous and that the time spans and external depositional influences were downplayed or ignored. Partridge (1975) agreed with Butzer and erected a new schema for the deposits. He named the Limeworks Cave infillings within the Malmani Dolomite the 'Makapansgat Formation', with an areal extent of some 230 by 100 m (see comments earlier). The sequence of members, based on Brock *et al.* (1977), from the basal disconformity over the Malmani Dolomite, and with faunal elements included, is given in Figure 2.

Materials and List of Specimens

The Limeworks *H. lybicum* dental sample comprises the crowns of two upper milk incisors, 33 isolated whole or partial upper milk premolars, one isolated permanent second premolar (LM 193), 11 isolated whole or partial lower milk premolars, and one fragment of a right juvenile dentary with p_{2-4} (181-488; Table 1). *E. capensis* is represented by two crushed horizontal rami with damaged and well worn (LM 197) and newly worn dentitions (181-488), respectively, and a lower molar series embedded on matrix (No Number), all from Cave of the Horse's Mandible (Table 2). No postcranial elements from *Equus* have been recognised from Limeworks Cave. Some assorted hipparion postcranial elements from Limeworks Cave are in the collections of the BPI (M.A. Raath, *pers. comm.*, Feb., 1999) but were not examined by me.

In the account that follows, teeth will be identified as permanent or milk by capital and lower case letters respectively, with numbers written superscript for upper and subscript for lower teeth, and L and R indicating left and right side of the animal, e.g., Lp^4 for left milk fourth upper premolar, and RM_3 for right permanent third lower molar.

The *Hipparion lybicum* teeth derive from juveniles in which the teeth are either unworn or only newly worn, except for LM 2475, which is from a late juvenile in which the permanent premolars are well developed with P^2 entering wear (Figure 4). All specimens derive from Member 3.

The informative *Equus capensis* jaw fragments represent a single mature individual (LM 197) with well-developed enamel patterns on the molars (Figure 5), and a young individual (181-488) in which wear has scarcely revealed an enamel pattern. The *E. capensis* specimens derive from the breccia in the Cave of the Horse's Mandible at the entrance to the east adit. The cave gains its name from the mandible LM 197.

The specimens are listed under *Hipparion lybicum* (Table 1) and *Equus capensis* (Table 2), and the teeth of the former by incisors and upper and lower premolars. Many of the *H. lybicum* teeth have lost all or most of the outer cement, a few have calcite crystals formed on them, and most are some shade of brown. All measurements are given in millimetres (mm).

Descriptions of the milk premolars of *Hipparion lybicum*

The premolar specimens are generally unworn and the enamel patterns obscured by cement or not fully developed by wear (Figure 4). Measurements of measurable specimens are given in Table 3. Among the upper milk premolars, only LM 2483 (Lp^2), 2481 (Lp^3), 2480 (Lp^4) and 2496 (LP^3) show stages of early wear (Figure 3). No definite plis caballine are present in any milk premolars but promontories reaching towards the protocone confuse their recognition: 1 or 2 plis protoloph, 2 or 3 plis protoconule, 2 or 4 plis prefossette, 1-3 plis postfossette, and 0-2 plis hypoloph may be seen. However, as wear is just beginning, characters and pli

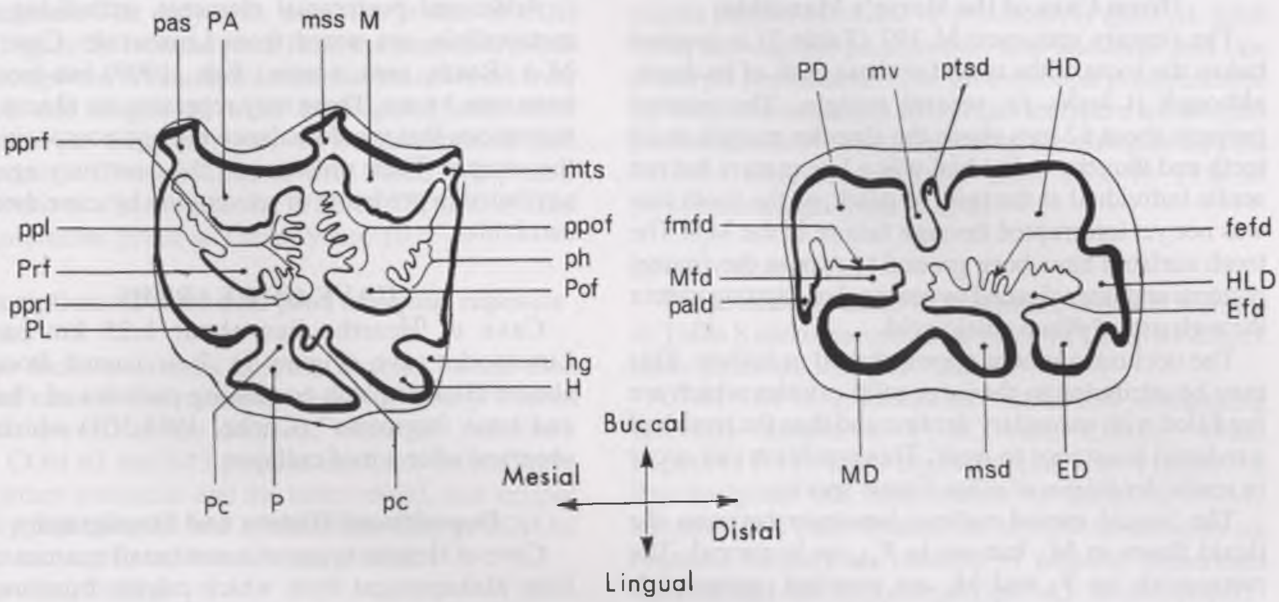

Figure 3. Generalised enamel patterns of upper and lower cheekteeth of advanced equids.

counts are probably unreliable because of small sample size and poor pattern development. No attempt has been made to review the qualitative characters of these upper and lower milk cheek teeth.

The permanent upper right fourth premolar (LM 2475, Figure 4) has been sectioned as the crown is unworn. The revealed enamel pattern shows a separate oval protocone, a double isthmus or commissure, and a rudimentary pli caballine. The paraconule is bulbous and rounded, and separated from the main protoloph by strong valley or glyph. There are two plis protoconule, a complex pli protocone, two plis prefossette (one large and one small), two plis postfossette (one large and one squarish), and one pli hypoloph. The parastyle is simply rounded and the mesostyle a smooth rise. Most of the cement ring has spalled away from the outer enamel walls.

The sectioned permanent right upper second premolar (LM 193, Figure 4) shows a double isthmus, a large pli protoloph with an incipient rise buccally, one medium and two small plis protoconule, one pli prefossette, two plis postfossette and a buccal thickening, and a small pli hypoloph. An additional small pli lies mesial to the isthmus and may represent the pli caballine.

The lower milk premolars are also generally unworn, and enamel patterns are revealed only in early stages of wear in LM 2505 ($Lp_{3/4}$) and 2474 ($Rp_{3/4}$). The typically elongate sectioned buccal pillars are present on all milk premolars and lie just distal to the buccal mesial valley with their mesial edges about level with the valley. LM 2173 has an additional oval distal buccal pillar placed off the distobuccal angle of the hypoconid and oriented nearly transversely. The floor of the entoflexid is sinuous in LM 2474 and less so in 2505.

Measurements of the milk premolars (Table 3) appear larger than those recorded for *H. lybicum* (cf. Table 4), although the lower premolars are small. Unfortunately only permanent premolars are recognised from Kromdraai (KA 729+1351, LP^2; Churcher, 1970) and Swartkrans (SK 3278, LP^3; 3982, LP^4; 2307, RP^4; Churcher, 1970: SKX 1706+1708, RP^2; Churcher & Watson, 1993) so comparisons with *H. lybicum* from other Transvaal cave deposits is restricted to comparison of LM 2475 RP^2 with KA 729+1351 and SKX 1706+1708; the latter is too damaged for meaningful comparison. The enamel patterns are similar, size is comparable, and the protocones similarly compressed (cf. Tables 3 and 4). There is no specimen comparable to that recorded from Swartkrans Member 3 which yielded a five tooth P_3 - M_3 fully adult row that lacks its ventral margin (Churcher & Watson, 1993).

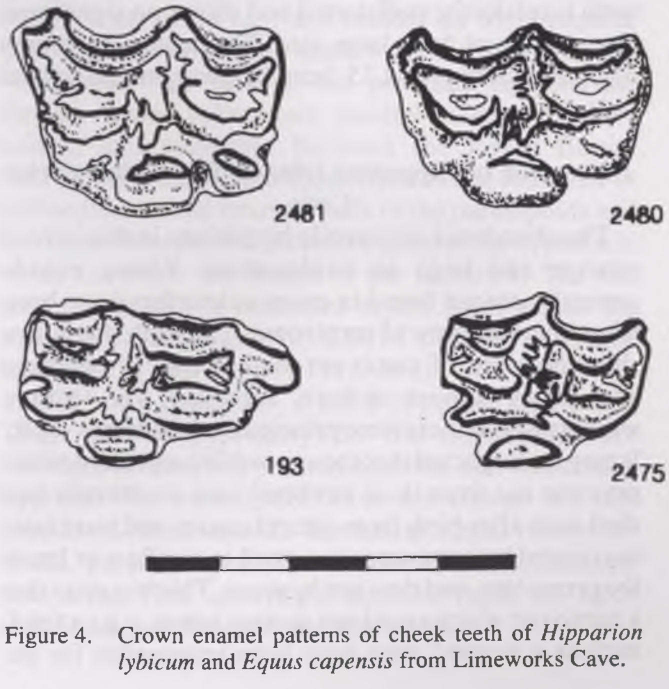

Figure 4. Crown enamel patterns of cheek teeth of *Hipparion lybicum* and *Equus capensis* from Limeworks Cave.

Descriptions of teeth and jaws of *Equus capensis* (from Cave of the Horse's Mandible)

The dentary specimen M 197 (Table 2) is crushed below the roots of the teeth for about 60% of its depth, although it lacks its ventral margin. The enamel projects about 12 mm above the alveolar margin on all teeth and thus the individual was a late mature but not senile individual at the time of death, as the tooth row was not yet interrupted through failure of the M_1s. The tooth surfaces have been ground to expose the enamel patterns and later cleaned by removal of capping matrix through use of dilute acetic acid.

The occlusal surfaces appear dished or hollow. This may be attributed to the large pulp cavities which are not filled with secondary dentine and thus the teeth had a reduced resistance to wear. This condition can occur in senile dentitions of other *Equus* species.

The buccal mesial valleys penetrate between the flexid floors in M_1, but not in P_{3-4}, as is normal. The metaconids on P_3 and M_1 are rounded, metastylids pointed but not strongly inflated, entoconids squarely inflated, and no hypoconid spur is visible. Measurements of these teeth (Table 5) are normal for those reported in the literature (cf. Churcher, 1970; Churcher & Watson, 1993) and compare well with those reported below for *E. capensis* from the Cave of Hearths (see below and Table 10).

The juvenile left lower dentition p_{2-4} LM 181-488 is newly worn and slightly damaged. The cusps are all proportionately elongate, as is normal in milk cheek teeth, especially when in early wear, as is p_4. The characters of the cusps are not fully developed and inflation is reduced by lateral compression of the pattern. However, the metaconids are rounded, metastylids pointed distolingually and entoconids elongatedly oval in p_{2-3} and squarely rounded in p_4. The distal parts of the floors of the entoflexids are smooth but in p_{3-4} the mesial parts are bent. There are no ptychostylids. The dentary fragment which bears these teeth is relatively undistorted and shows no significant character apart from large size. The dentary measures 33.5mm below p_2 and 35.5mm below p_3 on the lingual face.

Discussion of *Hipparion lybicum* from Limeworks Cave

The abundance of juvenile hipparions in this cave is strange and begs an explanation. Young equids generally are not found in caves unless they have been taken there as prey of carnivores. The milk premolars show no signs of carnivore tooth marks or breakage and, being almost unworn, represent very young animals whose diets were principally their mares' milk. It may be suspected that these juveniles represent either prey cut out from their mothers' care or animals that died soon after birth from natural causes and were later scavenged by carnivores too small to swallow or break the premolars, and thus not hyaenas. This suggests that a carnivore which could not destroy bones, e.g., a felid, such as a leopard, may have been responsible for the accumulation of the animals whose teeth are preserved.

Additional postcranial elements, includidng some metapodials, are noted from Limeworks Cave (*fide* M.A. Raath, *pers. comm.*, Feb., 1999) but have not been seen by me. These may represent the absent adult hipparions that would balance the age composition of the sample. Their presence in the cave may again be attributed to predation or scavenging by cave dwelling carnivores.

CAVE OF HEARTHS

Cave of Hearths lies about 1.25 km east of Limeworks cave (Figure 1). It is named from "an almost circular patch containing particles of charcoal and bone fragments" (Cooke, 1988:507) which was observed after a roof collapse.

Depositional History and Stratigraphy

Cave of Hearths is one of a number of quarries on the farm Makapansgat from which calcite dripstone was excavated for lime. These excavations exposed much breccia, in which many bones and hand-axes were included, and which exposed the larger circular patch of charcoal and bone fragments from which it gained its name (Cooke, 1988; Mason, 1988). Most of the breccia was too poor in calcite to warrant burning for lime and was removed and stacked outside the adits (Figure 1, insert). The cavity is an elongate hall that was divided by a travertine septum into the eastern Cave of Hearths and western Hyaena Cave; to the east it connects with the Historic Cave (Brain, 1988).

Most of the fossils were obtained from the breccia dumps and thus lack adequate stratigraphic provenance. These breccia blocks are termed 'loose breccia' in many publications, and almost certainly derive from the Early Stone Age/Later Acheulean horizons, designated Beds 1 to 3 by Mason (1988:67), and equivalent to the 'Fauresmith' stage of other writers (e.g., Cooke, 1988). About two-thirds of the breccia derives from a pipe-like trap called the 'Swallow Hole', which perhaps connected with the passage linking to the Historic Cave to the east.

Materials and List of Specimens

Cooke (1988:514) noted that 'equine teeth are very abundant' and that 'the majority (more than 500) cannot be distinguished from corresponding teeth of the living bontequagga, *Equus burchelli* ...' He also recorded 'some 65 specimens that are of much larger size and these are referred to the extinct *Equus capensis*.' Only these will be considered here.

The *Equus capensis* sample from the Cave of Hearths includes two maxillary fragments with P^4-M^1 (COH 41) and P^4-M^2 (No Number), six mandibular fragments with one series of P_2-M_3 (415), two series of P_{3-4} (537 & 557), and one each of p_3-M_2 (550), P_3M_1 (OQ/25-25/14-16') and P_3-M_3 (404). Isolated teeth comprise three permanent incisors and 89 isolated cheek teeth (Tables 5-7). All are catalogued with the prefix 'COH'. Field numbers, levels, horizons or square designations, where known, are given in parentheses. The only milk dentition is that of COH 550 (Figure 5). Isolated teeth from the same individual are recognised when interdental facets, occlusal wear angles and stages of wear correspond and allow positions in the tooth row to be determined (see Materials). The specimens are listed with their qualitative characters in Tables 7 and 8 and measurements given in Tables 9 and 10.

Descriptions of teeth and jaws of *Equus capensis*

Incisors

The incisive crowns possess heavier buccal than lingual enamel and resemble those of Grevy's zebra (*Equus grevyi*) or the domestic horse (*E. caballus*). Both COH 62 and 623 possess marks or infundibula, the former lenticular and the latter round, and located mainly in the lingual half of the tooth. That in COH 62 has a wavy or fluted buccal enamel wall.

Upper Cheek Teeth

These are listed in Table 6, qualitative dental features are summarised in Table 7, and measurements given in Table 9.

COH 41 is a small maxillary fragment containing P^4-M^1 with buccal surfaces damaged on P^4 and ectoloph missing on M^1 (Figure 6). Single plis prefossette occur in both teeth and a single pli hypoloph in M^1. The fossettes in M^1 have pits in the cement.

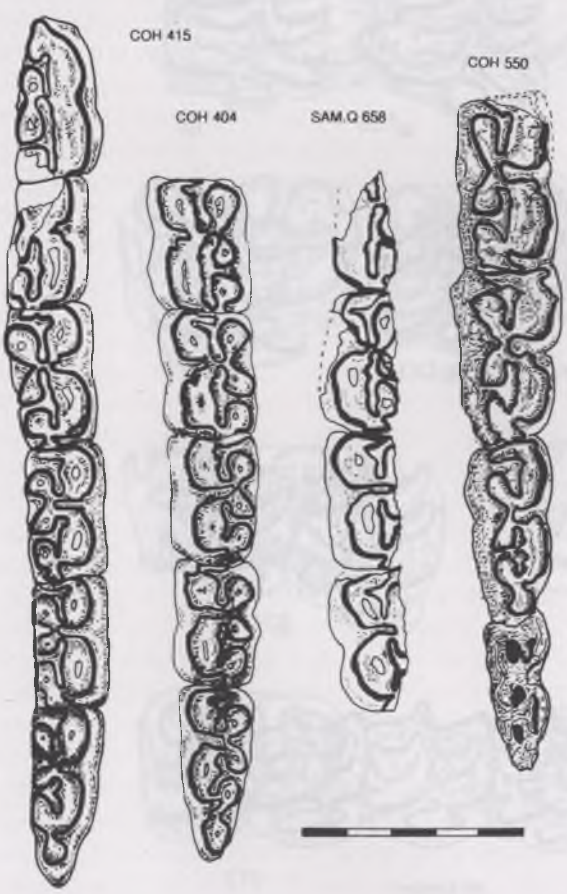

Figure 5. Crown enamel patterns of mandibular cheek teeth of *Equus capensis* COH 415, 404, 550 compared with that of the holotype SAM Q.658.

The No Number maxillary specimen with P^4-M^2 shows no plis caballine or protoloph (Figure 6). Each tooth has one pli protoconule, and one large and one small pli postfossette. The pli hypoloph is represented by small waves only in the molars and there are two plis prefossette in P^4. The protocones are elongate and the isthmus migrates mesially from 25% to 15% of protocone length from P^4 to M^2.

Lower Cheek Teeth

These teeth are listed with qualitative dental features in Table 8 and measurements given in Table 10. Cheek teeth series are listed in Table 6.

COH 404 is a partial left tooth row comprising laterally displaced P_3-M_3 (see Cooke, 1988, Figure111.1) and reassembled in Figure 5. Ptychostylids are represented by kinks in P_3-M_3, strongest on P_3 and weakest on M_1. The metaconids are rounded, metastylids rounded or pointed, entoconids squared and the hypoconulid on M3 'acorn shaped'. The floors of the metaflexids are smoothly curved (P_3-M_1) or bent (M_{2-3}) and of the entoflexids lightly wavy (P_{3-4}) or crested (M_{1-3}). The buccal mesial valleys are broad, parallel sided and terminally rounded, but square in M_3. Those of P_{2-3} approach the isthmus between the flexid floors but those of M_{1-3} penetrate into the metaconid-metastylid junction and meet the lingual valley wall. Interdental wear by the hypoconulids has abraded the paraconid-paralophid areas resulting in a reduced length to the toothrow.

COH 415 (F/2/15) is a slightly warped but worn entire right lower cheek tooth row with damage to the lingual and mesial surfaces of P_3 and the entoconid of P_2 (Figure 5). Ptychostylids are represented by kinks in P_2-M_2, but not in M_3. The metaconids are rounded, metastylids round pointed, entoconids squared, and the hypoconulid on M_3 rounded. The floors of the metaflexids are bent or strongly curved in P_4-M_3 and flat in P_2, and of entoflexids shallowly wavy on premolars, slightly curved on M_{1-2} and crested on M_3. Premolar buccal mesial valleys are shallow (almost absent on P_2), with broad 'Vs' and do not penetrate between the flexids; molar valleys are parallel sided and round ended, and penetrate between the flexid floors. Interdental wear by the hypoconulids has removed or thinned the mesial enamel walls of the paralophids and by the protoconids some cement distal to the hypoconid so as to reduce the length of the toothrow. The full toothrow length is estimated at 201.9mm versus the measured 192.5 (Table 10). COH 415 is also illustrated by Cooke (1988, Figures 111.2 & 3).

COH 537 comprises a left P_3-P_4 pair (Figure 7a). There are no ptychostylids; the metaconids are rounded, metastylids pointed deltoids, and entoconids squared. The metaflexid floors are curved and the entoflexid floors smooth. The buccal mesial valleys are broad, parallel sided, with rounded ends and incline mesially. This specimen derives from an aged individual and the teeth are very worn.

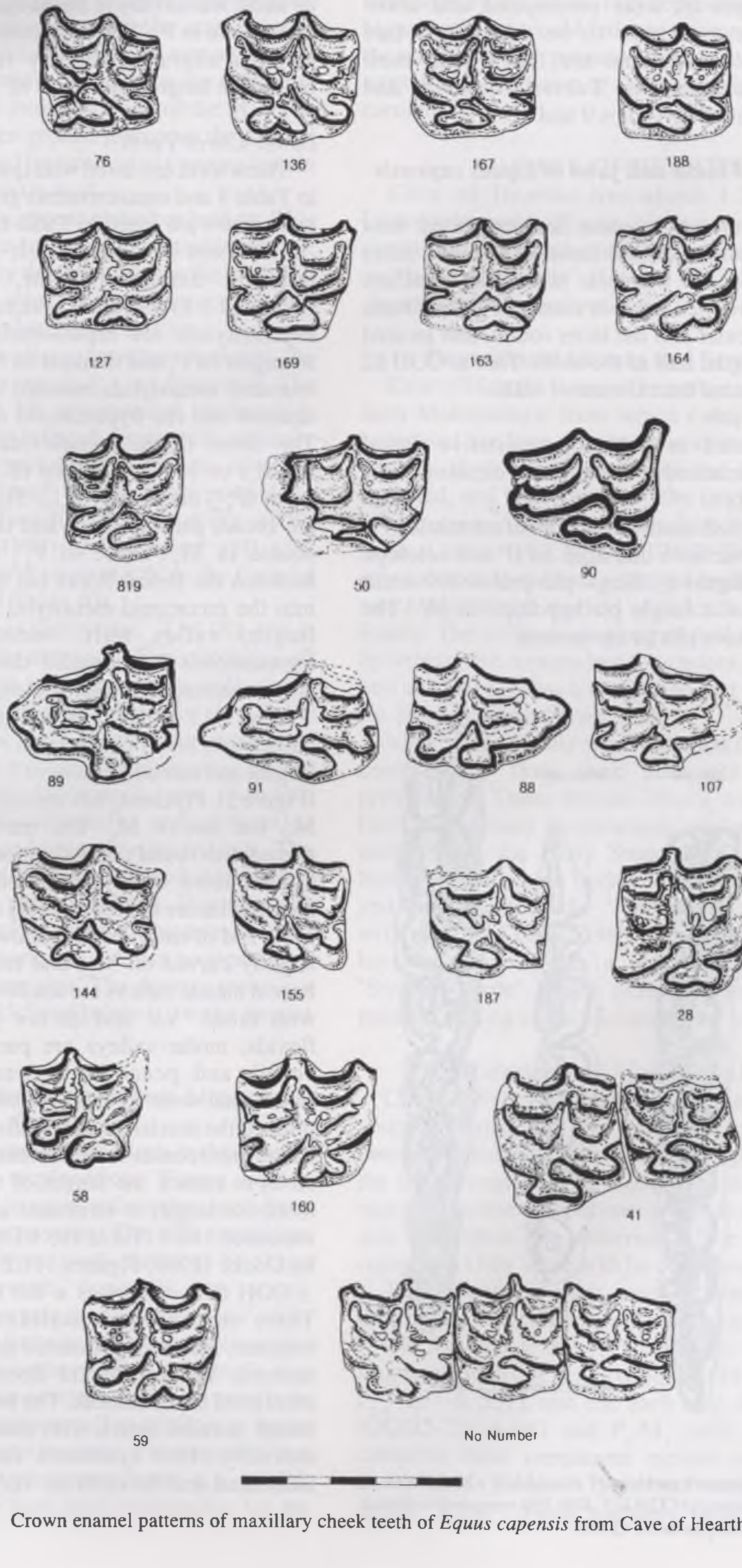

Figure 6. Crown enamel patterns of maxillary cheek teeth of *Equus capensis* from Cave of Hearths.

COH 550 comprises associated right milk p_{3-4} and permanent M_1 in an early stage of wear, with M_2 emerging (Figure 5). Ptychostylids are short and robust on p_3-M_1. In p_{3-4}, the milk metaconids are rounded, metastylids squarely pointed, and entoconids rounded wedges: the hypoconulid is prominent in p_4 and compressed in p_2. In M_1, the metaconid is elongate and not as rounded as in p_3-p_4, the entoconid pointed, and hypoconulid squared. The floors of the metaflexids are smooth or shallowly arced in p_3-p_4 and irregularly wavy in M_1.

COH 557 comprises associated left P_3-P_4 (Figure7). Ptychostylids are absent. The metaconids are rounded, metastylids pointed, and hypoconids squared. The metaflexid floors are curved or bent and entoflexid floors smooth. The buccal mesial valleys are wide, inclined mesially, and penetrate to the level of the medial wall of the protoconid (100%) in P_4.

The left dentary fragment OQ/25-25/14-16' contains a partial tooth row with P_3-M_1 (Figure 7). Ptychostylids are represented by kinks. The metaconids are rounded, metastylids pointed and entoconids squarish. The metaflexid floors are bent and entoflexid floors crested, slightly more so in M_1 than in P_{3-4}. The buccal valleys are broad, V-shaped in P_3 and parallel sided in P_4-M_1, and penetrate 80% of the width of the protocone in P_3, 100% in P_4, and 130% in M_1.

Discussion of *E. capensis* from Cave of Hearths

Cooke (1988) briefly considers the Perissodactyla from Cave of Hearths. Apart from the major sample of some 450 teeth assigned to *E. burchelli*, he noted 65 specimens identified as or ascribed to *E. capensis*. COH 415 is noted as from Bed 2 in the Acheulean deposits and COH 404 as from the 'swallow hole'. Both of these are considered closely comparable to specimens from

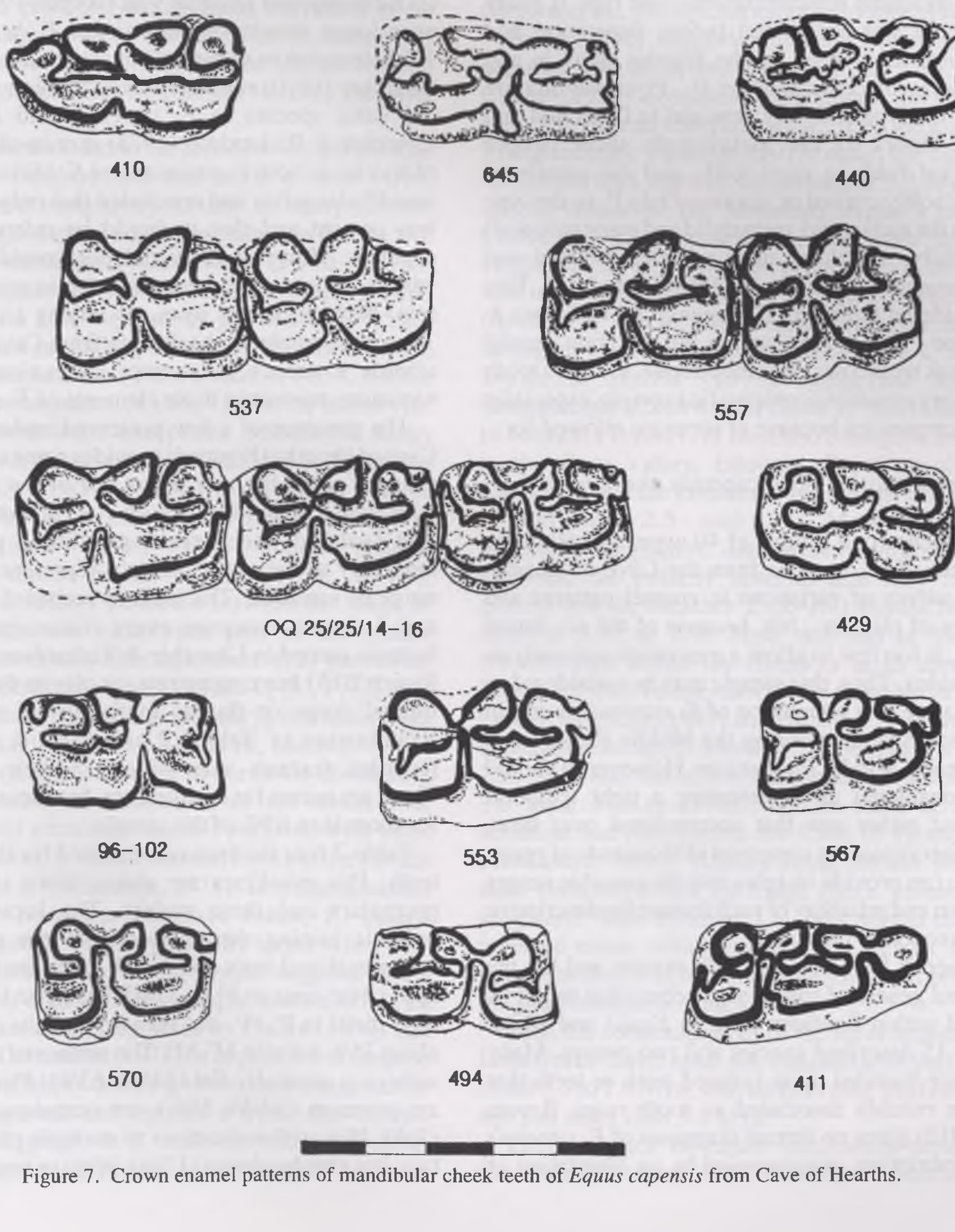

Figure 7. Crown enamel patterns of mandibular cheek teeth of *Equus capensis* from Cave of Hearths.

COH 550 comprises associated right milk p_{3-4} and permanent M_1 in an early stage of wear, with M_2 emerging (Figure 5). Ptychostylids are short and robust on p_3-M_1. In p_{3-4}, the milk metaconids are rounded, metastylids squarely pointed, and entoconids rounded wedges: the hypoconulid is prominent in p_4 and compressed in p_2. In M_1, the metaconid is elongate and not as rounded as in p_3-p_4, the entoconid pointed, and hypoconulid squared. The floors of the metaflexids are smooth or shallowly arced in p_3-p_4 and irregularly wavy in M_1.

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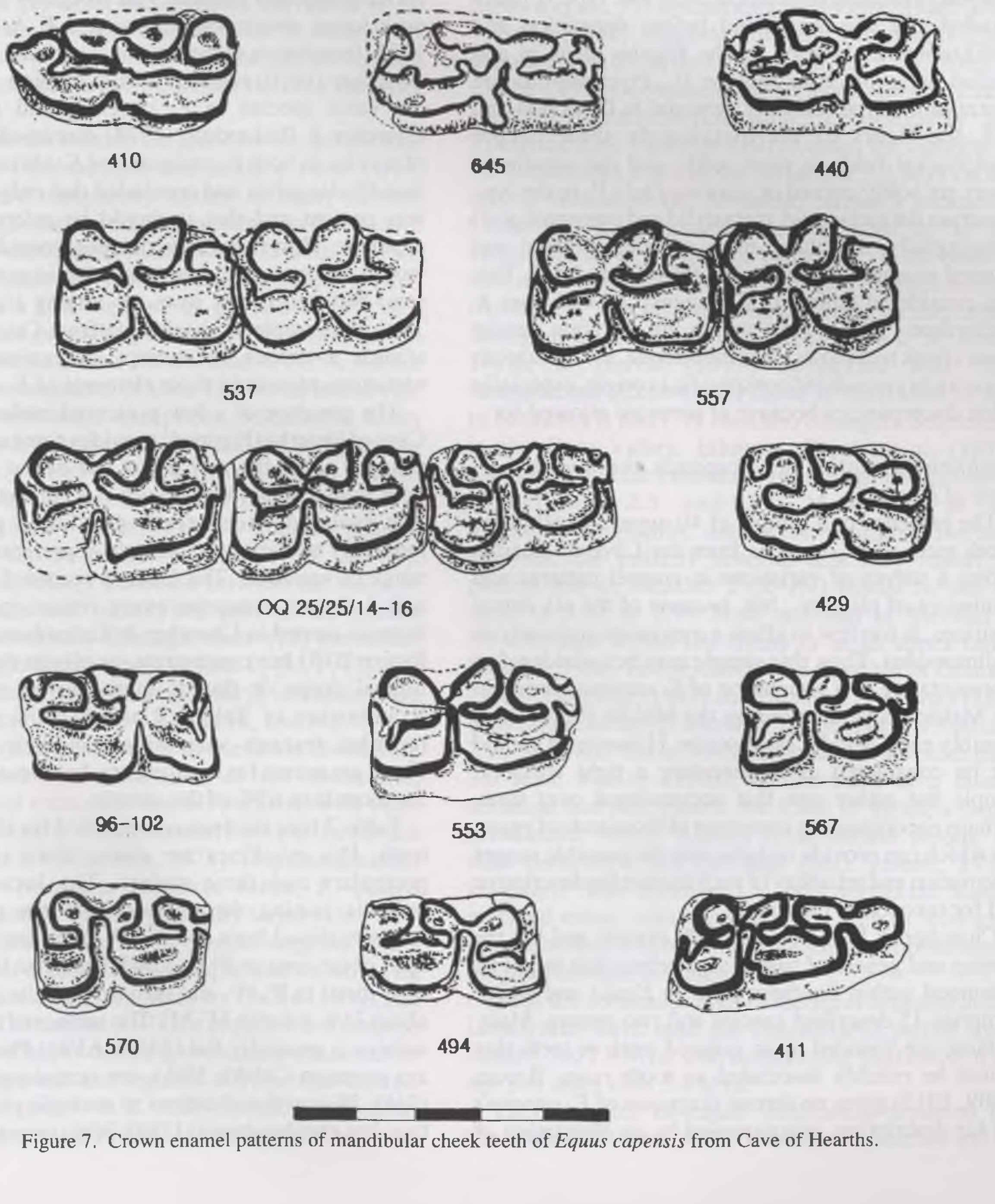

Figure 7. Crown enamel patterns of mandibular cheek teeth of *Equus capensis* from Cave of Hearths.

Vlakkraal (Wells *et al.*, 1942) and Florisbad (Dreyer, 1931).

Cooke (1988, Table 2) lists the fauna from Cave of Hearths by Early (ESA or Pietersburg) or Middle Stone Age (MSA or Acheulean), or mixed categories. Both *E. capensis* and *E. burchelli* are present in all three categories. Because of the paucity of materials known certainly to originate from these layers, and the majority of the materials originating from mixed or statrigraphically unknown horizons, Cooke (1988, 518) is unsure whether 'the differences between the ESA and MSA assmblages as listed are real or are the consequences of inadequate diagnosis.'

Comparison of the full right dental row of COH 415 with the type specimen SAM.Q 658 of *E. capensis* (Broom, 1909), a damaged partial left row P_3-M_2 (Figure 5), from Ysterplaats, near Cape Town, shows two rows of similar size and portions of the crown enamel patterns of P_3-M_2 available for comparison. The type is badly abraded and was weathered before deposition and fossilisation; as evinced by the angular break in and spalled areas of cementum on P_4. Ptychostylids are absent in the type and only vestigial in COH 404 and 415, the floors of the metaflexids show deeper mesiobuccal folds in most teeth, and the entoflexid floors are softly curved or sinuous. Only P_4 in the type preserves the metaconid, metastylid and entoconid at all meaningfully, and these show rounded, pointed and squared enamel outlines as in COH 404 and 415. This was considered typical of *E. capensis* by Churcher & Richardson (1978). Thus within the variation among lower cheek teeth rows described above, the three tooth rows can be considered conspecific in origin, especially when discrepancies because of wear are allowed for.

Qualitative variation in E. capensis *cheek teeth from Cave of Hearths*

The presence of a sample of 40 upper and 60 lower cheek teeth of *E. capensis* from the Cave of Hearths allows a survey of variations in enamel patterns and incidences of plis, etc., but, because of the six dental positions, is too few to allow a mensurational analysis of dimensions. Thus, this sample may be considered as representative of a population of *E. capensis* living in the Makapansgat area during the Middle Pleistocene, possibly early Middle Pleistocene. However, it should not be considered as representing a tight temporal sample but rather one that accumulated over time, perhaps encompassing some tens of thousands of years, but which can provide insights into the possible ranges of variation and reliablity of each feature for descriptive and for taxonomic purposes.

Churcher & Richardson (1978) review and list the species and genera of fossil large zebras that might be subsumed within Southern African *Equus* and which comprise 15 described species and two genera. Many of these are founded upon isolated teeth or teeth that cannot be reliably associated as tooth rows. Broom (1909, 1913) gives no formal diagnosis of *E. capensis* but his description, accompanied by an illustration of the jaw fragment, effectively allows identification of the taxon, despite Wells' (1959) opinion that *E. capensis* is indeterminable. Broom's founding of *E. capensis* on a lower jaw fragment requires associated upper and lower molar rows, of which the lower resemble that of the type, to allow a diagnosis for the upper dentition. Cooke (1950) provided this but did not consider either variation along a molar row or variation between teeth of different individuals, and instead provided a description of the features of an average upper cheek tooth. However, he originally recognised as separate eight of the then described 14 species but, in an appendix added just prior to publication, noted Broom's (1948) description of a further species and reduced it and three others to synonymy within a surviving five species. Later, he (1963) accepted Wells' (1959) decision of the invalidity of the type specimen of *E. capensis* and recognised only *E. (= Kolpohippus) plicatus* Van Hoepen 1930 (founded on a lower cheektooth series) and *E. helmei* Dreyer 1931 (founded on apparently unassociated cheekteeth). Churcher (1970) rejected Wells' opinion and reduced the valid species to *E. capensis* and *E. plicatus*. Churcher & Richardson (1978) discussed this duality of species as both *E. capensis* and *E. plicatus* represent mandibular series and concluded that only one species was present and that it should be referred to as *E. capensis*. However, they did not consider variation within a population, between teeth in a single molar row, between molar rows, or among isolated teeth. Thus, the sample of cheek teeth from Cave of Hearths affords a chance to attempt an evaluation of the variations present in these elements of *E. capensis*.

The presence of a few preserved molar rows from Cave of Hearths (Figure 4) provides some control in the changes along the row and a test of the randomness with which individual features occur between teeth. The isolated cheek teeth provide a presumedly randomly accumulated sample representative of the range of variation. The features recorded in Tables 7 and 8 do not comprise every feature possible (see features named in Churcher & Richardson, 1978, 387, Figure 20.5) but concentrate on plis in the upper and lingual cusps or flexids in the lower cheek teeth. Examination of Tables 7 and 8 show that all the recorded features vary widely in their expression. There are norms for each feature, but these are unusual for more than 65% of the sample.

Table 7 lists the features recorded for the maxillary teeth. Plis caballines are absent from all but three premolars and three molars. The location of the isthmus joining the protocone to the protoconule migrates distad from about 10% distal from the mesial apex of the cone on P^2, to 35-45% distal in P^3, and to 45-50% distal in P^4-M^1, and then reverses its migration to about 35% distal in M^2-M^3. The surface of the ectoloph valleys is generally flat (24/38, 63%). Plis protolophs are common (20/40, 50%), are occasionally twinned (2/40, 5%), with indications of multiple plis in another two, but may be absent (12/40, 30%) or vestigial (7/40, 17.5%). Plis protocones are also comon (25/40, 62.5%) or absent (13/40, 32.5%), but twinned in two (2/40, 5%). Plis prefossettes occur (16/40, 40%), are absent (13/40, 32.5%), twinned (5/40, 12.5%), triple in one, or vestigial (6/40, 15%). Plis postfossettes are very common (31/40, 77.5%), twinned (6/40, 15%) with others (12/40, 30%) showing indications of additional plis, absent (4/40, 10%), and vestigial in one. Plis hypolophs are present (15/40, 35.5%), twinned in one, absent (16/40, 40%), or vestigial (6/40, 15%).

From these summations from Table 7, plis prefossettes occur most frequently and are twinned most often, plis protolophs, protoconules and prefossettes are about as frequently present as absent, plis postfossettes are the most likely to be multiple, and all plis can be twinned or multiple. Within a single animal, e.g., COH 41 or No Number (Figure 6), the teeth all tend to reflect a dominant molar morphology throughout a premolar-molar field, but there is no obvious linkage between the presence or absence of different features, e.g., plis protocone and prefossette are both present in COH No Number but only the latter in COH 41.

Table 8 lists the features recorded for the mandibular cheek teeth. Ptychostylids are rarely present (4/60, 6.6%) and are completely absent in many (24/60, 40%), although there are kinks or bumps in the smooth curve of the shoulder in many others (29/60, 48.3%). Metaconids generally have a rounded shape (51/57, 89.5%) with a few wedged or pointed (3/57, 5%). Metastylids are generally pointed (53/58, 91.4%), with a round conformation as the alternative (4/58, 6.8%). Entoconids are squared (43/60, 71.7%) or round (16/60, 26.7%) with some exceptions. Metaflexid floors are bent, arced, or curved, with the distal end pointing bucccodistally (43/54, 79.6%), with a few flat or smooth (9/54, 16.7%). Entoflexid floors are mostly wavy or sinuous (24/56, 42.9%), smooth (12/56, 21.4%), but can be crested or bent (17/56, 30.4%). Buccal mesial valleys penetrate between the bases of the metaconids and metastylids only in the molars (>100% penetration), although some (12) premolars attain 100% penetration, and include P_4 (8), P_3 (3), and P_2 (1). Penetration of the buccal valleys increases from mesial to distal, with 120-130% in M_2 and M_3.

The most reliable character of the lower cheekteeth of *E. capensis* is the inflation of the metaconid, metastylid and entoconid enamel outlines, with thick enamel, and usually simple enamel floors to the flexids (see Churcher & Richardson, 1978). This distinguishes *E. capensis* from the common zebra, *E. quaga burchelli*, together with its generally larger size.

This assessment of a small sample suggests that a broader survey of an enlarged sample, and including all characters considered important by Cooke (1950) and Churcher & Richardson (1978), is required to attempt to evaluate the reliabilty of trying to use such characters to identify *E. capensis* and separate it from other zebras, particularly *E. grevyi* or *E. oldowayensis*. At present, these large grevyine zebras are recognised on size, robustness of their teeth, and perhaps the degree of inflation of the lingual enamel outlines in the lower molars and the robust ectoloph, flattened or grooved crests to the ectostyles, especially the mesostyle, and the broader protocone and hypocone in the upper molars.

DISCUSSION AND CONCLUSIONS

Hipparion lybicum ethiopicum is reported in Shungura Formation Members F-L in the Omo sequence (Hooijer & Churcher 1985, 100) although "the documentation is not as good as one would wish."

Equus oldowayensis first appears in the Omo sequence in Shungura Formation Member G (Churcher & Hooijer, 1980). It also appears in Members H and J-L and in the Kalam Outcrop. Member G corresponds to Bed I in Olduvai Gorge and both cover the times from earliest Early Pleistocene (G) to late Early Pleistocene (K-L). These are dated between 1.93 and 1.34 Mya (Brown *et al.*, 1978; Churcher & Hooijer, 1980: 279).

Brain (1956) suggested that the Limeworks Cave deposits span the period from 3.5 to 2.5 Mya. Wells & Cooke (1956) considered the faunas to be 'Latest Kageran or earliest Kamasian', i.e., probably late Villafranchian. Partridge (1973) dated the opening of the Limeworks Cave to the surface at 3.7 Mya on the rate of retreat of the Mwadziri stream's nickpoint. Cooke (1970) suggested that the fauna is "in the vicinity of 2.5 to 3.0 million years old" on the basis of suid morphology and, on the presence of *Notochoerus capensis*, a species intermediate between the upper Shungura B *N. euilus* and the Shungura C *N. scotti*. White & Harris (1977) suggested that "the Makapansgat [Limeworks] fauna is equivalent in age to Members B and C of the Omo Shungura Sequence" in the Omo Valley, Ethiopia. Brock *et al.* (1977) concluded that the consensus for the age of Member 3 is between 2.5 and 3.0 Mya but, as no magnetostratigraphic data were available for this member, the polarity reversal that they report as present low in Member 2 (R→N) should be one of those at 3.32 or 2.94 Mya, and that in Member 4 (N→R) high within the Gauss or at its upper limit. Member 5 may be coeval with the Réunion or Olduvai events. Partridge (1983) and Partridge & Talma (1986) considered the age of Member 3 to be between 3.40 and 2.92 Mya, and that of lower Member 4 to be older than 2.0 Mya. McKee (1995), on the basis of a faunal seriation analysis, placed the Cave of Hearths fauna penultimate before Klasies River Mouth among 18 sites considered and Partridge (*pers. comm.*, 1998) suggested "that Member 3 ... falls within the Kaena reversed event, which lasted from 3.11 to 3.04 myr (based on the most recent astronomical calibrations of the palaeomagnetic timescale)".

Thus the consensus ages of the infill deposits in the Limeworks Cave span the considerable period from about 3.5 to 1.8 Mya, with an emerging likelihood of an age just older than 3.0 Mya.

The sequence of equid succession reported by Churcher & Watson (1993) in which *H. lybicum* and *E.*

capensis exist together before *E. burchelli* appears in the Swartkrans sequence suggests that the Limeworks Cave's record with only the hipparion is very early and earlier than the deposit in the Cave of the Horse's Mandible, where only *E. capensis* is present. *E. capensis* probably entered southern Africa slightly later than in East Africa (1.8 Mya in Bed 1, Olduvai Gorge and 1.9 Mya in Member G, Shungura Formation, Omo Valley; Churcher, 1981), possibly about 1.8-1.75 Mya or ealiest Pleistocene. Thus the Cave of the Horse's Mandible may be at oldest 1.8 Mya while the body of Limeworks cave with only *H. lybicum* is older and possibly about 3.0 My.

The Cave of Hearths has provided a reasonable sample of *E. capensis* and many *E. burchelli* specimens, most of which derive from a Later Acheulean (= 'Fauresmith') horizon considered to be Mason's (1988) Beds 1-3. The presence of both monodactylous equids coexisting in this site suggests an age less than about 2.0 or 1.8 Mya, dates at which *E. burchelli* is first recorded from Laetoli and Olduvai Gorge, respectively (Churcher & Richardson, 1978, 414/415, Figure 20.7) or when *E. capensis* is first recorded in East Africa (Churcher, 1981). However, *E. burchelli* is not known from coeval beds in the Omo sequence. Cave of Hearths Beds 1-3 lie beneath a debris layer some 6 m deep and perhaps representing passage of a hundred thousands years. Bed 4 records the change from unifacial to bifacial tools and may be dated at about 100 000 BP or more (see below). Thus the equid fossils are minimally at least 200 000 years old.

More recent dates for the 'Fauresmith' Late (Terminal) Acheulean (e.g., from Florisbad, Grün *et al.*, 1996) indicate the actual age may well be of the order of 300 000 yr. BP or even older. Upper Acheulean tools from Refruf Pass (Wadi el-Refruf) in the Libyan Escarpment to the northeast of Kharga Oasis, Egypt (Caton-Thompson, 1952, Locus V) are dated at $\geq$ 400 000 BP and 'Lower Levalloisian' (= older Middle Stone Age, Caton-Thompson, 1952, Locus IV) at 220 000 $\pm$ 20 000 BP (Isotope stage 7) (Kleindienst *et al.*, 1996). Recent recoveries of early Middle Stone Age tools and associated fauna from Dakhleh Oasis, Egypt (Churcher *et al.*, in press) also associate a fauna containing a northern *E. capensis* population and other mammals with earlier Middle Stone Age lithics. These are estimated on geomorphological evidence and by correlation with the Kharga record to date from about 250 000 yr BP.

The Twin Rivers Cave site (Barham, 1998), near Lusaka, Zambia, contains a breccia with artifacts and bones, which was sealed by roof collapse in the late Middle Pleistocene. The tools comprise a combination of flake and core forms which place the doposit early in the Middle Stone Age. $^{230}Th/^{234}U$ analysis of a sample of speleothem (F Block) from the top of the breccia gave an age of 230 000 +35 000/-28 000 yr BP. Analysis by mass spectrometer also supports a late Middle Pleistocene age for the speleothem (F Block) at 195 000 ± 19 000 yr BP (error at 2 sigma). A second but weathered speleothem sample (A Block) yielded an infinite mass spectrometer date (>350 000 yr BP) which, after removal of a source of error, has a minimum age of 300 000 years. Barham (1998) concludes that the Acheulean-Middle Stone Age transformation as shown in Twin Rivers Cave occurred earlier than 200 000 yr BP. As all the 'real' Acheulean in the Western Desert is beyond U-series dating range (>400 000 Uyrs), the Early to Middle Stone Age transformation may be earlier than 300 000 yr BP (M.R. Kleindienst, *pers. comm.*, June 1999) .

The recovery of the Cave of Hearth equids from the blocks of breccia mined and stacked outside the adit makes any attempt at a stratigraphic separation of *E. capensis* and *E. burchelli* at this site wasted effort. As both species existed into Recent times, a date close to the present of 17 000 years, proposed by Mason (1962), is possible but unlikely as the evidence from Florisbad (South Africa), Twin Rivers (Zambia) and Karga and Daklhleh Oases (Egypt) suggests that the early Middle Stone Age transition occurred between 300 000 and 200 000 years ago. The relatively greater abundance of *E. burchelli* fossils compared to those of *E. capensis* may reflect a coexistant herding behaviour between the two species similar to that between the extant *E. grevyi* and *E. burchelli* observable to-day (Churcher, 1982, 1993), and thus that this behaviour has an ancient source. The greater frequency of common zebra should not be taken to indicate a date towards the end of a replacement process of *E.capensis* by *E.burchelli.*

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TABLE 1.
Specimens of *Hipparion lybicum* from Limeworks Cave, Makapansgat.
(LM prefix to accession numbers)

Specimen No.	Tooth	Description
Incisors		
196	L i^2 or R i_2	rootless, unworn
2478	R i^2 or L i^2	rootless, unworn
Upper Premolars		
187	R p^3	rootless, unworn
188	L p^4	rootless, unworn
190	R p4	lacking paracone and roots, unworn
192	R p^2 or P^2	lacking mesial half and distolingual corner, in jaw fragment
193	R P^2	newly worn, buccal cement damaged
546	R p^3	damaged on hypoglyph, rootless, unworn
2167	R p?	paracone only, rootless, unworn, cement
2168	R p^4	rootless, unworn
2169	L p^3	lacking mesial half of paracone and protoconule, rootless, unworn
2171	L $p^{2/3}$	central fragment, rootless, unworn
2185	L p^3	rootless, unworn
2475	R P^4	rootless, newly worn, cement (sectioned)
2480	L p^4	rootless, early wear, complete cement
2481	L p^3	rootless, worn, cemented. M 2480 and 2481 derive from one individual as they share matching interdental facets
2483	L p^2	damaged on mesial style, rootless, early wear, cement
2485	R p^2	damaged on mesial style and protoconule, rootless, unworn
2486	L p^2	rootless, unworn, little cement
2487	R p^4	damaged on protocone and protoconule, rootless, unworn
2488	L p^4	damaged, protocone absent, rootless, early wear
2490	L $p^?$	protocone, hypocone and fossettes only, rootless, unworn, calcite crystals in pulp cavities
2491	R p^4	damaged metacone, rootless, unworn
2492	R p^4	rootless, unworn
2494	L p^3	damaged buccally, rootless, newly worn, cement
2495	R $p^?$	buccal area and prefossette only, rootless, unworn
2496	L p^3	rootless, early wear, cement
2497	L p^2	lacks mesial process, rootless, unworn, some cement
2498	R p^4	damaged distally and on parastyle, rootless, unworn, some cement
2499	L $p^?$	lacking paracone and protoconule, rootless, unworn
2500	R p^4	lacking distal half of hypocone and metacone, broken on paracone and hypocone cusps, unworn, calcite crystals in pulp cavities
2501	R p^4	enamel damaged buccally and distally near margin, rootless, unworn
2502	R p^4	damaged mesial half of paracone and on metacone cusps, rootless, unworn, cement
2509	R $p^{2?}$	damaged on crown and lingually, rootless, unworn, some cement
No number	R p^4	rootless, unworn, little cement
No number	R p^2	rootless, unworn, little cement, calcite encrusted
No number	L p^3	mesial halves of metacone and hypocone only, rootless, worn, cement
Lower Premolars		
182	R p_2	damaged mesially, rootless, unworn, additional long enamel pillar on buccal surface near valley
2166	R p^{3-4}	abraded and damaged crown, buccal face absent, rootless, calcite encrusted
2170	L $p_{3/4}$	lacking distal halves of hypoconid and entoconid, rootless, unworn, little cement, calcite encrusted
2172	L $p_{3/4}$	protoconid, paraconid and mesial metastylid only, rootless, calcite encrusted
2173	R $p_{2/3}$	lacking distal halves of metaconid and hypoconid, rootless, calcite encrusted, with additional pillar buccal to mesiobuccal angle separate from protoconid
2474	L p_4	mesial protoconid, paraconid and metastylid only, and roots of p_3, in dentary fragment, with calcite infillings, early wear
2503	L $p_{3/4}$	rootless, unworn, little cement
2504	R $p_{3/4}$	rootless, newly worn, little cement, calcite in pulp cavities
2505	L $p_{3/4}$	rootless, newly worn, little cement, calcite in pulp cavities, fused pillar
2506	L $p_{3/4}$	rootless, newly worn, little cement, calcite in pulp cavities, pillar broken
2508	L $p_{3/4}$	rootless, unworn, little cement, calcite in pulp cavities
2510	L $p_{3/4}$	rootless, unworn, little cement, calcite in pulp cavities, damaged
2511	R $p_{3/4}$	rootless, unworn, little cement, calcite in pulp cavities
2512	–	Five equid (2 upper and 3 lower) tooth fragments, and 2 bovid (possibly alcelaphine) tooth fragments

TABLE 2.
Specimens of *Equus capensis* from Cave of the Horse's Mandible, Limeworks Site, Makapansgat.
(LM prefix to accession numbers)

Specimen No.	Description of Specimen
197	Left dentary fragment with distal portion of P_3, P_4–M_1, and damaged crowns of M_2–M_3. Dentary crushed below teeth, and thus individual is late mature to old.
181–488	Right dentary fragment with slightly damaged p_2–p_4; damaged protoconids on p_2 and p_4, and some damage buccally on p_3; unworn, cement, juvenile.
No Number	Left M_{1-3}, in dentary fragment, with matrix over crown.

TABLE 3.
Measurements of isolated premolars of *Hipparion libycum* from Limeworks Cave, Level 3, Makapansgat.
(LM prefix to accession numbers)

Abbreviations: MDD - mesiodistal diameter midway between enamel and occlusal margins on upper and just above enamel margin on lower premolars; BLD - buccolingual diameter over enamel only; PaH - height of paracone; PrH - height of protocone or protoconid; PrL - greater diameter of protoconid pillar. e - estimated measurement, w - measurement reduced because of wear, + indicates a minimal value due to damage PrD - lesser diameter of protoconid pillar.

Specimen No.	Tooth	MDD	BLD	PaH	PrH	PrL
Upper dentition						
Permanent premolar						
193	R P^2	37.9	22e	56.5e	53e	10.8
2475	R P^4	Unrecorded				
Milk premolars						
2483	L p^2	39.2+	27.0	30.2	21.4	11.0
2485	R p^2	45.3+	22.2+	–	21.7	9.4
2486	L p^2	43.8	23.1	29.3	21.6	9.2
No Number	R p^2	47.5	19.5	27.2	22.9	10.7
187	R $p^{3/4}$	33.1	25.2	33.6	25.1	9.1
188	L $p^{3/4}$	32.5	25.5	32.7	21.3	10.2
190	R $p^{3/4}$	–	–	31.0	23.0	11.9
546	R $p^{3/4}$	31.3	19.3	–	27.5e	10.2
2165	L $p^{3/4}$	34.2	25.8	–	27.2	10.4
2168	R $p^{3/4}$	32.9	25.1	31.4	25.1	10.8
2480	L $p^{3/4}$	32.3	28.9	29.2w	22.3w	11.2
2481	L $p^{3/4}$	29.6	27.9	35.7w	27.5w	12.3
2487	R $p^{3/4}$	33.2	24.8	29.6e	27.8	11.0
2492	R $p^{3/4}$	33.8	23.0	27.8	24.8	10.2
2494	L $p^{3/4}$	34.6	21.5	34.5e	28.0	12.6
2496	L $p^{3/4}$	31.5	25.5	30.0w	21.3w	8.4
2498	R $p^{3/4}$	33.0	24.2	32.0	22.9	10.6
2501	R $p^{3/4}$	32.5	24.4	34.5e	25.9	11.2
No Number	R $p^{3/4}$	33.3	23.0	35.1	26.5e	10.6

Lower dentition Specimen No.	Tooth	MDD	BLD	PrH	PrL	PrD
Milk premolars						
2503	L $p_{3/4}$	33.1	14.9	33.8	20.4	8.6
2504	R $p_{3/4}$	33.5	15.2	31e	20.5	9.8
2505	L $p_{3/4}$	34.9	15.2	33.9	15.9	7.8
2506	L $p_{3/4}$	33.7	11e	30.5	17.7e	8.9
2508	L $p_{3/4}$	33.8	16.6	–	23.3	8.8
2511	L $p_{3/4}$	33.7	14.1	29.8	21.5	7.1

TABLE 4.

Measurements of permanent maxillary teeth of *Hipparion lybicum* from Kromdraai (KA) and Swartkrans (SK) Caves.

Abbreviations: MDL - mesiodisal length; BLD -bucclingual diameter; PaH - paracone height; PH -protocone height; PL - protocone mesiodistal length. e - estimated measurement, + - minimal measurement, (1) data from Churcher (1970) or (2) from Churcher & Watson (1993) with revised measurements '*'.

Specimen No	Tooth	MDL	BLD	PaH	PH	PL	Source
KA 729–1351	L P^2	38.8	28.2	78.0+	59.2+	11.8	(1)
SK 3982	L P^4	24.2	26.0	61.4+	56.4+	9.0	(2)
SK 2307	R P^4	24.0*	27.3*	47e+	40.2+	9.0	(2)
SK 3278	L P^3	24.9	24e	43e+	41.0+	10.6	(2)

TABLE 5.

Measurements of mandibular cheek teeth of *Equus capensis* from Cave of the Horse's Mandible, Limeworks Site, Makapansgat.

(LM prefix to accession numbers).

Specimen No	Tooth	MDD	BLD	PrH	PrL	PrD
197	L P_2	–	–	17.7e	–	–
L P_3	30.7	–	18.7	18.9e	11.9e	
L P_4	30.2	20.1	18.5	17.9	9.9	
L M_1	26.1	18.8	16.4	14.0	7.4e	
L M_2	24.3e	–	14.9e	–	–	
L M_3		(roots only)				
		(mesiodistal length P_2-M_1 = 85.3e)				
181–488	L p_2	38.9	17.5e	12.4	17.6	15.4
L p_3	32.7	16.9	11.4	17.4	14.5	
L p_4	33.1	15.3	11.0	15.2	12.8	
		(mesiodistal length p_2-p_4 = 110.2)				

TABLE 6

Incisors and associated tooth rows of *Equus capensis* from Cave of Hearths, Makapansgat.

(COH prefix to accession numbers)

Abbreviations: MMD - mesiodistal diameter of protocone; BLD - buccolingual diameter over enamel only; PrH - height of protoconid; PrL - mesiodistal length of protoconid; PrD - buccolingual diameter of protonid.

Specimen No	Description
Incisors	
62	R I^1, in matrix sample. Mark present.
210	L I^3 or R I_3. Crown and root broken, no mark.
623	R I^1, but labelled 'lower I_1'. Root broken, mark present.
Maxillary Series	
41	Left maxillary fragment with P^4-M^1, damaged, and ectoloph of M^1 absent. No field data.
No Number	Left maxillary fragment with P^4-M^2. No field data.
Mandibular Series	
404 (KH 12)	Left dentary with series P_3-M_3, separated but in one matrix block; teeth well worn and preserved. No associated P_1 or P_2, but fragments of crushed bone *in situ* both against sides of teeth and in the matrix (Fig. 5).
415 (F/2/15)	Right dentary fragment with P_2-M_3; P_3 damaged mesiolingually, all well worn. Cement spalling on buccal faces. Acheulean level, Bed 2 (Fig. 5).
537	Left dentary fragment with P_{3-4}; well worn. No field data.
550 (K/14/14'-16')	Right p_{3-4}, M_{1-2}. Milk teeth maturely worn; M_1 worn just to reveal enamel pattern, but not fully developed, M_2 unworn (Fig. 5).
557	Left dentary fragment with P_{3-4}. Cement spalled from teeth, teeth rooted, old individual.
OQ/25-25/14-16'	Left dentary with series P_3-M_1; P_3 damaged mesiobuccally, teeth possibly rooted.

TABLE 7.
Maxillary cheek teeth of *Equus capensis* from Cave of Hearths, Makapansgat.
(COH prefix to accession numbers)

Annotated for qualitative characters. Abbreviations: PC - pli caballin; PI % - position of protocone isthmus from mesial extremity of protocone; Ectstyl - shape of enamel between ectostyles; Ppl - pli protoloph; Ppc - pli protocone; Ppf - pli prefossette; Pof - pli postfossette; PH - pli hypoloph. 0 - not developed , VS - very small, S, M, L, and XL - short, medium, long and very long mesiodistal lengths to the protocone, ? - partially expressed, numbers indicate number of plis, + indicates indication of pli only. Nos. 136 and 160 derive from the 'Swallow Hole' (SH) and 90 is noted as from an Acheulian (A) context.

Specimen No.	Tooth	PC	PI	Ectstyl	Ppl	Ppc	Ppf	Pof	PH
41	L P^4	0	M 45%	flat	0	0	0	1	bump
	L M^1	0	M 25%	missing	0	kink	0	1	0
No number	L P^4	0	M 25%	arc	0	1	2	1+	0
	L M^1	0	M 20%	missing	0	1	0	1+	wave
	L M^2	0	L 15%	flat	0	1	bump	1+	wave
Isolated teeth									
45	R P^2	0	S 10%	slight rise	?	0	?	?	?
79	R P^2	0	S 10%	flat	1	0	?	?	?
88	R P^2	0	S 10%	flat	1	0	1	1-wavy	0
89	L P^2	0	S 10%	ridge	1	0	1	2	1
91	L P^2	0	S 10%	concave	kink	0	1	1	bump
107	R P^2	1	S 35%	flat	1	1	0	bump	1
132	R P^2	0	M 15%	flat	0	bump	0	0	0
2179	R P^2	0	M 10%	ridge	0	1	0	1	1
28	R P^3	0	M 35%	flat	1	1	0	1	1
58	R P^3	1+	M 30%	arc	1	1	0	1	1
83	L P^3	missing	missing	flat	1	0	1	?	0
135	L P^3	0	S 50%	flat	1	0	1?	1	?
144	L P^3	0	M 45%	flat	1	1	2	1	0
155	L P^3	0	M 30%	flat	wavy	1	1	1+	1
160	R P^3	1	M 30%	flat	1	1	2+	1+	1
187	L P^3	1	M 30%	ridge	wavy	1	1	1+	bump
69	R P^4	0	L 30%	curve	2	1	1	2	1
106	R P^4	VS	S 50%	flat	1	1	bump	2	0
136 (SH)	L P^4	0	M 45%	flat	1	2	2	2+	0
76	L M^1	0	L 50%	flat	1+	1	wavy	1+	1
127	R M^1	bump	M 45%	arc	wavy	1	bump	1+	0
136	L M^1	1	L 45%	flat	2	1	bump	2	1
167	L M^1	1	L 40%	flat	1++	1	0	2	0
169	R M^1	0	L 30%	flat	0	0	1	1+	1
188	L M^1	bump	M 40%	flat	0	1	wavy	1	0
30	R M^2	0	M 45%	arc	?	0	0	0	0
141	L M^2	+	XL 45%	arc	1	2	2	1	2
160 (SH)	R M^2	0	M 40%	round	1	1	wavy	1	1
163	R M^2	0	L 35%	flat	0	1	wavy	1	1
164	R M^2	1	L 35%	flat	bump	1	wavy	1	0
819	L M^2	bump	L 35%	flat	bump	1	0	1+	0
No number	R M^2	bump	XL 30%	flat	0	1	3	1+	bump
(Tu/15-19/28-30 inscribed on this tooth)									
50	R M^3	0	XL 35%	low ridge	bump	0	0	0	0
90 (A)	R M^3	0	XL 30%	flat	1	0	1	?	1
129	R M^3	0	XL 35%	arc	0	0	0	0	0

TABLE 8.
Mandibular cheek teeth of *Equus capensis* from Cave of Hearths, Makapansgat.
(COH prefix to acession numbers)

Annotated for qualitative characters. PC - pli caballinid, Mc - metaconid shape, Ms - metastylid, Ent - entoconid, Mf - metaflexid floor, Ef - entoflexid floor, BMV - penetration of buccal mesial valley past protoconid (buccolingual diameter of protoconid = 100%). O - not developed or VS - very small, S, M, L, and XL - short, medium, long and very long mesiodistal lengths of the protocone, ? - partially expressed, numbers indicate number of plis, + indicates indication of pli only.

Specimen No.	Tooth	PC	Mc	Ms	Ent	Mf	Ef	BMV
404	L P_3	kink	round	point	square	arc	wavy	50%
	L P_4	kink	round?	point?	round	bent	wavy	50%
	L M_1	kink	round	point?	round	bent	wavy	110%
	L M_2	0	round	point	square	bent	crest	110%
	L M_3	kink	round	point	square	bent	wavy	110%
415	R P_2	0	round	point	square	flat	wavy	0%
	R P_3	bump	–	–	square?	–	dip	50%
	R P_4	bump	round	point	square	crest	wavy	90%
	R M_1	bump	round	point	round?	rise	crest	110%
	R M_2	bump	round	round	oblong	arc	rise	110%
	R M_3	0	round	round	point	arc	crest	105%
537	L P_3	0	round	point	square	curve	smooth	100%
	L P_4	0	round	point	square	curve	smooth	100%
550	R p_3	1	round	point	round	data	unrecorded	
	R p_4	1	round	point	round	..	..	..
	R M_1	1	long	point	square	..	..	..
557	L P_3	0	round	point	square	crest	flat	90%
	L P_4	0	round	point	square	crest	rise	90%
OQ/25	L P_3	kink	round	point	round	crest	wavy	90%
-25/	L P_4	bump	round	point	round	crest	wavy	100%
14/16'	L M_1	bump	round	point	square	rise	rise	120%
Isolated teeth								
410	L P_2	kink	round	point	square	wavy	wavy	30%
432	R P_2	?	–	–	round?	–	wavy	–
449	R P_2	0	round?	point	round	flat	smooth	30%
513	R P_2	+	wedge?	point	round	smooth	crest	50%
576	L P_2	0	round	point	square	smooth	smooth	50%
412	L P_2	1	wedge	point	round	crest	wavy	100%
485	L P_2	kink	round	point	square	crest	smooth	60%
586	L P_2	kink	wedge	point	square?	flat	smooth	40%
645	R P_2?	Unrecorded						
No number	L P_2	0	round	point	square	curve	wavy	–
440	R P_3	+	round?	point	square	angle	wavy	90%
488	R P_3	?	point	point	round	angle	wavy	60%
492	L P_3	0	round	point	square	smooth	wavy	100%
524	L P_3	0	round	point	square	smooth	smooth	100%
558	L P_3	0	round	point	square	curve	smooth	–
4512	R $P_{3/4}$	+	round	point	round	angle	wavy	100%
429	R P_4	kink	round	point	square	curve	wavy	80%
433	L P_4	kink	–	point	square?	–	wavy	80%
444	L P_4	0	round	point	square	curve	crest	100%
458	L P_4	0	round	point	square	angle	wavy	100%
487	R P_4	kink	round	point	square	curve	wavy	100%
497	L P_4	+	round	point	square	angle	smooth	90%
498	L P_4	kink	round	point	square	crest	wavy	90%
512	R P_4	0	round	point	square	crest	smooth	80%
540	R P_4	kink	square	point	square	crest	wavy	100%
616	R P_4	kink	round	point	square	curve	crest	90%
640	R P_4	kink	round	point	square	angle	smooth	60%
651	R P_4	kink	round	point	square	curve	crest	80%
652		Unrecorded						
96-102	R P_4/M_1	+	round	point	square	curve	wavy	100%
413	L M_1	0	round	point	square	crest	wavy	115%
453	L M_1	0	round	point	square	crest	crest	110%
553	L M_1	kink	round	point	round	crest	crest	110%
567	L M_1	0	round	round	square	crest	rise	115%
570	L M_1	0	round	point	square	flat	rise	130%
494	R M_2	0	round	point	square	curve	crest	120%
496	L M_2	0	round	point	square	curve	wavy	125%
538	R M_2	0	round	point	square	crest	crest	110%
645	R M_2	1	round	blunt	square	flat	–	110%
411	L M_3	kink	round	point	square	arc	crest	120%

TABLE 9.

Measurements of incisors and maxillary cheek teeth of *Equus capensis* from Cave of Hearths, Makapansgat.

COH prefix to accession numbers.

Abbreviations: BLD - buccolingual diameter, over cement below occulsal surface on cheekteeth; BLDE - buccolingual diameter over enamel of ectoloph and protocone; BLDM - buccolingual diameter of mark; MDD - mesiodistal diameter; MDDM - mesiodistal diameter of mark; PL - protocone length. e - estimated measurement, + indicates a minimal value due to damage. Specimen 819 (R M^2) is marked 'To/15-19/28-30' and 160 derives from the 'Swallow Hole' (SH).

Incisors

Specimen No.	**Tooth**	**BLD**	**MDD**	**BLDM**	**MDDM**	**Comment**
62	RI_1?	12.1	17e	5.8	10.2	Mark
210	LI^3 or RI_3	–	13.2	–	–	Mark absent
623	RI^1	15.6	18.7	7.7	8.0	Round mark

Upper Cheekteeth

Specimen No.	Tooth	BLD	MDD	BLDE	PL
41	L P^4	30.4	32.8+	31.9	13.7
	L M^1	25.7	28+	28.0	11.8
No number	L P^4	27.3	28.7	27.9	11.8
	L M^1	24.7	27.6	26.3	12.0
	L M^2	25.2	28.0	24.0	13.3
	Mesiodistal length P^4-M^2 = 77.7				
Isolated teeth					
45	R P^2	Unrecorded			
79	R P^2	Unrecorded			
88	R P^2	36.3	25.5	25.0	7.1
89	L P^2	38.4	29.9	28.8	10.3
91	L P^2	39.1	26.5	24.6	9.3
107	R P^2	46.5e	25.8	25.3	9.9
132	R P^2	Unrecorded			
2179	R P^2	41.5	30.3	29.7	10.3
28	R P^3	30.3	34.7	32.6	12.4
58	R P^3	27.7	27.5	26.0	11.9
83	L P^3	Unrecorded			
135	L P^3	30.3	32.7+	32.7	11.5
144	L P^3	32.1	29.6	28.4	10.2
155	L P^3	27.8	28.5	27.5	10.0
160	R P^3	32.1	30.3	29.0	11.1
187	L P^3	27.4	26.4	25.2	10.0
69	R P^4	31.4	30.8	28.9	13.5
106	R P^4	Unrecorded			
76	L M^1	28.8	29.6	28.2	16.0
127	R M^1	29.1	27.4	24.4	13.5
136	L M^1	31.8	30.9	28.2	13.6
167	L M^1	28.3	28.7	26.3	13.7
169	R M^1	28.5	28.2	27.5	13.3
188	L M^1	25.7	26.9	25.4	12.5
30	R M^2	Unrecorded			
141	L M^2	Unrecorded			
160 (SH)	R M^2	Unrecorded			
163	R M^2	28.4	28.3	26.0	15.2
164	R M^2	28.4	27.4	26.4	13.9
819	R M^2	29.0	29.0	26.6	14.3
50	R M^3	30.6	31.3	28.1	18.5
90	R M^3	26.7	31.0	24.7	15.8
129	R M^3	Unrecorded			

TABLE 10.
Measurements of mandibular cheek teeth of *Equus capensis* from Cave of Hearths, Makapansgat.

COH prefix to accession numbers.

Abbreviations: BLD - buccolingual diameter over cement below occlusal surface; BLDE - buccolingual diameter over enamel of ectoloph and protocone; EfxL - mesiodistal length of entoflexid; McMsL - mesiodistal length of metaconid-metastylid knot; MDD - mesiodistal diameter. e-estimated measurement, w - measurement reduced because of wear, + indicates a minimal value due to damage.

Specimen No.	Tooth	MDD	BLD	BLDE	McMsL	EfxL	Comment
404	L P_3	31.8	22.7	18.5	19.8	17.9	
	L P_4	31.3	22.4	17.6	17.6	15.0	
	L M_1	28.3	21.8	16.0	15.5	10.6	
	L M_2	28.3	19.8	15.6	15.2	11.0	
	L M_3	36.5	17.2	14.8	15.5	10.0	
	Mesiodistal lengths P_{2-4} = 95.6e; M_{1-3} = 93.3e; P_2-M_3 = 189e: all based on lengths of individual teeth.						
415	R P_2	36.3	21.7	17.9	19.7	18.8	
	R P_3	30.7	21.2	18.7	–	15.4	
	R P_4	34.1	23.7	17.5	18.9	14.6	
	R M_1	31.8	21.8	18.0	15.6	10.1	
	R M_2	31.6	21.0	15.3	16.3	10.9	
	R M_3	37.4	19.8	15.9	16.0	11.0	
	Mesiodistal lengths P_{2-4} = 100.0; M_{1-3} = 95.3; P_2-M_3 = 192.5.						
537	L P_3	30.1	19.4+	19.4	20.5	13.6	
	L P_4	29.2	19.3+	19.3	18.5	11.8	
550	R p_3	35.1	20.5	19.0	21.7	11.4	
	R p_4	37.2	22.5	19.5	20.2	11.2	
	R M_1	37.0	18.5+	18.5	17.9	9.7	
557	L P_3	31.2	20+	20.0	20.2	13.7	
	L P_4	29.2	20.2+	19.3	18.0	12.0	
OQ/25	L P_3	33.1	21.1	18.5	20.0	18.0	
25/	L P_4	33.3	19.9	17.7	17.9	15.5	
14-16	L M_1	28.9	19.2	16.5	15.8	9.5	
Isolated teeth							
410	L P_2	36.8	21.5	17.3	20.0	17.8	
412	L P_2	39.3	20.5	17.3	15.2	17.0	
485	L P_2	–	19.7	17.2	16.8	18.0	
576	L P_2	33.4	18.1+	18.1	16.0	15.9	
586	L P_2	Unrecorded					
645	R P_2?	38+	16.4	15.0	19.7	–	
No number	L P_2	38.0	17.1+	17.1	18.2	15.7	
440	R P_3	37.1	19.0	16.1	20.6	15.5	
472?	R P_3	32.6	20.1	16.1	17.4	16.6	
488	R P_3	35.0	19.2	16.5	21.8	18.7	
492	L P_3	28.9	17.9	14.4	16.7	12.1	
524	L P_3	28.1	17.7+	13.5	16.7	12.4	
558	L P_3	Unrecorded					
4512	R $P_3/_4$	Unrecorded					
429	R P_4	29.1	20.9	17.1	18.3	14.9	
433	L P_4	Unrecorded					
444	L P_4	26.7	21.1	16.8	16.5	11.7	?*burchelli*
458	L P_4	26.5	18.8	17.3	12.3	13.3	
487	R P_4	30.7	22.1	18.9	18.3	13.6	
497	L P_4	32.4	21.4	15.0	20.4	16.0	?P_3
512	R P_4	29.9	19.7	15.9	18.5	16.5	
540	R P_4	29.7	19.9	15.4	16.9	16.4	
616	R P_4	29.0	19.4	15.7	17.9	14.9	
640	R P_4	27.7	18.6	17.6	17.5	13.5	
652	R P_4	29.5	21.0	16.5	16.0	13.7	
96-102	R P_4 or M_1	30.4	19.6	16.4	19.0	14.7	
413	L M_1	Unrecorded					
453	L M_1	30.0	16.9+	16.9	15.8	12.3	
553	L M_1	33.3	20.4	18.0	20.4	13.7	
567	L M_1	28.7	19.6	16.5	14.8	11.3	?*burchelli*
570	L M_1	28.9	22.5	17.6	15.3	12.0	
494	R M_2	30.7	19.9	15.2	16.8	11.9	
496	L M_2	33.5	22.6	16.2	17.5	11.3	
538	R M_2	32.4	18.8	14.5	14.5	10.3	
411	L M_3	38.1	18.8	16.7	15.1	11.4	