ZOOLOGISCHE MEDEDELINGEN

UITGEGEVEN DOOR HET

RIJKSMUSEUM VAN NATUURLIJKE HISTORIE TE LEIDEN

(MINISTERIE VAN CULTUUR, RECREATIE EN MAATSCHAPPELIJK WERK)

Deel 55 no. 22 15 augustus 1980

THE OLDUVAI ZEBRA (*EQUUS OLDOWAYENSIS*) FROM THE LATER OMO BEDS, ETHIOPIA

by

C. S. CHURCHER

Department of Zoology, University of Toronto

and

D. A. HOOIJER

Rijksmuseum van Natuurlijke Historie, Leiden [1])

With 6 plates

Abstract

Shungura Members G, H, J, K and L, and the Kalam Outcrop, have yielded teeth and some postcranial elements assignable to *Equus oldowayensis* Hopwood, 1937. Member G (earliest Early Pleistocene) has yielded a sample of 21 upper and nine lower teeth and two complete and one partial metapodials. Member K (middle to late Early Pleistocene) has yielded nine upper and four lower teeth. The other members have yielded smaller samples. Positive identification of the species from Members G, K, and the Kalam Outcrop are based on series of associated teeth derived from single individuals. The recognition of *E. oldowayensis* from Shungura Members G-L corresponds to its known temporal range through Bed I at Olduvai Gorge and its existence in East Africa throughout the Early Pleistocene.

Introduction

Cooke (1963: tab. 4) assigned the large equid from the Omo deposits to *E. oldowayensis* Hopwood, 1937 or possibly to *E.* aff. *grevyi*, but without discussion. Hooijer (1976) recorded a large *Equus* that was considered indeterminate to species in the absence of skulls. However, he described characters (short protocones, V-shaped metaconid-metastylid valleys, or protocones occasionally long and valleys occasionally U-shaped) that are normal for *E. oldowayensis*. Coppens (1978) noted that 'True *Equus* appears in Member G together with *Hipparion aethiopicum* (sic; = *H. libycum ethiopicum*). Churcher & Richardson (1978: 381, tab. 20.1) list *Equus* (*Dolichohippus*) *oldowayensis* from the Shungura Formation Members F-J of the Omo

[1])Present address: Aert van Neslaan 101, 2341 HH Oegstgeest.

sequence and discuss (1978: 405) Hooijer's (1973; 1974, pers. comm. to Churcher & Richardson) observations on the *Equus* in Members G-J.

The opportunity to examine undescribed material from the later Shungura members allowed Churcher to confirm Cooke's listing and Churcher's and Richardson's deduction and for us to record the characteristics of the large equid present in the later Shungura Beds. The work was carried out at the Rijksmuseum van Natuurlijke Historie, Leiden, where comparisons with the extensive sample of *E. oldowayensis* from Olduvai Gorge was possible and allowed identifications of the variants observed in the smaller samples.

Type specimens

Hopwood (1937: 117) designated a lower jaw from an animal about two years old (Catalogue Number VIII, 353, in the Bayerische Palaeontologische Staatssammlung, Munich) as the holotype of *Equus oldowayensis*. He also designated a lower incisive region with the left incisors and right first incisor (Catalogue Number M. 14,199, in the British Museum [Natural History], London) as the paratype. The original Olduvai collection deposited in Munich, together with its catalogue, was destroyed during the 1939-1945 war, and included the type of *E. oldowayensis* (Dr. Kurt Heissig, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich).

The designation of a replacement neotype is therefore necessary. The original type was an immature mandible with p_2-M_1, with M_2 erupting, and consequently did not show the complete development of the dentition or of the adult molar patterns. The paratype, which normally would be the obvious replacement for a destroyed type, has damaged incisors and shows no distinctive characters by which it may be separated from other similar-sized *Equus* with any certainty. We have therefore chosen the new type from specimens derived from adult individuals, which show dental characters typical of the species and the complete dental sequence. We have considered the new materials recovered from Olduvai Gorge after the original collections and, as there is no skull with a preserved adult palate and dentition, found no reason to choose an undescribed specimen. We select the British Museum (Natural History) dentary (M. 14,184), for which Hopwood (1937: 125) gave measurements, as the replacement neotype. Hopwood's alternative specimen (M. 14,134), for which comparable measurements are also given, is from an old individual (Hopwood: 118) and has an enamel pattern closely similar to the neotype. The occlusal patterns and proportions of M. 14,184 reflect the variety observed in the *E. oldowayensis* lower jaws subsequently recovered from Olduvai Gorge and thus the neotype is considered typical and truly representative of the Olduvai Gorge *Equus oldowayensis* populations from the Middle Pleistocene.

Materials

The samples are not equal and the specimens are not distributed evenly throughout the sequence. Member G has yielded 21 upper and nine lower teeth, of which six upper and five lower teeth derive from single upper and lower jaws, essentially entire specimens of metacarpal III and metatarsal III and the distal end of another metacarpal III. Member H yielded three fragmentary teeth, Member J one whole and three fragmentary teeth, Member K ten upper and four lower teeth, of which eight upper teeth probably derive from one palate, and Member L five damaged teeth, one damaged ungual phalanx III and the distal end of a metacarpal III. The Kalam Outcrop has yielded five associated and one isolated teeth, and a fragment of a right dentary with three teeth is recorded only as from 'Omo'.

These specimens comprise part of the collection obtained by Dr. F. Clark Howell and the American contingent from the Omo Group deposits in Ethiopia during 1967 to 1974 and, although not extensive, do constitute a valid sample on which to base identifications, especially for Members G and K, and the Kalam Outcrop. The catalogue numbers used to identify the specimens in this report have prefixes that identify the locality: L = Shungura locality, F = F.H. Brown's field locality, and P = J. de Heinzelin's field locality, both in the Shungura Formation.

The specimens are considered by member in stratigraphic order.

1. Member G

Materials. — The dental specimens vary in preservation from dark, heavy and mineralised to light in colour and weight, some with encrusted minerals and some badly weathered. The postcranial specimens are well preserved, unweathered, partly mineralised and dark brown to yellow stained on the surface and dark brown internally. Occlusal enamel patterns of the cheek-teeth are shown in plates 1 and 2 and postcranial elements in plates 5 and 6. Measurements are given in tables 1 and 2.

Upper dentitions:

L.490-4a	Level	G5	I^2 dext., root broken
L.490-4b	„	G5	P^2 dext., rooted, well worn
L.490-4c	„	G5	P^4 sin., rooted, very well worn
L.490-4d	„	G5	M^1 dext., rooted, very well worn
L.490-4e	„	G5	P^3 dext., rooted, well worn
L.490-4f	„	G5	M^3 dext., rooted
L.490-4g	„	G5	M^3 sin., rooted, lacking buccal ectoloph

The series L. 490-4a to 4g probably derive from a single palate on the evidence of preservation and wear.

TABLE Ia

Measurements of upper cheekteeth of *Equus oldowayensis* from Shungura Formation Members G, J and K

'e' indicates estimated measurements because of damage to the tooth, and '+' indicates measurements to be greater than figure given. Measurements are in mm

	SHUNGURA FORMATION, MEMBERS G, J and K					
	G	G	G	G	K	K
P^2	L.490-4b	L.67-129			F.17-9	F.17-7
Mesiodistal diameter	39.0	40.4			-	37.5
Buccolingual diameter over protocone	24.9	27.6			25.7	27.4
Buccolingual diameter over hypocone	22.5	24.8			20+	25.2
Length of protocone	6.9	7.7			8.0	7.7
P^3	L.490-4e		F.24-7		F.17-6	F.17-10
Mesiodistal diameter	29.2		30.3		28.8	28.6
Buccolingual diameter over protocone	25.9		27.9		-	28.3
Buccolingual diameter over hypocone	23.8		24.2		-	23.3
Length of protocone	8.5		9.4		9.1	9.6
P^4		L.7-155a	F.513-13	L.626-35	F.17-8	F.17-14
Mesiodistal diameter		30.9	31.0	33.3	26.9	28.5
Buccolingual diameter over protocone		29.8	28.0	28e	-	-
Buccolingual diameter over hypocone		-	25.8	-	-	-
Length of protocone		11.0	10.8	12.3	9.9	-
M^1	L.490-4d	L.490-4c	L.427-9	L.627-95		
Mesiodistal diameter	25.4	24.4	25.8	26.5		
Buccolingual diameter over protocone	25.2	25.1	25.6	27.4		
Buccolingual diameter over hypocone	22.4	22.5	23.2	24.7		
Length of protocone	8.5	8.6	9.2	10.4		
M^2		F.163.3	F.740-25	F.165-2		F.17-5
Mesiodistal diameter		27.2	31.4	30.5		29.5
Buccolingual diameter over protocone		27.1	30.0	28.1		27.8
Buccolingual diameter over hypocone		21.6	24.7	-		25.6
Length of protocone		10.3	10.6	12.3		11.4
					J	
M^3	L.490-4f	L.490-4g	L.7-281		F.23-1	P.996-26
Mesiodistal diameter	25.6	25.8	30.0		26.2	27.3
Buccolingual diameter over protocone	21.5	-	26.8		21.2	22.2
Buccolingual diameter over hypocone	16.6	-	19.9		17e	15.3
Length of protocone	9.9	9.5	-		11.4	12.5

L.67-129 Level G7 P^2 sin., rooted
F.24-7 „ G2 P^3 sin., rooted, very well worn, damaged
L.7-155a „ G5 P^4 sin., rooted
F.513-13 „ G27 P^4 dext., rooted
L.73-55 „ G12 P^4 sin., rooted, lacking paraloph and most of protocone
L.626-35 „ G12 P^4 sin., rooted, very well worn, damaged
L.740-25 „ G M^2 sin., roots forming
L.427-9 „ G4 M^1 dext., rooted
L.627-95 „ G13 M^1 dext., rooted, well worn
F.163-3 „ G28 M^2 sin., roots forming, slightly worn
F.165-2 „ G13 M^2 dext., lacking metastyle, metacone and hypoglyph
L.7-281 „ G5 M^3 sin., rooted, worn, damaged mesiolingually
L.7-63 „ G5 M^3 dext., roots forming, slightly worn, prefossette, protocone and hypocone only
L.48-20a „ G13 central interfossette area of upper molar

TABLE 1b

Measurements of lower cheekteeth of *Equus oldowayensis* from Shungura Formation Members G, H, J and K

	SHUNGURA FORMATION, MEMBERS G, H, J and K						KALAM OUTCROP	OMO
	G	G	H	J	K	K		(Not located)
P_2	L.508-1a			F.23-3			P.1000-6d	
Mesiodistal diameter	34.8			36.3			34.5	
Buccolingual diameter over metaconid	13.4			13.1			11.6	
Buccolingual diameter over metastylid	16.1			15.9			15.7	
Length of metaconid-metastylid	14.5			15.4			16.0	
P_3	L.508-1a						P.1000-6a	67 - 57
Mesiodistal diameter	32.0						31.2	29.0
Buccolingual diameter over metaconid	15.9						14.8	14.4
Buccolingual diameter over metastylid	15.3						14.8	14.9
Length of metaconid-metastylid	19.3						17.5	17.3
P_4	L.508-1a	L.851-1					P.1000-6b	67 - 57
Mesiodistal diameter	29.4	31.0					30.3	26.2
Buccolingual diameter over metaconid	16.7	16.4					14.9	15.3
Buccolingual diameter over metastylid	16.2	16.3					12.3	13.6
Length of metaconid-metastylid	18.3	18.3					16.1	15.7
M_1	L.508-1a	L.626-87			P.996-7		P.1000-6c	67 - 57
Mesiodistal diameter	27.7	26.4			25.8		29.7	-
Buccolingual diameter over metaconid	14.4	13.6			12.8		13.4	14.4
Buccolingual diameter over metastylid	13.1	13.3			11.0		12.3	-
Length of metaconid-metastylid	14.9	14.9			14.9		14.5	-
M_2	L.508-1a	L.48-21	F.161-56	P.994-5	P.996-25	P.996-39	P.1000-5	
Mesiodistal diameter	27.6	27.8	27.9	25.2	23.9	26.4	26.9	
Buccolingual diameter over metaconid	14.4	14.8	12.9	13.3	14.0	13.6	13.5	
Buccolingual diameter over metastylid	13.3	14.4	11.9	12.3	13.8	13.2	12.4	
Length of metaconid-metastylid	14.9	15.1	14.3	14.5	15.8	15.0	14.9	
M_3	L.627-366	L.627-211						
Mesiodistal diameter	34.1	-						
Buccolingual diameter over metaconid	14.8	13.6						
Buccolingual diameter over metastylid	11.8	11.7						
Length of metaconid-metastylid	14.9	14.9						

Lower dentitions:

L.508-1a	Level	G9	P_2-M_2 sin., in alveolar bone, rooted
F.513-14	„	G27	P_3 or P_4 dext., metaconid to entoconid and flexids only, ?rooted
L.48-20b	„	G13	M_1 or M_2 sin., metastylid, entoconid and metaflexid only, ?unrooted
L.851-1	„	G1	P_3 or P_4 sin., badly damaged, ?rooted
L.626-87	„	G12	M_1 sin., rooted
L.48-21	„	G13	M_2 sin., rooted, damaged on hypoconid
L.627-366	„	G13	M_3 dext., rooted, slightly damaged
L.527-211	„	G13	M_3 dext., ?rooted, lacking hypoconulid
L.608-6	„	G5	M_3 dext., rootless, damaged distally and at base, unworn

Appendicular elements:

L.7-3	Level	G5	metacarpal III sin.
F.513-34	„	G27	metacarpal III dext., distal end
L.7-4	„	G5	metatarsal III dext., shaft damaged

TABLE 2

Measurements of the postcranial elements of the Omo Valley *Equus oldowayensis* from Shungura Formation Members G and L, compared with ranges for similar dimensions of *E. oldowayensis* from Olduvai Gorge

Specimens are identified as "G L.7-3" to indicate Member G, Locality L, No. 7-3. The ranges of variation for the Olduvai samples are derived from samples in which not all dimensions are measurable. Measurements are in mm.

DIMENSIONS	SHUNGURA MEMBERS G AND L				OLDUVAI GORGE	
Metapodials	Mc III s G L.7-3	Mc III d G F.513-34	Mc III s L F.410-5	Mt III d G L.7-4	Mc III Range Max.-Min.	Mt III Range Max.-Min.
Proximo-distal length	235	-	-	259	247 - 209	273 - 251
Proximal transverse diameter	46.5	-	-	44.5	57.7 - 47.7	59.2 - 43.0
Proximal anteroposterior diameter	31.4	-	-	38.5	38.7 - 30.2	47.9 - 38.5
Midshaft transverse diameter	29.9	-	-	30.5	37.6 - 30.0	40.8 - 32.8
Midshaft anteroposterior diameter	25.1	-	-	27.4	31.0 - 24.6	38.3 - 30.0
Distal transverse diameter	42.1	44.9	42.3	44.8	52.0 - 44.1	61.6 - 45.0
Transverse diameter of distal articulation	41.8	45.2	42.5	40.9	53.2 - 40.9	53.6 - 44.2
Anteroposterior diameter of trochlear keel	32.8	36.2	31.4	34.0	37.7 - 28.5	41.5 - 33.0
Anteroposterior diameter of medial trochlea	28.4	31.5	27.8	28.3	34.3 - 21.3	36.0 - 28.5
Anteroposterior diameter of lateral trochlea	25.0	28.8	25.5	24.2	30.0 - 19.6	32.7 - 26.9
Least anteroposterior diameter of diaphysis proximal to distal articulation	21.2	21.1	19.0	23.5	26.1 - 18.3 N = 44 - 15	32.0 - 23.8 N = 30 - 16

Ungual Phalanx	Ph III L F.356-4	Ph III Range Max.-Min.
Proximo-distal length on anterior surface	46.1	60.1 - 44.0
Anteroposterior diameter of articulation	26.7	27.8 - 20.1
Height of coronoid above plantar plane	38.5	48.1 - 33.8
Height of ventral margin of articulation above plantar plane	23.0	28.6 - 18.8 N = 20 - 15

Descriptions and discussion. — The single upper incisor (I^2 dext., L.490-4a) measures 16.3 mm mesiodistally by 11.6 mm buccolingually on the occlusal surface. The infundibulum or mark is a lozenge in cross-section, measures 8.2 mm by 5.3 mm, and is situated near the lingual boundary. Cement is present on the root, but not obviously within the mark, and no secondary dentine ring is visible. This tooth is similar in proportions to those of *E. oldowayensis* from Olduvai Gorge, but the mark is more often round, oval or elongate in that population. Marks in *E. burchellii* are also variable, and include lozenge-shaped examples.

The upper premolars have flattened crests to the parastyles and mesostyles on the ectoloph, some of which are longitudinally grooved. The parastyles of P^3 and P^4 are broader and flattened mesiobuccally, and may be channelled (L.513-13, pl. 1 fig. 9; F.24-7). Those of P^2 are often less broad and less obvious. The mesostyles of P^2 are broad and may be channelled (L.67-129, pl. 1 fig. 7; L.490-4b, pl. 1 fig. 1), but those of P^3 and P^4 are thinner than the parastyle, more rounded and with less of a flattened surface, lean slightly mesiad, and often overhang the ectoloph valleys (F.513-13,

L.490-4e, pl. 1 fig. 2; F.24-7). The floors of the ectoloph valleys are buccally concave, and vary from nearly flat in well worn specimens (F.24-7) from aged animals to arcuate in maturely worn specimens (F.513-13) from prime adults, and with a slight median convexity in newly worn crowns (L.73-55). The protocones are small and nearly as buccolingually wide as they are mesiodistally long in P^2. In P^3 and P^4 they are mesiodistally elongate, and may be flattened (F.24-7) or concave on the lingual margin and semicircular in buccal outline (F.513-13). The buccal arm of the postfossette extends more buccad to the base of the mesostyle and beyond that of the prefossette, even in well worn specimens where the difference is lessened.

Plis caballins vary from absent through vestigial kinks or bends and simple or small loops (L.490-4b, 4e) to double and large (F.513-13). Plis protolophs may be simple (L.490-4b; F.513-13; F.24-7), double (L.67-129) or vestigial, plis hypolophs may be small or vestigial (L.490-4b; L.67-129) or large and simple (F.513-13), plis protoconules are large and single (L.490-4b, 4e; F.24-7; L.626-35) or double (F.513-13), plis prefossettes vary from one (L.626-35) to two small, vestigial folds (L.490-4b, 4e; L.67-129) or three small folds (F.24-7) to six of various sizes (F.513-13), and plis postfossettes have one large and one or two vestigial folds. Specimen F.513-13 has an additional pli mesial to the pli caballin across the protocone isthmus.

The molars are similar to the premolars, but smaller and the characters are less emphasized. The ectoloph crests are slimmer and narrower, seldom as flattened as in the premolars, and then on the parastyle only, where it may be channelled (F.165-2; L.740-25, pl. 1 fig. 8). The ectoloph valleys are flatter and may have a slight median rise along their length. The styles do not overhang the valleys noticeably and the mesostyles do not appear tilted mesiad, except in the very well worn specimens. The protocones are more elongated mesiodistally, those of M^1 resembling those of P^3 and P^4, but those of M^2 strongly elongate when newly worn and attached in the mesial third of their length and those of M^3 elongate even when well worn and attached by their mesial extremities.

Plis caballins are vestigial or absent; plis protolophs are simple (F.165-2; L.740-25), vestigial or absent; plis hypolophs simple (F.165-2; L.740-25; L.490-4g, pl. 1 fig. 6), double (L.490-4f, pl. 1 fig. 4) or absent; plis protoconules may be simple, small (L.490-4g; L.627-95, pl. 1 fig. 10; L.429-9), double (L.490-4g) or branched (L.490-4f); plis prefossettes may be two or three vestigial (L.427-9), two to four well developed folds (F.165-2; L.490-4f, 4g), absent or vestigial (L.627-95); and plis postfossettes may show one major fold and vestigial or no other folds or graded folds as in a premolar (F.165-2).

The characteristics of the ectolophs and protocones and the distribution of the plis correspond to those in *E. oldowayensis* from Olduvai Gorge.

The lower premolars are represented only by P_2-P_4 in L.508-1a (pl. 2 fig. 1) and in the damaged L.851-1 and fragmentary F.513-14 specimens. The worn series in L.508-1a shows the typical equid buccal valley penetrating lingually no further than the level of the flexid floors in P_4 and not as far in P_2 and P_3. No pli caballinid or ptychostylid is visible, although a kink in the enamel is present in P_2 of L.851-1a. The metaconids are large and round in P_3-P_4, and the metastylids are broad with a strong distolingual angle. The floors of the metaflexids are slightly sinuous with a broad bend opposite the mouth of the flexid in P_4 of L.851-1a. In this and F.513-14 the floors are similar and have small bends in the position of the pli hypolophid of *Hipparion*. The molars are similar to the premolars, but slighter, with the buccal valley penetrating between the flexid floors in all specimens where they are observable. Plis caballinids or ptychostylids are absent, but kinks are present in the walls of the hypoconids (L. 626-89; L.48-21, pl. 2 fig. 2; L.627-366, pl. 2 fig. 3). The floors of the metaflexids bend towards the mouths of the flexids in all observable cases and a small kink in the pli hypolophid position occurs in L.626-87 (pl. 2 fig. 4).

In the shapes of the metaconids and metastylids, the lack of ptychostylids, the conformation of the metaflexid floors and the massiveness of the third and fourth premolars, the equid teeth from Shungura Member G correspond to those of *E. oldowayensis* from Olduvai Gorge. No observable character of either the upper or the lower dentitions suggests a taxon other than the large extinct zebra (*E. oldowayensis*) and no dental material suggests another zebra such as *E. burchellii* or a true horse.

The postcranial elements comprise only one whole left metacarpal III (L.7-3, pl. 6 figs. 1-3), the distal end of a right metacarpal III (F.513-34, pl. 5 fig. 3) and a right metatarsal III (L.7-4, pl. 6 figs. 4-6). These are slender, gracile bones, not typical of the larger bones of *E. oldowayensis* in massiveness, but may be matched with the more lightly built elements of the species obtained from Olduvai Gorge and may represent females.

The two metacarpal III specimens both show marked concave depressions proximal to the distal articulations on the posterior surface of the shaft. The comparable area on the metatarsal L.7-4 has a central ridge running proximally from the trochlear keel to the margin of the depression (compare lateral aspects, pl. 6 figs. 2 and 5). This is absent in F.513-34 and slight in L.7-3, and does not reach the margin of the depression in either specimen. This condition distinguishes the extinct *E. oldowayensis* and many recent *E. grevyi* from *E. burchellii* and supports the dental similarities of

the Shungura Member G equid and *E. oldowayensis* from the type locality of Olduvai Gorge.

2. Member H

Materials. — The specimens are fragmentary, weathered, partly mineralised and coloured black, reddish brown and yellow, with whitish enamel. The occlusal pattern of F.161-56 is shown in plate 2 and its measurements are given in table 1.

L.781-8 Level H1 M^3 dext., rooted, buccal portion only
L.781-9 „ H1 P_2 sin., distobuccal fragment with valley, hypoconid and metaflexid, rooted
F.161-56 „ H4 M_2 sin., lacking lingual cement, rootless

Descriptions and discussion. — The fragmentary M^3 (L.781-8) shows a flattened mesiobuccal surface to the parastyle and a rounded mesostyle that tilts mesiad. The mesial ectoloph valley floor is buccally concave and the distal flat. No pli protoloph, a single pli hypoloph, a large lingual and two small buccal plis postfossettes, and three or four plis prefossettes can be seen.

The fragmentary P_2 (L.781-9) shows a vestigial ptychostylid and a sinuous floor to the metaflexid with a small kink in the position of the pli hypolophid. The metastylid is broad and has an angular distolingual corner. The M_2 (F.161-56, pl. 2 fig. 6) shows no ptychostylid, but has broad metaconid and metastylid, and a pli hypolophid in the metaflexid.

All three specimens show characteristics typical of *E. oldowayensis*. The occurrence of ptychostylids on P_2's of *E. oldowayensis* is more common than on other teeth, and the flattened distal valley on M^3's is also a common feature. These specimens are not diagnostic, but fall within the ranges of morphology observable in *E. oldowayensis* from Olduvai Gorge and may be assigned to that species.

3. Member J

Materials. — All four specimens are stained mottled black or bleached cream, and F.23-3 is stained red on part of its lingual surface. The three specimens (except F.23-3) are incomplete, fissured and broken, apparently by weathering. Occlusal enamel patterns are shown in plate 4 and measurements given in table 1.

F.23-1 Level J3 M^3 sin., very well worn, rooted, lacking mesiobuccal corner
F.23-3 „ J3 P_2 dext., very well worn, rooted, entire
P.994-5 „ J6 M_2 dext., very well worn, rooted, slightly damaged mesiobuccally
P.993-6 „ J6 ?P_4 dext., well worn, rooted, damaged lingually and distally

Descriptions and discussion. — The sole upper molar specimen (M^3 sin., F.23-1, pl. 4 fig. 1) shows few taxonomic characters. It is small and lightly built, with a thin mesostyle, flat distal and probably buccally concave mesial floors to the ectoloph valleys, three small plis prefossettes, the most lingual of which might be a pli protoconule, two vestigial plis postfossettes, and one vestigial pli hypoloph. No pli caballin is present. The protocone is mesiodistally elongate, has a smooth lingual margin and the isthmus to the protoconule is located at about 15-20% of its length from the mesial end. No hypoglyph is obvious as the posterior wall has enclosed it, and it is confluent with the postfossette. On these characters it is possible to assign F.23-1 to either *E. burchellii* or *E. oldowayensis*, with the latter being more likely in view of the shapes of the valley floors and the protocone margins.

The lower cheekteeth show no ptychostylids, although shallow bends are visible in the appropriate locations, the floors of the metaflexids are nearly straight in the well worn P_2 (F.23-3, pl. 4 fig. 2) and M_2 (P.994-5, pl. 4 fig. 3), but do bend slightly towards the mouth of the flexid; the less worn $?P_4$ (P.993-6) shows both the bend towards the mouth and the pli hypolophid bend. The metaconid and metastylid in P_2 and M_2 are broad and the metastylids have sharp distolingual angles.

All three specimens are small and too well worn or damaged to provide confidence in identification, but can be matched well with specimens of *E. oldowayensis* from Olduvai Gorge and do not suggest *E. burchellii*.

4. Member K

Materials. — The upper dental specimens are all stained black in the dentine and cementum, and the enamel is often a creamy white or amber where exposed. The lower dental specimens are similar, except that some have more reddish staining to the enamel or cement and some have yellowish cement or secondary dentine. Specimen P.996-39, as conserved, is chiefly dark cream with some dark patches on the enamel. The specimens are partly mineralised and all except P.996-39 have been weathered and have lost their roots. Occlusal enamel patterns of cheekteeth are shown in Plates 3 and 4, and measurements are given in table 1.

Upper dentitions:

F.17-9	Level K4	P^2 sin., lacking mesial spur and lingual eminences
F.17-6	„ K4	P^3 sin., lacking ectoloph and hypoloph areas
F.17-8	„ K4	P^4 sin., lacking ectoloph and hypoloph areas

Specimens F.17-9, F.17-6 and F.17-8 derive from a single individual.

F.17-7 Level K4 P^2 dext., almost entire (includes F.17-12)
F.17-10 „ K4 P^3 dext., lacking parastyle, hypostyle damaged
F.17-14 „ K4 P^4 dext., lacking ectoloph, protocone and hypocone (includes F.17-11)

Specimens F.17-7, F.17-10 and F.17-14 derive from a single individual. All six specimens F.17-6 to F.17-10 and F.17-14 may represent the same individual on the evidence of wear and preservation. Specimens F.17-5 and F.17-13 may also derive from his individual.

F.17-5 Level K4 M^2 dext., slightly damaged on crown
F.17-13 „ K4 M^3 sin., distal half only
P.996-23 „ K? P^3 dext., ectoloph and fossettes only
P.996-26 „ K? M^3 dext., damaged mesially on crown and towards root on parastyle

Lower dentitions:

P.996-7 Level K? M_1 dext., ?rootless
P.996-24 „ K? ?P_4 sin., ?rooted, lacking buccal and distal faces
P.996-39 „ K? M_2 dext., rooted
P.996-25 „ K M_2 sin., rooted, damaged on crown and distally

Descriptions and discussion. — The upper premolar sequences and the possibly associated molars (P^2-P^4 sin., F. 17-7, F. 17-10, F.17-14; dext., F.17-9, F.17-6, F.17-8, pl. 3 figs. 1-6; M^3 sin. F.17-13; M^2 dext. F.17-5, pl. 3 fig. 7) are very well worn and so stained that some plis are not easily visible. Most of the ectolophs are destroyed and only the mesostyles on P^2's F.17-7, F.17-9, and P^3 F.17-6 and the parastyle and mesostyle on M^2 F.17-5 survive to show flattened crests tilted mesiobuccally. The valleys on the ectolophs are flat or concave buccally where preserved on P^2 F.17-7, P^3 F.17-10, P^2 F.17-9, P^3 F.17-6, P^4 F.17-8 and M^2 F.17-5. On the well worn P^3 P.996-23 (pl. 3 fig. 9) the same characters are visible and the mesostyle is grooved. The protocones are mesiodistally short and buccolingually broad, with flat lingual faces on the premolars and a concave face on M^2 F.17-5. Plis caballins are present on all premolars, but not on M^2 F.17-5. No pli caballin is visible on M^3 P.996-26 (pl. 3 fig. 8) and its protocone is elongated and attached at about 20% from the mesial end. Simple plis protolophs are present on all seven teeth; simple plis hypolophs are visible only on P^3-P^4 of F.17-6 and F.17-8; plis prefossettes are absent or vestigial; a simple pli protoconule is present on all premolars, but the area on M^2 F.17-5 is anomalous and atypical with the protoconule forming an arc into the prefossette; and simple plis postfossettes exist in all seven teeth with some small indications of other plis in a few specimens. M^3 P.996-26 has one pli protoconule, two plis prefossettes, two plis postfossettes and one pli hypoloph.

The lower premolars and molars all have small ptychostylids, broad metaconids and metastylids, and metastylids with distolingual angles.

All the specimens are large and represent massive teeth, and can be matched with cheekteeth of *E. oldowayensis* from Olduvai Gorge. Because of the associated upper dental series derived from one individual, this sample can be more certainly identified as *E. oldowayensis*. The possibility of misidentification is also small, since none of the teeth show characteristics of *E. burchellii* or other African equids.

5. Member L

Materials. — The upper cheekteeth are mainly black on the dentine and cement with lighter stained enamel and some red superficial encrustations. The lower cheektooth is similarly coloured, but not as darkly stained, and the incisor is yellow and black. The postcranial elements are stained black. The cheekteeth are too poorly preserved for illustrations or measurements to be informative. The appendicular elements are illustrated in Plates 5 and 6 and measurements given in table 2.

Dentitions:

F.400-28	Level	L2	?I_2 sin.
F.355-4	„	L	M^3 dext., lacking cement and ectoloph
F.354-2	„	L	M^1 or M^2 dext., lacking buccal and mesial surfaces
F.408-39	„	L1	M_2 sin., lacking cement and slightly damaged
F.356-3	„	L	M^3 sin., distal part of protocone only

Appendicular elements:

F.410-5	Level	L2-3	metacarpal III sin., distal end
F.356-4	„	L	ungual phalanx III, central section only

Descriptions and discussion. — The lower incisor (F.400-28) is worn, so that the mark is placed on the lingual margin of the occlusal surface. The tooth measures 14.0 mm mesiodistally by 9.6 mm buccolingually on the crown and the mark 8.6 mm by 4.2 mm. The mark is lozenge-shaped and lined with a layer of cement 1.5 mm thick buccally and 1.0 mm thick lingually.

The upper molar fragments show none of the ectolophs' characters. The protocones are attached at their mesial ends, and have buccally convex buccal margins and flat or lingually convex lingual margins. A single pli caballin is present in F.354-2; it is vestigial in F.355-4 and none is visible in the fragment F.356-3. No pli protoloph or pli protoconule is present in F.345-4, or pli hypoloph in F.356-3. A pli protoconule is present in F.356-3, as are two vestigial plis prefossettes and one simple lingual and some vestigial signs of plis postfossettes. In F.355-4 the plis prefossettes and postfossettes appear vestigial.

The lower M_2 (F.408-39) shows a small ptychostylid fold, large metaconid

and metastylid with a distolingual angle to the latter, a metaflexid floor with a pli hypolophid, and a bend towards the mouth of the flexid.

The fragmentary cheekteeth and the incisor can be matched with teeth of *E. oldowayensis* and resemble them both in size and proportions; they do not correspond to those of *E. burchellii.*

The postcranial specimens are small and lightly built, as are those from Member G. The distal end of a left metacarpal III (F.410-5, pl. 5 fig. 4) is small, and has the hollow area proximal to the distal articulation on the posterior surface typical of *E. oldowayensis.* The partial ungual phalanx III (F.356-4, pl. 5 fig. 5) is small and can only be identified to a small species of *Equus,* but is not *Hipparion.*

The specimens from Member G all conform to the characteristics and morphologies within the size ranges of *E. oldowayensis* from Olduvai Gorge, and are assigned to that species.

6. Kalam Outcrop

Materials. — These specimens derive from the western end of the outcrop and were obtained as part of a mixed fauna collected from above a shell bed and from within gravels. They are unweathered, light yellow or reddish with black surface staining, except P.1000-5 and P.1000-21, which are weathered, stained black with some reddening on the cement. Occlusal enamel patterns of the cheekteeth are shown in plates 2 and 4 and measurements are given in table I.

P.1000-21 M^2 dext., very well worn, rooted, crown slightly damaged and parastyle missing
P.1000-6d P_2 sin., well worn, rooted
P.1000-6a P_3 sin., worn, rooted
P.1000-6b P_4 sin., worn, rooted
P.1000-6c M_1 sin., worn, rooted

Specimens P.1000-6a to P.1000-6d comprise a dental series. P_2 to M_1 and derive from one individual.
P.1000-5 M_2 dext., worn, ?rootless

Descriptions and discussion. — The upper molar fragment P.1000-21 (pl. 2 fig. 6) is badly preserved, but shows a mesostyle that overlaps both mesially and distally the flattish floors of the ectoloph valleys. No pli caballin, pli protoloph, or pli hypoloph is visible. The plis prefossettes and postfossettes are vestigal with a single lingual pli postfossette. Two plis protoconules are present.

The series P_2-M_1 (P.1000-6a to P.1000-6d, pl. 4 fig. 6) shows broad, short ptychostylids, and P_3, P_4 and M_1 show oblong, inflated metaconules

and broad, elongate parallelogram-shaped metaconids with strong distolingual angles. P_2 has an abnormal broad metastylid with a groove on the lingual surface, but with a strong distolingual angle. The floors of the metaflexids are very sinuous in P_2-P_4, with single plis hypophids, double crested bends opposite the mouths of the flexids and one or more small plis distal to them. On M_2 the pli hypolophid is small, the bend opposite the mouth of the flexid is smooth and no distal plis are visible. M_2 P.1000-5 (pl. 2 fig. 8) is similar to M_1 P.1000-6c in its morphology.

The series of lower cheekteeth are typical of *E. oldowayensis* and the isolated M_2 P. 1000-5 and fragmentary M^2 P.1000-21 both show no characters that are unusual for that species. Because these teeth represent at most one or two mature and one aged individuals, their constancy of morphology supports strongly the identification to *E. oldowayensis*.

7. Omo — No locality or horizon

Material. — An isolated portion of an equid right dentary (OMO 1967 (57), pl. 5 figs. 1 and 2) with P_3-P_4, the mesial third of M_1, the resorbed alveolar area of P_2 and the inferior margin beneath these teeth, provides sufficient dental characters to identify the taxon. The specimen is well preserved and partly mineralised, stained reddish khaki over much of the surface, the teeth have lost most of their cement and only the distal portion of M_1 appears to have been lost in collecting. Occlusal enamel patterns are shown in plate 5 fig. 1, and the specimen is illustrated in buccal aspect in plate 5 fig. 2. Measurements of the teeth are given in table 1.

Descriptions and discussion. — Ptychostylids are vestigial on both P_3 and P_4, the metaconids are large and rounded and the metastylids are similar with strongly developed distolingual angles. The floors of the metaflexids bend towards the mouths of the flexids and there is a small pli on the metaconid-metastylid isthmus, projecting mesially into the entoflexid. The cement was thick, especially buccally.

The specimen resembles specimens of *E. oldowayensis* from Olduvai Gorge with which it can be matched. It also resembles modern *E. grevyi*. It is assigned to *E. oldowayensis* on its morphology and because of its stratigraphic age.

General discussion and conclusions

No description of the *Equus* from the upper levels of the Shungura Formation exists in the literature. Only the mentions of *Equus* by Hooijer (1973, 1976) and Coppens (1978), of *Equus oldowayensis* by Cooke (1963) or *Equus* (*Dolichohippus*) *oldowayensis* by Churcher & Richardson (1978) provide probable taxonomic identifications.

The materials from the Shungura Members G to L and from the Kalam Outcrop of comparable age are all assignable to *Equus oldowayensis*, are comparable to specimens of that species from Olduvai Gorge, mainly from Bed II, with which they have been compared, and no individual specimens have been examined that suggest another species of *Equus*, whether zebra, horse or ass.

Table 1 gives measurements of the better preserved dental elements for possible comparisons with measurements of teeth of other equids and to record the observed ranges of size. The patterns of the enamel on the occlusal surfaces of the cheekteeth, illustrated in plates 1 to 5, show similar variations to those seen in teeth of *E. oldowayensis* from Olduvai Gorge. The patterns and dimensions are similar to those examined by Churcher (unpublished) from Olduvai Gorge.

Table 2 records dimensions of the few postcranial elements available. The metapodial dimensions fall within or close to those observed for *E. oldowayensis* from Olduvai Gorge measured by Churcher.

The later members of the Shungura Formation (Members G to L) are probably equivalent in age to the deposits of the Koobi Fora Formation above the Tulu Bor Tuff (Brown, Howell & Eck, 1978). The age is from about 1.93 to 1.34 My ago, and extends from the time of the middle or last Reunion Event in the Matuyama Reversed Epoch possibly to as late as the Jaramillo Event. *E. oldowayensis* existed throughout this time at its type locality in Tanzania, while the deposits of the Olduvai Gorge sequence were being deposited, from about 1.8 My ago. The Shungura record from Members G to L corresponds to the earlier part of the Olduvai Gorge record. It is reassuring, therefore, to find that the Shungura Members G to L yield the same equids, *Equus oldowayensis* and *Hipparion libycum*, as are common in the Olduvai deposits. Teeth probably derived from *E. burchellii* have been recognised by Churcher (unpublished) among the extensive sample of *Equus* from Olduvai Gorge, and its scarcity in the Olduvai deposits and thus probably in the coeval faunas during the Early and Middle Pleistocene may be the reason for its absence in the relatively small samples available from the Shungura Formation.

The earliest record of *E. oldowayensis* in the Shungura Formation is from Member G, approximately 1.9 My ago. The specimens were recovered from levels G1-13, and in the upper levels G27 & 28, but not from the levels G14-20, which represent a lake sequence. Churcher & Richardson (1968: 416-417) suggest that *E. oldowayensis* may have descended from *E. numidicus*. The stratigraphic records of *E. numidicus* are from the Late Pliocene of Algeria, and possibly the Sudan and Uganda, or Early Pleistocene of Algeria. *E. oldowayensis* is recorded from the Early Pleistocene

at Omo, Ethiopia, Olduvai Gorge, Tanzania, and Malawi, with the related species *E. capensis* recorded from the Late Pliocene at Langebaanweg, Cape Province, and from Makapansgat and later sites in the Transvaal, South Africa (Churcher & Richardson, 1978: 414-415, fig. 20.7). Thus there appears to be no time stratigraphic progression that records the north to south colonisation of Africa by this lineage of zebras.

Acknowledgements

We wish to thank Dr. F. Clark Howell and the members of the American Expedition to the Omo River Valley, Ethiopia, for collecting these equid specimens during 1967 to 1974, and Dr. Howell for allowing us to study them at our leisure. Churcher thanks Dr. W. Vervoort, Director, and the staff of the Rijksmuseum van Natuurlijke Historie for the courtesy and facilities made available to him during his vist to Leiden in May and June, 1979, when most of this report was compiled. Churcher's work and travel was supported by National Research Council of Canada Grant A 1704.

We wish to thank Dr. T. S. Parsons of the Department of Zoology, University of Toronto, for critically reading the draft version of the report. We thank Mr. John Glover of the Faculty of Arts and Science, University of Toronto, Photographic Facility, for printing the photographs included and from which the line diagrams were made.

References

Brown, F. H., F. C. Howell & G. G. Eck, 1978. Observations on problems of correlation of late Cenozoic hominid-bearing formations in the North Lake Turkana Basin. In: Bishop, W. W. (editor), Geological Background to Fossil Man. Recent Researches in the Gregory Rift Valley, East Africa: 473-498. Published for the Geological Society of London by Scottish Academic Press / University of Toronto Press.

Churcher, C. S. & M. L. Richardson, 1978. Equidae. Chapter 20 in: Maglio, V. J. & H. B. S. Cooke (editors), Evolution of African Mammals: 379-422. Harvard University Press, Cambridge, Mass.

Cooke, H. B. S., 1963. Pleistocene mammal faunas of Africa with particular reference to Southern Africa. In: Howell, F. C. & F. Boulière (editors), African Ecology and Human Evolution: 65-116. Aldine Publishing Company Chicago.

Coppens, Y., 1978. Evolution of the hominids and of their environment during the Plio-Pleistocene in the lower Omo Valley, Ethiopia: In: Bishop, W. W. (editor), Geological Background to Fossil Man. Recent Researches in the Gregory Rift Valley, East Africa: 499-506. Published for the Geological Society of London by Scottish Academic Press / University of Toronto Press.

Hooijer, D. A., 1973. Stratigraphy, paleoecology and evolution in the Lake Rudolf Basin. Mimeographed paper presented at the Wenner-Gren Foundation for Anthropological Research, New York, Sept. 8-20, 1973: 1-5.

——, 1976. Evolution of the Perissodactyla of the Omo Group deposits. Part 17 in: Coppens, Y. & F. C. Howell (editors), Earliest Man and Environments in the Lake Rudolf Basin: 209-213. University of Chicago Press, Chicago/London.

Hopwood, A. T., 1937. Die fossilen Pferde von Oldoway. — Wiss. Erg. Oldoway-Exp. 1913, (n.s.) 4: 112-136.

EXPLANATION OF THE PLATES

PL. 1

Equus oldowayensis. Occlusal aspects of upper cheekteeth from Shungura Formation Member G. Scale in cm. Figs. 1-6, no. L.490-4 (a-d), cheekteeth from one individual from Member G 5. Figs. 1-4, right side and figs. 5-6, left side of palate: fig. 1, no. L.490-4b, P^2 dext.; fig. 2, no. L.490-4e, P^3 dext.; fig. 3, no. L.490-4d, P^4 dext.; fig. 4, no. L.490-4f, M^3 dext.; fig. 5, no. L.490-4c, P^4 sin.; fig. 6, no. L.490-4g, partial M^3 sin. Fig. 7, no. L.67-129, P^2 sin., Member G 7. Fig. 8, no. L.740-25, M^2 sin., Member G. Fig. 9, no. L.513-13, P^3 or P^4 dext., Member G 27. Fig. 10, no. L.627-95, M^1 dext., Member G 13.

PL. 2

Equus oldowayensis. Occlusal aspects of lower cheekteeth from Shungura Formation Members G and H, and isolated teeth from the Kalam Outcrop. Scale in cm. Fig. 1, no. L.508-1a, P_2-M_2 sin., Member G 9. Fig. 2, no. L.48-21, M_1 sin., Member G 13. Fig. 3, no. L.627-366, M_3 dext., Member G 13. Fig. 4, no. L.626-87, M_1 sin., Member G 12. Fig. 5, no. L.627-211, partial M_3 dext., Member G 13. Fig. 6, no. F.161-56, damaged M_2 sin., Member H 4. Fig. 7, no. P.1000-21, partial M^1 dext., Kalam Outcrop. Fig. 8, no. P.1000-5, M_2 dext., Kalam Outcrop.

PL. 3

Equus oldowayensis. Occlusal aspects of upper cheekteeth from Shungura Formation Member K. Scale in cm. Figs. 1-6, damaged cheekteeth from one individual from Member K 4. Figs. 1-3, P^2-P^4 dext., figs. 4-6, P^2-P^4 sin.: fig. 1, no. F.17-7, P^2 dext.; fig. 2, no. F.17-10, P^3 dext.; fig. 3, no. F.17-14, P^4 dext.; fig. 4, no. F.17-9, P^2 sin.; fig. 5, no. F.17-6, P^3 sin.; fig. 6, no. F.17-8, P^4 sin. Fig. 7, no. F.17-5, damaged M^2 dext., Member K 4. Fig. 8, no. P.996-26, partial M^3 dext., Member K. Fig. 9, no. P.996-23, fragmentary P^3 dext., Member K.

PL. 4

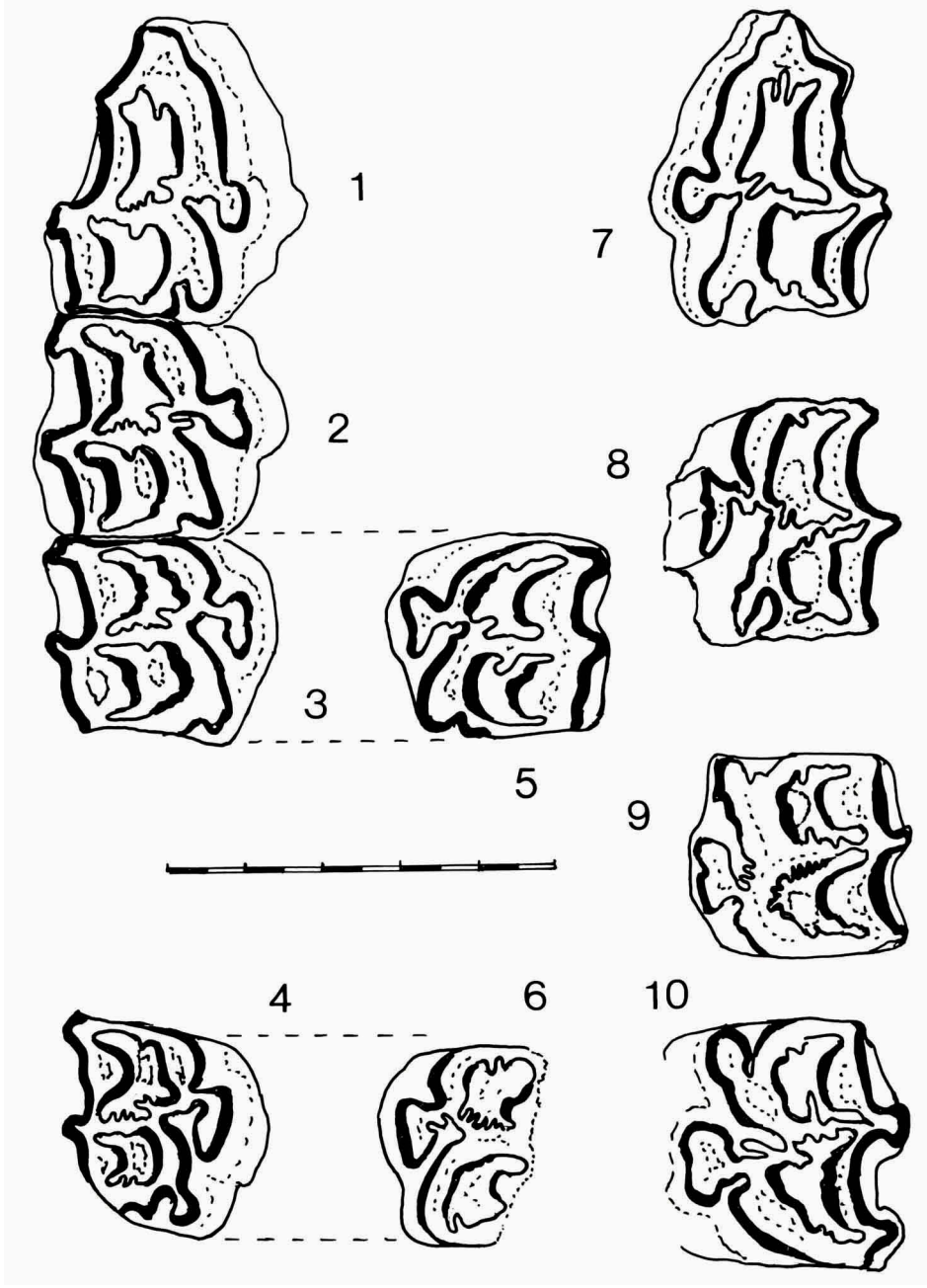
Equus oldowayensis. Occlusal aspects of upper and lower cheekteeth from Shungura Formation Members J and K and from the Kalam Outcrop. Scale in cm. Fig. 1, no. F.23-1, partial M^3 sin., Member J. Fig. 2, no. F.23-3, P^2 dext., Member J 3. Fig. 3, no. P.994-5, damaged M_2 dext., Member J 6. Fig. 4, no. P.996-39, M_1 dext., Member K. Fig. 5, no. P.996-7, M_1 dext., Member K. Fig. 6, no. P.1000-6 (a-c), P_2 sin. (d), P_3 sin. (a), P_4 sin. (b), M_1 sin. (c), Kalam Outcrop.

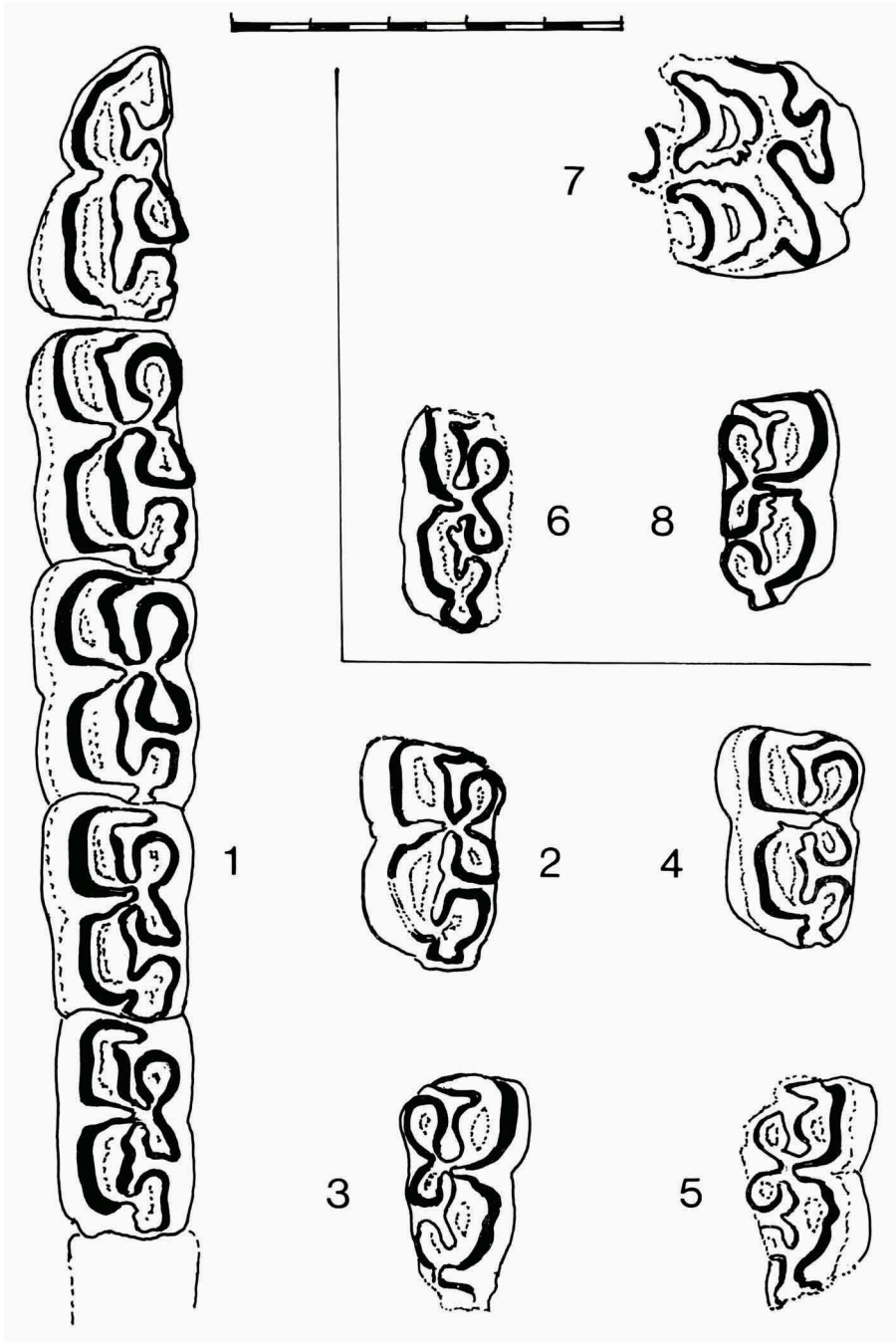
PL. 5

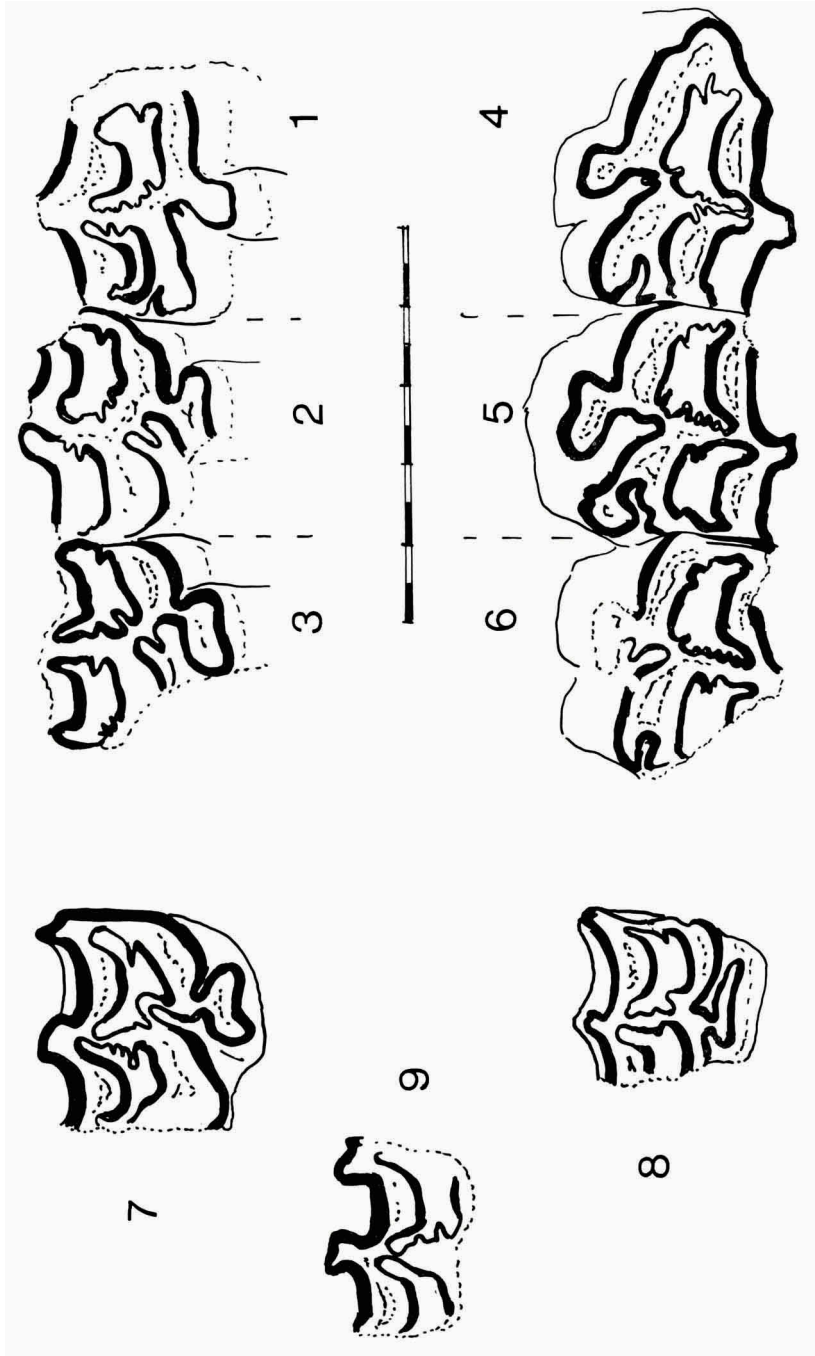
Equus oldowayensis from the Shungura Formation Members G and L, and unlocated. Scales in cm. Figs. 1-2, OMO 1967 (57), fragment of right dentary with P_2, P_3, and mesial half of P_4, no horizon or locality: fig. 1, occlusal pattern; fig. 2, buccal aspect. Fig. 3, no. F.513-34, distal end of metacarpal III dext., posterior aspect, Member G 27. Fig. 4, no. F.410-5, distal end of metacarpal III sin., posterior aspect, Member L 2-3. Fig. 5, no. F.356-4, partial ungual phalanx III, anterior aspect, Member L.

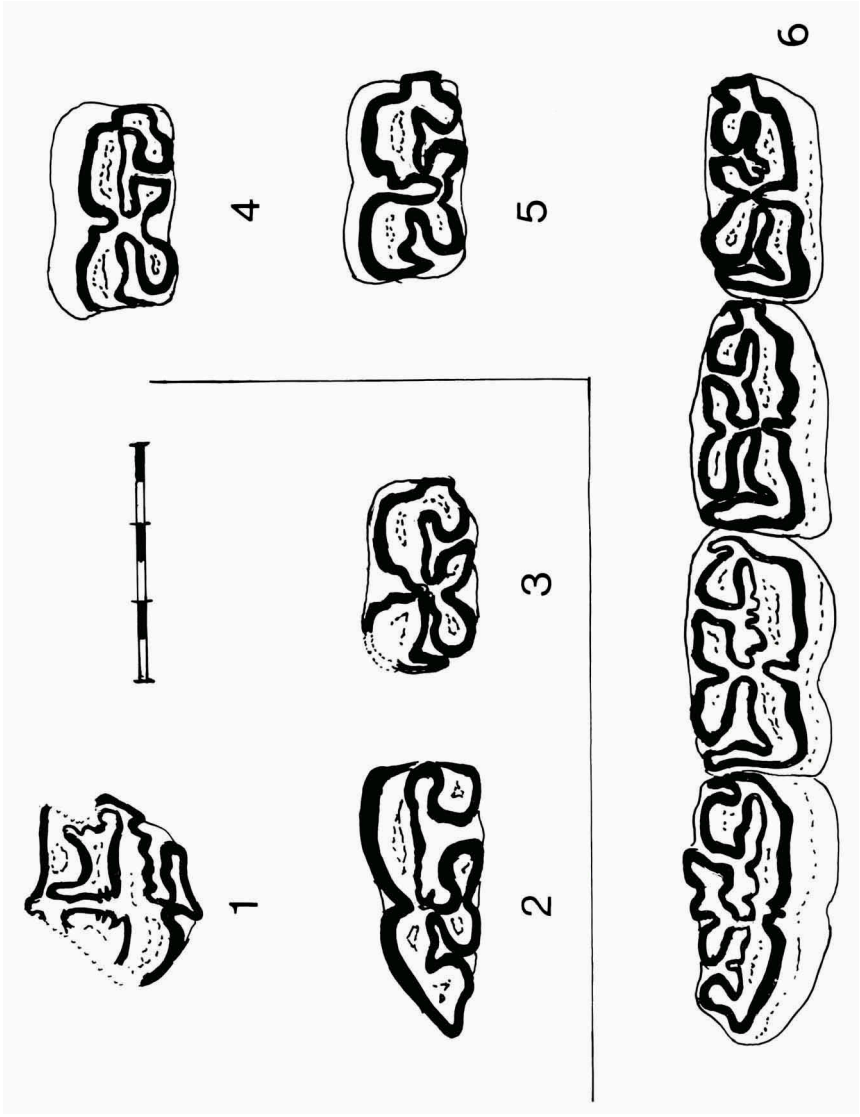
PL. 6

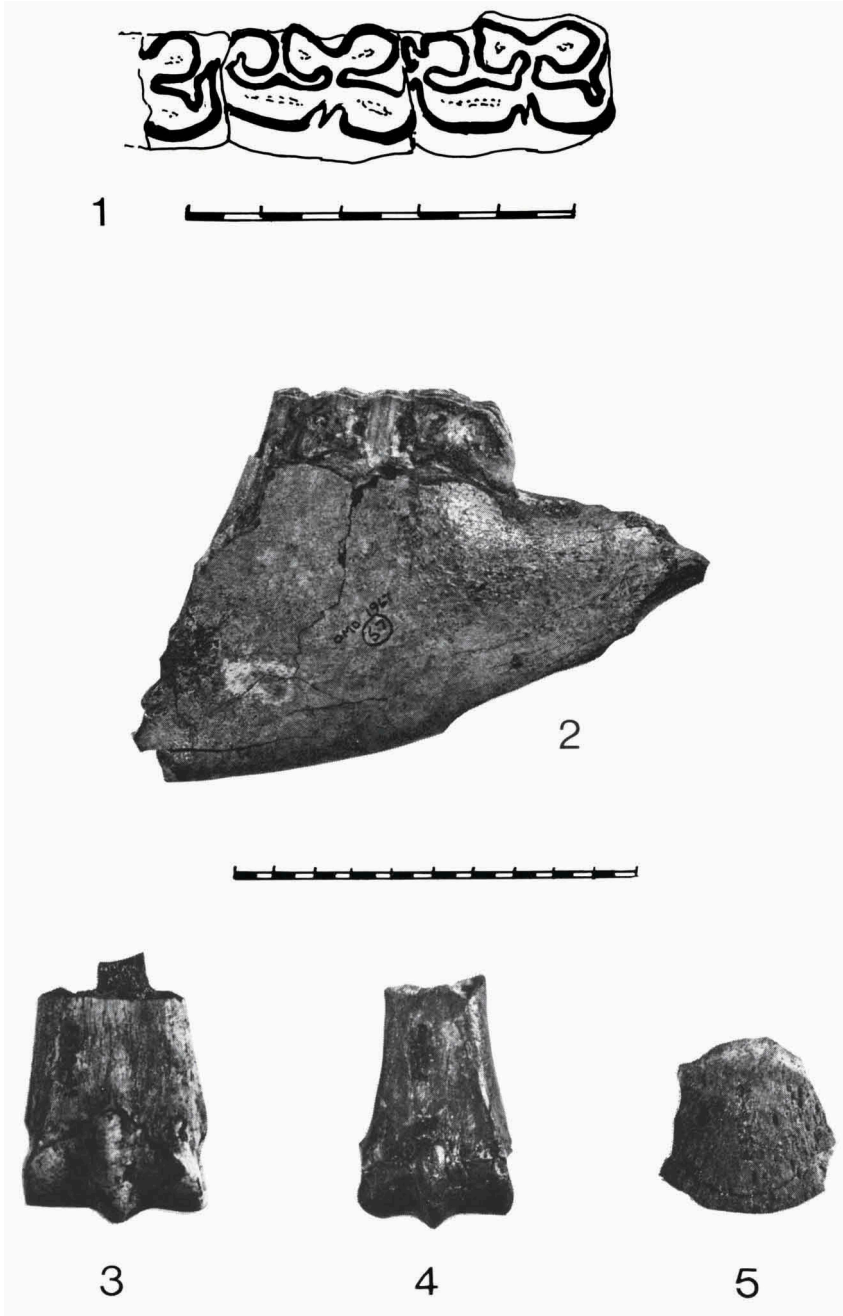
Equus oldowayensis. Metapodials from the Shungura Formation Member G. Scale in cm. Figs. 1-3, no. L.7-3, metacarpal III sin.: fig. 1, anterior aspect; fig. 2, lateral aspect; fig. 3, posterior aspect, Member G 5. Figs. 4-6, no. L.7-4, damaged metatarsal III dext.: fig. 4, anterior aspect; fig. 5. medial aspect; fig. 6, posterior aspect, Member G 5. Note concavity of posterodistal areas and lack of median ridges proximal to distal articulation.

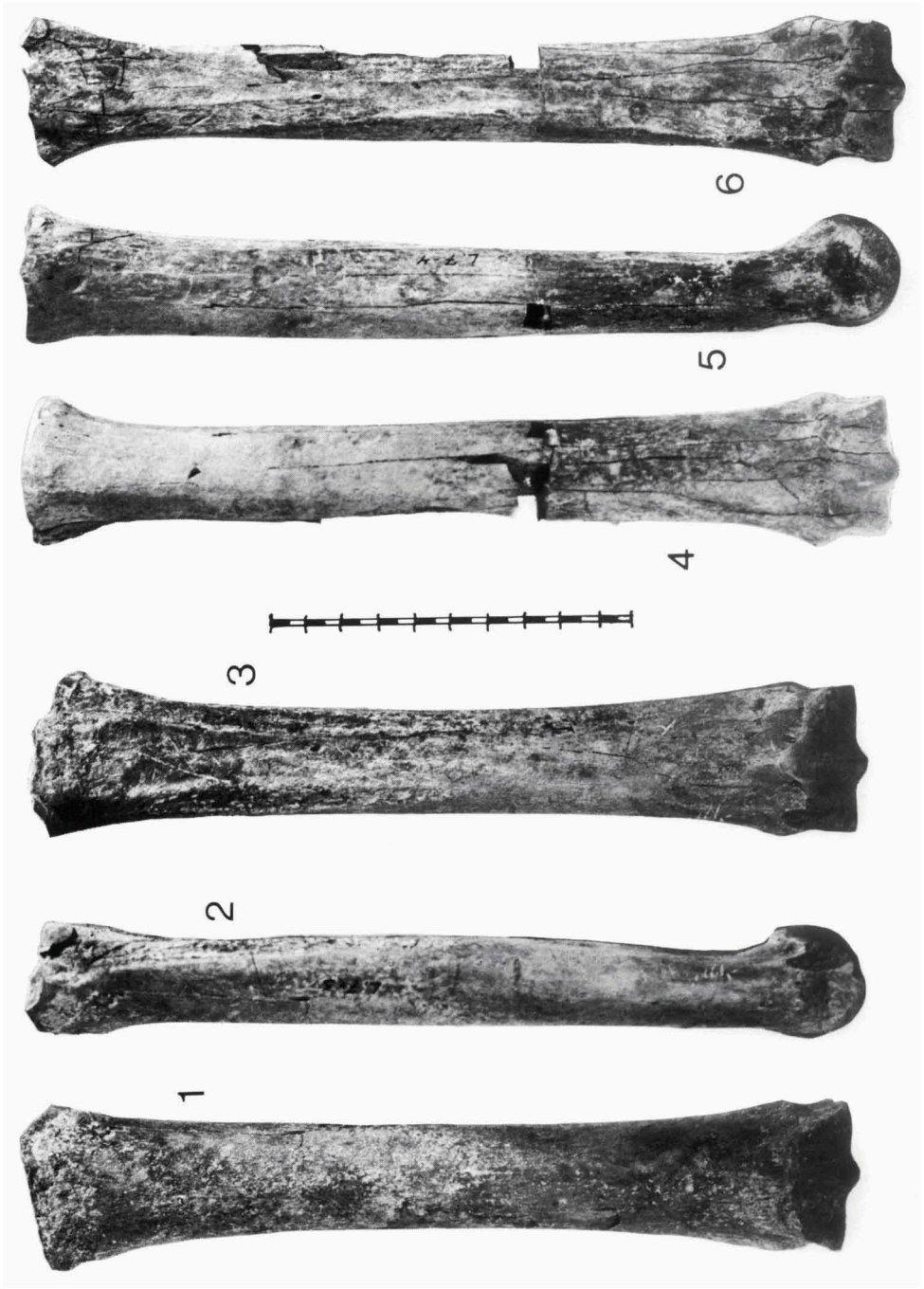

1
2
3
4
5
6
7
8
9
10


1
2
3
4
5
6
7
8


1
2
3
4
5
6
7
8
9


1
2
3
4
5
6


1
2
3
4
5


6
5
4
3
2
1