

Taxonomic review of fossil Proboscidea (Mammalia) from Langebaanweg, South Africa

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Comparative morphological and metric study of proboscidean dental fossils from the Quartzose (QSM) and Pelletal Phosphate (PPM) Members of the Varswater Formation at Langebaanweg, South Africa, identifies the presence in the fauna of an anancine gomphothere and two species of elephant. The gomphothere, from the QSM and PPM, displays a unique combination of primitive and derived molar features, and consequently is placed in a new species (*Anancus capensis* sp. nov.) that is regionally distinct from other African species of *Anancus*. A new species of loxodont elephant (*Loxodonta cookei* sp. nov.) is identified from the PPM, distinguished from penecontemporaneous *L. adaurora* by having anterior and posterior accessory central conules that contribute to the formation of strong median sinuses throughout its molar crowns. It is further differentiated from other loxodont elephants by its primitive retention of permanent premolars, lower crown height, fewer molar plates, thicker enamel, and lower lamellar frequency, and extends the *L. exoptata*-*L. africana* lineage back into the late Miocene. A second elephant species, from the QSM, is referable to *Mammuthus subplanifrons*, and represents the most archaic stage of mammoth evolution. The elephants appear to have been more cosmopolitan in distribution than the gomphothere. Together, these taxa support a latest Miocene–early Pliocene age of ca. 5.0 Ma for the Varswater Formation. Based on isotopic analyses of congeners from other African sites, it may be inferred from the occurrence of these taxa that open conditions were present locally and abundant grazing resources were available in the ecosystems of Langebaanweg during the time of deposition of the QSM and PPM.

INTRODUCTION

The Quartzose (QSM) and Pelletal Phosphate (PPM) Members of the Varswater Formation, exposed in the 'E' Quarry at Langebaanweg, Western Cape Province, South Africa (Figure 1), have yielded a rich collection of invertebrates and vertebrates estimated to be latest Miocene–early Pliocene in age (Hendey, 1981, 1982). The Langebaanweg fauna is the best documentation of animal life in southern Africa from this interval, and its vertebrate sample is comprised of a unique amalgam of amphibians, birds, reptiles, and mammals, notably including penguins, bears, sabre-toothed cats, seals, peccaries, and cetaceans (see Hendey, 1981: 45–53). Among the mammals from the site are abundant proboscidean fossils from both the QSM and PPM, assignable to three species. Despite the utility of fossil proboscideans for biochronological correlation (e.g., Cooke & Maglio, 1972; Maglio, 1970a, 1973; Beden, 1980) and palaeoecological reconstruction (e.g., Cerling *et al.*, 1999, 2003; Zazzo *et al.*, 2000; Harris *et al.*, 2003; Schoeninger *et al.*, 2003; Kingston & Harrison, 2007), the Langebaanweg proboscidean assemblage has not previously been properly classified or assessed morphologically. One of the proboscidean taxa, from the QSM, was originally misidentified as a stegolophodont (Singer & Hooijer, 1958), but later was correctly recognised as an elephant and placed in *Mammuthus subplanifrons* (Maglio & Hendey, 1970). Although a second taxon, from the QSM and PPM, was established to be a gomphothere (Hendey, 1970, 1976), and was later identified to the genus *Anancus* (Coppens *et al.*, 1978), it has not been formally described and no further taxonomic refinement has been attempted. The third taxon, a loxodont elephant from the PPM, also has not been described, and appears to have been inappropriately lumped into *M. subplanifrons* (Hendey, 1981: 51). The present investigation of the Langebaanweg proboscidean assemblage was under-

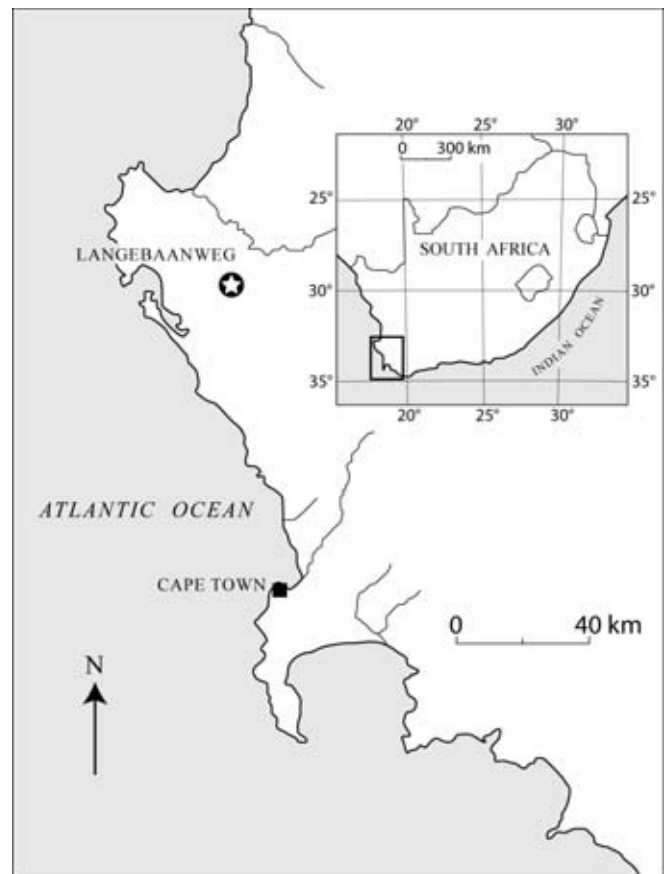


Figure 1. Map showing the position of Langebaanweg in the Western Cape Province, South Africa (modified from Klein *et al.*, 2007: figure 1).

taken in part to address these discrepancies, focusing on comparative dental anatomy and taxonomy.

The latest Miocene–early Pliocene interval represented at Langebaanweg by the deposits of the Varswater Formation was a time of dynamic transformation of African ecosystems (Franz-Odenaal *et al.*, 2003) and for African proboscideans (Maglio, 1973; Beden, 1985; Todd & Roth, 1996; Sanders, 2004). Just prior to this period, mammutids and gomphotheres went into precipitous decline, leaving anancine gomphotheres as remnants of a once highly speciose Miocene radiation (Todd, 2006). Their arrival in Africa was simultaneous with the emergence of the first elephants (Todd & Roth, 1996; Shoshani & Tassy, 1996), apparently linked ecologically and adaptively with increased distribution of grasses on the continent (Cerling *et al.*, 1993). Among the earliest elephants were the archaic forms *Stegotetrabelodon*, *Primelephas*, and *Stegodibelodon* (Coppens *et al.*, 1978), coincident or nearly contemporaneous with the first appearances of the crown elephant genera *Loxodonta*, *Mammuthus*, and *Elephas* (Beden, 1980, 1985; Tassy, 1986, 1995, 2003; Kalb & Mebrate, 1993; Brunet *et al.*, 2000; Sanders, 2004). By the late Pliocene, the archaic forms had disappeared, and the crown genera had undergone episodes of evolutionary change, evidenced by parallel acquisition of enhanced craniodental specialisations for grazing (Maglio, 1972, 1973). Unfortunately, in part because of the strong degree of homoplasy in craniodental adaptations among elephants, latest Miocene–early Pliocene phylogenetic relationships among the basal members of crown elephant genera, and links between them and their modern–near modern congeners remain poorly documented and less well understood (Thomas *et al.*, 2000; Sanders, 2004). African anancine gomphotheres also continued to evolve during the Pliocene, exhibiting increasingly complicated molar occlusal platforms (Mebrate & Kalb, 1985; Kalb & Mebrate, 1993; Sanders *et al.*, in prep.) until their disappearance from the continent at the close of the epoch (perhaps ultimately in failed competition with other grazers, including elephants, for the same resources; see Cerling *et al.*, 1999, 2003; Zazzo *et al.*, 2000; Harris *et al.*, 2003; Semaw *et al.*, 2005). The extent and geographic patterning of their diversity and morphological transformation during this latest Miocene–early Pliocene phase, however, have never been comprehensively delineated.

From a region otherwise unknown for this interval, the proboscidean assemblage from the Varswater Formation at Langebaanweg has proven to be critically important for the consideration of these issues. Although the phylogenetic systematics of early elephants and African anancine gomphotheres requires broader analysis than is possible here, comparative study of the Langebaanweg proboscideans has: (1) provided more precise identification of the constituent taxa from the site; (2) helped establish the evolutionary position of these taxa within their lineages and to link basal and Recent members of lineages phylogenetically; and (3) contributed new information for biochronological correlation and palaeoecological reconstruction of the Varswater Formation. These results confirm earlier estimates of an age *ca.* 5.0 Ma for the Varswater Formation; suggest that little time passed between the deposition of the QSM and PPM; indicate the availability of substantial grazing resources in both members; show strong regionalism in the evolution of African anancine gomphotheres; and extend the apparent phylogenetic connection between Recent and fossil mammoths and loxodont elephants back into the late Miocene.

Abbreviations. ET, enamel thickness; H, height; HI, hypsodonty index (crown height \times 100/width); I, upper incisor;

L, length; l, left; LF, lamellar frequency, number of plates per 100 mm; M or m, molar (for example, M1 is the first upper molar and m1 is the first lower molar); Ma, Mega annum (10⁶ years); mm, millimetres; P or p, premolar (for example, P3 is the third upper premolar and p3 is the third lower premolar); r., right; W, width; x, denotes an anterior or posterior cingulum(id) not constituting a full loph(id) or plate; +, indicates a missing portion of a tooth, and that the original dimension was greater.

Definitions. Accessory central conules, enamel-covered pillars situated at the anterior and/or posterior faces of the loph(id)s or plates, or in the transverse valleys, partially blocking them centrally (Tobien, 1973a); anancoidy, antero-posterior alternation of paired half-loph(id)s, in which the lingual half-loph(id)s are anterior to buccal half-loph(id)s (Tobien, 1973a); posttrite, refers to the less worn half of each loph(id), which is lingual in lower and buccal in upper molars (Vacek, 1877); pretrite, refers to the more worn half of each loph(id), which is buccal in lower and lingual in upper molars (Vacek, 1877).

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Order PROBOSCIDEA Illiger, 1811

Suborder ELEPHANTIFORMES Tassy, 1988

Superfamily ELEPHANTOIDEA Gray, 1821

Family GOMPHOTHERIIDAE Hay, 1922

Subfamily ANANCINAE Hay, 1922

Genus ANANCUS Aymard, 1855

***Anancus capensis* sp. nov.**, Figures 2–3

Gomphotheriidae *incertae sedis* Hendey, 1970: 125.

Gomphotheriidae gen. et sp. indet. Hendey, 1976: 236.

Anancus sp. Coppens *et al.*, 1978: 346, 348.

Anancus sp. Hendey, 1981: 51.

cf. *Anancus* sp. Mol, 2006: 190.

Anancus sp. nov. Sanders, 2006: 196.

Holotype

South African Museum, Cape Town, South Africa, SAM-PQ-L 41692, associated l. M1 and M3, r. M2 and M3 (Figure 2A–E; Table 1).

Paratypes. SAM-PQ-L 2550, r. m3 frag; -PQ-L 2551, l. M3 frag; -PQ-L 2554, partial ?M3; -PQ-L 2555, r. M2 frag; -PQ-L 2556, r. M3 frag; -PQ-L 2559, r. m3 frag (same individual as -L 2556); -PQ-L 2560, r. m3 frag; -PQ-L 2561, l. M3 frag; -PQ-L 6042, r. M2 frag; -PQ-L 22079A, B, r. and l. partial M3 (Figure 3B); -PQ-L 31390, l. m3 frag; -PQ-L 40007, l. M3; -PQ-L 40012, r. M1 (Figure 3A); -PQ-L 40014, r. ?M3; -PQ-L 40115, r. M3 frag; -PQ-L 40116, r. m3 frag; -PQ-L 40117, r. M3 frag; -PQ-L 40983, l. m3 frag; -PQ-L 41018, l. m2; -PQ-L 43038, l. dp4 or m1 frag; -PQ-L 55000, r. M2 frag and M3; -PQ-L 69080, l. M3 (Table 1).

Type locality

E' Quarry, Langebaanweg, South Africa (Hendey, 1981).

Age and occurrence

Latest Miocene–early Pliocene, southern Africa (known only from the type site).

Diagnosis

Contrasted with *Anancus petrocchii* and the advanced form of *A. kenyensis* by its tetralophodont intermediate molars. More advanced than the primitive form of *A. kenyensis* and *A. osiris* in

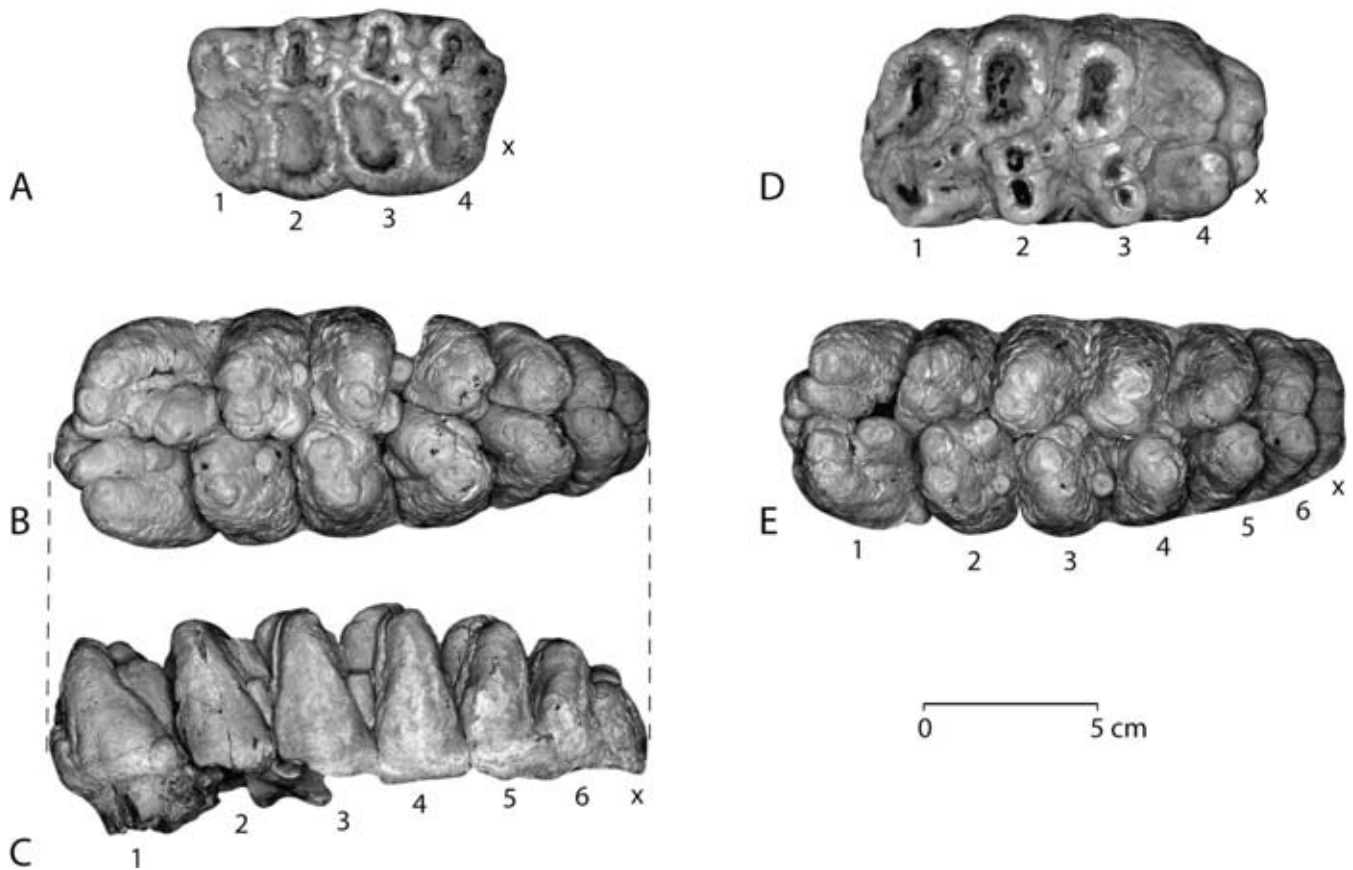


Figure 2. Type specimen of *Anancus capensis* sp. nov., SAM-PQ-L 41692. Anterior is to the left. **A**, Occlusal view, l. M1. **B**, Occlusal view, l. M3. **C**, Lingual view, l. M3. **D**, Occlusal view, r. M2. **E**, Occlusal view, r. M3.

having more complex molars, with greater folding of enamel, an incipient seventh loph in M3, more pronounced anancoidy, and posttrite posterior accessory conules occurring nearly throughout the crown in M3.

Etymology

Capensis is a geographic name derived from the occurrence of the type locality in the southern Cape region of Africa.

Description

Although the Langebaanweg material has been recognised for some time as representative of a new *Anancus* species (Coppens *et al.*, 1978; Hendey, 1981), this is its first formal description. Cementum coats sides of molar loph(id)s and may fill transverse valley floors. Intermediate molars have four loph(id)s (Figs 2A,D and 3A), half-loph(id)s each consist of two conelets, and posttrite posterior accessory conules are present to the third or fourth loph(id). Pretrite posterior accessory conules vary in development, and may occur in association with loph(id)s 1–3. Enamel is thick (about 4.5 mm in M1, 5.0–6.0 mm in M2) and enamel rims of occlusal wear figures are undulated to well folded. Third molars are low-crowned ($H = 57\text{--}58\text{ mm}$) with thick enamel (4.5–6.0 mm), and have pre- and posttrite posterior accessory conules well distributed throughout the crown, occasionally accompanied by multiple additional accessory conules (Figures 2B,C,E and 3B). Third molars also have low lamellar frequencies ($LF = 3.5\text{--}4.0$), and their postcingulae(id)s are formed of three to six conelets.

In the type specimen, the intermediate molars are tetralophodont (Figure 2A,D) and have thick, coarsely undulating enamel. The third molars of the type (Figure 2B,C,E) each have six lochs and a prominent distocingulum (or incipient

seventh loph), are modest in size, and are brachyodont (Table 1). Accessory central conules in these molars are associated on the pre- and posttrite sides with lochs 1–4, and each half-loph is formed of two conelets. Anancoidy is conspicuous in the third molars of this specimen (Figure 2B,E).

Remarks

Anancine gomphotheres (*Anancus* spp.) originated in Eurasia, probably deriving from *Tetralophodon*, and were widely distributed throughout the Old World during the late Miocene–early Pleistocene (Tobien, 1973b; Coppens *et al.*, 1978; Mebrate & Kalb, 1985; Tassy, 1985, 1986, 1996; Tobien *et al.*, 1988; Metz-Muller, 1995; Kalb *et al.*, 1996a; Shoshani, 1996; Göhlich, 1999). They immigrated into Africa near the end of the Miocene, coincident with the first appearance there of elephants (Tassy, 1986), and persisted on the continent well into the late Pliocene, though they are absent from the East African fossil record after the mid-Pliocene (Tassy, 1986; Kalb *et al.*, 1996b).

Anancus is characterised by straight upper tusks lacking enamel, brevirostrine mandibles with no lower tusks, tetralophodont-pentalophodont intermediate molars (DP4-M2), and especially anancoidy of pre- and posttrite half-loph(id)s (Petrocchi, 1954; Coppens, 1967; Coppens *et al.*, 1978; Mebrate & Kalb, 1985; Tassy, 1985, 1986; Kalb & Mebrate, 1993). Although their skulls are absent from the site, a series of well preserved molars exhibiting the distinctive anancoid pattern is sufficient to confirm the occurrence of *Anancus* at Langebaanweg, from the Quartzose and Pelletal Phosphate Members of the Varswater Formation (Hendey, 1976, 1981).

Other than this rare southern African occurrence of anancine gomphotheres, the subfamily is far better represented regionally

Table 1. Dimensions and indices of proboscidean dental specimens from Langebaanweg, South Africa and conspecifics from other African sites. Linear dimensions in mm. Abbreviations: ET, enamel thickness; H, height; HI, hypsodonty index ($H \times 100/W$); L, length; LF, lamellar frequency (average number of plates per 100 mm); W, width; +, indicates missing portion of tooth; x, indicates presence of anterior or posterior cingulum(id). Numbers in parentheses refer to the plate on which a measurement was taken. Supplemental data are from Meiring (1955), Cooke & Coryndon (1970), Maglio & Hendeby (1970), Tassy (1986, 1995), Vanoverstraeten *et al.* (1990), Kalb & Mebrate (1993), Haile-Selassie (2001) and Sanders (2005).

Taxon/Accession number	Element	No. plates/loph(id)s	LF	L	W	H	HI	ET
<i>Anancus capensis</i> sp. nov.								
Langebaanweg, South Africa								
SAM-PQ-L 40012	r. M1	x4x	4.5	90.6	62.0 (2)	worn	—	4.0–4.7
PQ-L 41692 (type)	l. M1	4x	—	93.8	57.5	worn	—	3.7–5.6
	r. M2	x4x	4.0	117.8	65.0	worn	—	5.2–5.5
	r. M3	x6x	4.0	175.0	71.6 (3)	58 (1)	81	—
	l. M3	x6x	4.0	170.0	70.5 (2)	58 (1)	82	—
PQ-L 2561	l. M3	x4+	3.5	151.8+	89.0 (2)	57.0	64	5.0
PQ-L 22079A	r. M3	6x	3.5	205.0	87.5 (4)	worn	—	6.0
PQ-L 22079B	l. M3	+4x	3.5	+147.0	89.0 (4)	worn	—	6.0
PQ-L 40007	l. M3	6x	4.0	175.0	83.3 (2)	worn	—	4.8–5.7
PQ-L 40014	r. ?M3	7x	4.0	175.0	82.1 (3)	worn	—	4.6–5.0
PQ-L 55000	l. M3	x6x or x7	4.0	190.0	77.8 (3)	58.0	75	—
PQ-L 69080	l. ?M3	+5x	4.0	+146.5	82.4 (3)	worn	—	5.2–6.0
PQ-L 41018	l. m2	x4x	4.0	125.1	66.0 (4)	worn	—	6.0–6.8
<i>Loxodonta cookei</i> sp. nov.								
Langebaanweg, South Africa								
PQ-L 45789	l. DP3	x4 or 5	—	55.4	40.5	worn	—	1.4–1.6
PQ-L 46541	l. DP4	x5x or x6	—	101.7	53.5 (4)	37.5	70	1.8
PQ-L 45616	r. P3	3x	—	57.3	53.6 (1)	worn	—	2.3–2.9
	r. P4	x4	—	69.3	52.0 (1)	worn	—	2.6–3.0
	r. M1	x6	4.0	142.0	79.0 (2)	worn	—	2.8–3.4
PQ-L 50434	?r. P3	3x or 4	—	42.8	37.7 (2)	worn	—	1.6–1.8
PQ-L 69072	?l. P3	x3x	—	52.6	50.0 (2)	worn	—	1.8
PQ-L 45617	l. M1	5x or 6	4.0	141.8	77.7 (2)	worn	—	3.1–3.4
PQ-L 45618	l. M2	x6x	4.0	195.0	93.5 (4)	96	103	—
PQ-L 45619	l. M2	x6x	4.0	205.0	93.8 (4)	85.0 (4)	91	—
PQ-L 45627 (type)	r. M2	x6x	4.0	202.0	92.0 (4)	83.0 (4)	90	—
PQ-L 69077	l. M2	x6x	5.0	155.0	75.0 (3)	worn	—	3.0
PQ-L 69069	dp2	3x	—	26.3	17.4	20.0	—	—
PQ-L 69070	?l. dp2	x3	—	26.0	15.5	worn	—	v. thin
PQ-L 46996	l. dp3	x4x or 5x	—	61.8	38.2 (3)	worn	—	1.2
	l. dp4	x6x	—	100.7	52.2 (4)	—	—	2.1
	r. dp4	x6x	—	101.7	52.0 (4)	43.0 (3)	83	2.1
PQ-L 69075	r. dp3	x4x	—	62.2	38.8 (3)	worn	—	1.4–1.6
PQ-L 46259	r. dp4	x4+	—	+75.0+	+51.8	37.3+	—	1.5–2.0
PQ-L 69067	?l. p3	x3x	—	57.1	38.1 (2)	35.0	—	—
PQ-L 69071	?r. p3	x4x	—	54.7	39.5 (4)	25.0+	—	2.0
PQ-L 45608	l. p4	x4x	—	66.0	47.4	worn	—	2.5–3.0
PQ-L 45782	?l. ?p4	x4x	—	66.5	45.3 (1)	worn	—	3.2–3.7
PQ-L 50864	?r. ?p4	x4x	—	63.9	44.0 (1)	worn	—	2.4–3.3
PQ-L 45611	l. m1	+5x	4.0	+133.7	76.4 (4)	worn	—	3.4–4.1
PQ-L 45613	r. ?m1	+4x	4.0	+107.5	75.0 (4)	worn	—	3.3–3.6
PQ-L 50433	r. m1	+3x	—	+77.0	+70.0	worn	—	3.3–3.6
PQ-L 50865	r. ?m1	+5x	4.0	+110.3	72.5	worn	—	2.6–3.4
PQ-L 46561 + 50863 + 46220	l. m2	x7x	4.0	210.0	81.2 (5)	83.0 (5)	102	—
PQ-L 50862	r. m2	x7x	4.0	210.0	81.2 (5)	83.0 (5)	102	thick
PQ-L 42224	l. m3	x8x	3.5	290.0	93.5 (2)	76.0	81	—
PQ-L 45784	molar plate	—	—	—	81.7	61.3	75	—
PQ-L 45785	molar plate	—	—	—	84.3	—	—	—
PQ-L 45766A	m2 or m3 fragment	+3+	—	+103.2+	84.4	71.0	84	5.0–5.1
PQ-L 45788A	l. m3	x8x	4.0	260.0	92.0 (6)	worn	—	4.9–6.2
PQ-L 45788B	r. m3	x8x	4.0	270.0	91.4 (6)	worn	—	4.9–6.2

Continued on p. 5

Table 1 (continued)

Taxon/Accession number	Element	No. plates/loph-(id)s	LF	L	W	H	HI	ET
PQ-L 49736	l. m3	+5x	3.5	+160.0	+90.0	75.5	—	5.0
Tugen Hills, Kenya								
KNM-BC 1761	l. M1	+6x	4.3	+140.0	66.8 (3)	worn	—	3.0–3.5
KNM-BC 32	r. M3 fragment	x4+	4.0	106.2+	93.2 (4)	—	—	3.3
KNM-BC 189	r. M3	x7x	4.0	235.0	92.2 (4)	worn	—	4.0
KNM-BC 917	l. M3 fragment	x4+	4.0	110.0+	98.9 (4)	80.0 (4)	81	4.0–5.2
KNM-LU 67	r. m3	x8x	4.0	217.8	85.0	worn	—	3.8
Endolele, Tanzania								
L5/BK(E) 35	third molar fragment	+4+	4.0	+137.5+	93.6	79.0	84	—
Western Rift, Uganda								
NK 252'86	r. M2	x5x	3.3	158.6+	82.1 (3)	68.5 (5)	91	3.9
NK 253'86	l. M2	x5x	—	167.0	82.6 (4)	71.0 (5)	90	—
NK 787'89	r. M2	x6x	3.7	177.2	77.5 (5)	78.6 (5)	101	4.1
NK 62'89	r. M3	x7 or 8	3.5	202.0	86.4 (3)	—	—	—
NK 373'86	?M3 fragment	—	4.2	—	—	—	100	—
NK 439'86	M3 fragment	+5+	3.4	—	—	—	91	4.5
NK 496'89	r. m3 fragment	—	3.7	—	—	—	—	5.2
NK 2500'89	molar plate	—	—	—	—	—	102	—
<i>Mammuthus subplanifrons</i>								
Langebaanweg, South Africa								
PQ-L 40430	?l. l2	—	—	+830.0	58.0 (mid-point)	103.0 (mid-point)	—	—
PQ-L 20192	r. M3	x6+	—	175.0+	100.4	worn	—	4.4
PQ-L 69078	l. M3	+4+	—	+126.9+	111.8	worn	—	4.7–5.5
PQ-L 12723	l. m3	x9x	3.8	325.0	110.5 (3)	76	69	4.8–5.4
	r. m3	—	3.2	—	101.1	66.6	67	—
Tugen Hills, Kenya								
KNM-LU 7597	l. m3	9x	3.1	272.2	108.4	worn	—	v. thick
Virginia, South Africa								
A2882	l. l2	—	—	2489.0	155.0 (mid-point)	175.0 (mid-point)	—	—
	l. m3	+9x	4.5–5.0	+196.0	91.0	worn	—	4.0–5.0
Middle Awash, Ethiopia								
L27-1a	l. m3	x8x	3.5	245.0	101.0	76.0	76	4.0–4.5
L27-1b	l. M3	+5+	3.5	+154.0+	102.0	91.0	89	2.0–4.0
ALA-VP-2/309	r. M3	9	—	—	87.0+	—	—	4.0–4.5
ASK-VP-3/16	l. M3	8x	—	—	—	—	—	4.7–5.8
Vaal River, South Africa								
MMK 3920(type)	r. m3	+5x	4.5	+151.6	101.4	worn	—	3.3–4.5
MMK 4334	l. m3	+8x	4.0	+265.0	104.3	worn	—	4.0
	r. M3	+5x	3.3	+181.2	104.8	worn	—	4.3–4.7
Western Rift, Uganda								
M 25160	l. M3	+3x	—	+112.0	104.0	worn	—	5.0–7.0
Western Rift, Democratic Republic of Congo								
Ishasha unnumbered molar	l. m3 fragment	+4+	3.2	+120.0+	109.6	worn	—	3.7

on the continent in the north (*Anancus osiris* and *A. petrocchii*), and east-central regions (primitive and advanced morphs of *A. kenyensis*). *Anancus petrocchii* is found only in the latest Miocene-earliest Pliocene site of Sahabi, Libya, and has pentalophodont intermediate molars, third molars with six lophs, and simple, primitive crowns with weak anancoidy (Figure 3C; Petrocchi, 1943, 1954; Coppens, 1965; Coppens *et al.*, 1978). The molars of this species are massively constructed, with little or no development of accessory conules, and are among the largest known for anancine gomphotheres. The

primarily late Pliocene species *A. osiris* also has heavy, pyramidal loph(id)s and simple third molar crowns with few or no accessory conules, but in contrast its intermediate molars are tetralophodont and anancoidy is conspicuous (Figure 3F; Arambourg, 1945, 1970; Coppens *et al.*, 1978; Tassy, 1986). *Anancus kenyensis* is the most well known species of the subfamily, with an abundant fossil record. It has been divided into two morphs by Tassy (1986). The primitive morph ranges in age from late Miocene–early Pliocene, and is characterised by tetralophodont intermediate molars, weak anancoidy,

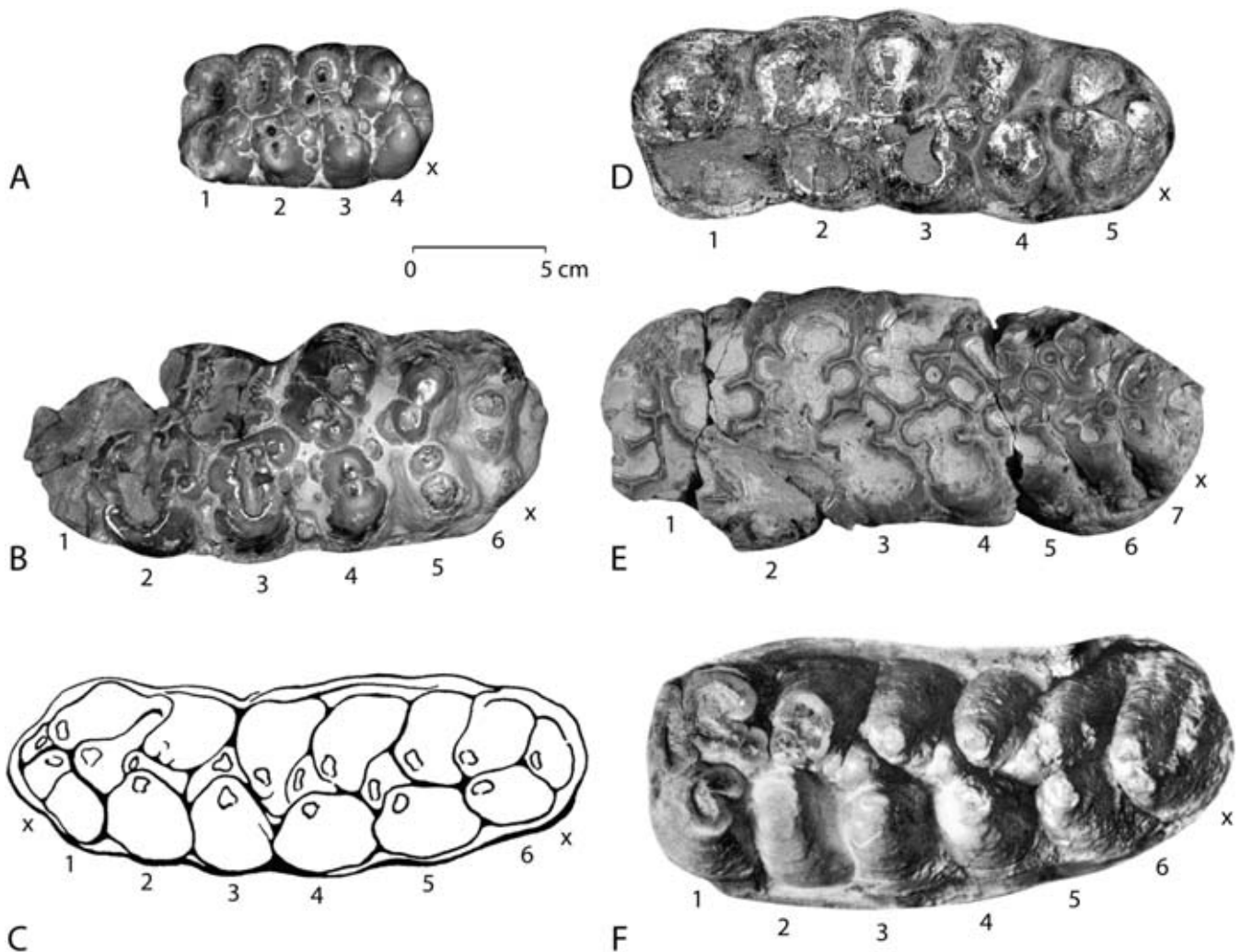


Figure 3. Representative molars of African *Anancus* species. Anterior is to the left. All specimens in occlusal view. **A**, SAM-PQ-L 40012, *A. capensis* sp. nov., r. M1. **B**, SAM-PQ-L 22079A, *A. capensis* sp. nov., r. M3. **C**, Sahabi molar no. 8, *A. petrocchii*, r. m3 (after Petrocchi, 1954: figure 20B). **D**, KNM-LU 57, *A. kenyensis* primitive morph, Tugen Hills, Kenya, r. m3. **E**, EP 197/05, *A. kenyensis* advanced morph, Laetoli, Tanzania, l. m3. **F**, 1956-4: A1, *A. osiris*, Ain Boucherit, Algeria, r. m3.

thick, unfolded enamel, simple occlusal morphology with posttrite accessory conules limited to the anterior half of molar crowns, and loph(id)s that are bulbous and massive in lateral view (Figure 3D; MacInnes, 1942; Mebrate & Kalb, 1985; Tassy, 1986, 1995; Kalb & Mebrate, 1993; Sanders, 1997). The advanced morph is an early–mid Pliocene form that is distinct enough to warrant erection of a new species (Sanders *et al.*, in prep.), with pentalophodont intermediate molars, more pronounced anancoidy, complex occlusal morphology with greater expression of accessory conules, third molars with six or seven loph(id)s, and enamel that may be finely folded (Figure 3E). No other species of African anancine gomphothere exhibits this combination of features (Table 2).

Molars of anancine gomphotheres from Langebaanweg also exhibit a novel mix of primitive (low crowned, tetralophodonty, thick enamel) and advanced (enamel folding, complex distribution of accessory conules, six–seven third molar loph(id)s, pronounced anancoidy) features (Table 2; Sanders, 2006). This mix suggests that the progressive evolutionary transformation to *A. capensis* sp. nov. from a primitive, *A. kenyensis*-like molar pattern occurred independently from that in the East-Central African lineage, where over time increasing crown complexity was accompanied by pentalophodonty, and from that in northern Africa, where the acquisition of pentalophodonty in *A. petrocchii* was not associated with more

intricate occlusal morphology (Coppens *et al.*, 1978).

Only a single anancine molar is known from Baard's Quarry at Langebaanweg, and it differs from molars of *A. capensis* sp. nov. in having laterally elongated, antero-posteriorly compressed posttrite half-lophids (Hendey, 1978, 1981). Unfortunately, it is too fragmentary to assign more precisely than to *Anancus* sp. Further study is necessary to determine if specimens from Karonga and Uraha, Malawi attributed to *A. kenyensis* and *Anancus* sp. (Mawby, 1970; Bromage *et al.*, 1995) might instead belong in *A. capensis* sp. nov.

Despite the brachyodont condition of their molars, stable isotope analyses of tooth enamel from a number of African sites indicate that *Anancus* spp. were grazers with a predominantly C_4 -based diet (Cerling *et al.*, 1999; 2003; Zazzo *et al.*, 2000; Harris *et al.*, 2003; Semaw *et al.*, 2005). At Langebaanweg, however, C_3 grasses are inferred to have been prevalent (Franz-Odenaal *et al.*, 2002) and, although anancine gomphotheres from the site have not yet been sampled for carbon isotopes, there is no reason to suspect that they differed ecologically from other African congeners. As the Pliocene progressed, this emphasis on grazing may have contributed to the decline and extinction of *Anancus* in Africa, as it placed its congeners in increasingly crowded competition with an expanding number of hypsodont elephants and other ungulate grazing specialists (Cerling *et al.*, 2003).

Table 2. Comparison of dental features in African anancine gomphotheres. Derived features in bold type.

Species	Anancoidy	No. loph(id)s, intermediate molars	No. loph(id)s, M3/m3	Enamel folding	Molar crown	Age complexity
<i>Anancus kenyensis</i> 'primitive morph'	weak	4	5–6	absent–coarse	simple	late Miocene–early Pliocene
<i>Anancus kenyensis</i> 'advanced morph'	pronounced	5	6–7	coarse–fine	complex	early–mid Pliocene
<i>Anancus capensis</i> sp. nov.	pronounced	4	6–7	moderate–fine	complex	late Miocene or early Pliocene
<i>Anancus petrocchii</i> Pliocene	weak	5	6	absent	simple	late Miocene or early
<i>Anancus osiris</i>	pronounced	4	5–6	absent–coarse	simple	?early–late Pliocene

Family ELEPHANTIDAE Gray, 1821
Subfamily ELEPHANTINAE Gray, 1821

(Endolele, Tanzania) Endo L5/BK(E) 35, third molar fragment (Table 1).

Genus LOXODONTA Cuvier, 1825 (anonymous emendation, 1827)

Type locality

'E' Quarry, Langebaanweg, South Africa (Hendey, 1981).

***Loxodonta cookei* sp. nov.**, Figure 4A–J

Mammuthus subplanifrons (in part) Hendey, 1976: 236.

Mammuthus subplanifrons (in part) Hendey, 1981: 51, 56.

Elephantinae indet., cf. *Loxodonta* Tassy, 1986: 115–117, pl. 14, figure 6.

Loxodonta sp. 'Lukeino stage' Tassy, 1995: 237–239, figure 5, pl. 4, figures 1–4.

Loxodonta sp. nov. Sanders, 2006: 196.

Age and occurrence

Late Miocene–early Pliocene, southern and eastern Africa.

Diagnosis

Primitive loxodont elephant retaining permanent third and fourth premolars. Distinguished from *L. adaurora*, *L. exoptata*, *L. atlantica*, and *L. africana* by fewer molar plates, especially in posterior teeth, and lower hypsodonty indices, and from non-loxodont elephants by presence of anterior and posterior accessory conules and tendency for enamel rims of plates to form median sinuses with wear, throughout molar crowns (Table 3).

Holotype

South African Museum, Cape Town, South Africa, SAM-PQ-L 45627, r. M2 (Figure 4A–B; Table 1; probable antimer of -PQ-L 45619).

Etymology

Named in honour of H. Basil S. Cooke, for his numerous and important contributions to African mammalian palaeontology.

Paratypes

SAM-PQ-L 42224, l. m3; -PQ-L 45608, l. p4 (Figure 4C–D); -PQ-L 45611, l. m1; -PQ-L 45613, r. ?m1; -PQ-L 45616, r. maxilla fragment with P3, P4, and M1 (Figure 4I–J); -PQ-L 45617, l. M1; -PQ-L 45618, l. M2; -PQ-L 45619, l. M2 (probable antimer of type -PQ-L 45627); -PQ-L 45766A, m2 or m3 fragment; -PQ-L 45782, ?l. p4 (?antimer of -PQ-L 50864); -PQ-L 45784, molar plate (Figure 4G); PQ-L 45785, molar plate; -PQ-L 45788, l. and r. m3 (Figure 4H); -PQ-L 45789, l. DP3; -PQ-L 46220 + 46561 + 50863, l. m2 (antimer of -PQ-L 50862); -PQ-L 46259, r. partial dp4; -PQ-L 46541, l. DP4; -PQ-L 46996, l. dp3, l. and r. dp4; -PQ-L 49736, l. partial m3; -PQ-L 50433, r. partial m1; -PQ-L 50434, ?r. P3; -PQ-L 50862, r. m2 (antimer of -PQ-L 46220 + 46561 + 50863); -PQ-L 50864, ?r. p4 (?antimer of -PQ-L 45782); -PQ-L 50865, r. partial ?m1; -PQ-L 69067, ?l. p3 (Figure 4E–F); -PQ-L 69069, dp2; -PQ-L 69070, ?l. dp2; -PQ-L 69071, ?r. p3; -PQ-L 69072, ?l. P3; -PQ-L 69075, r. dp3; -PQ-L 69077, l. M2.

Referred specimens

(Western Rift, Uganda) NK 252'86, r. M2; NK 253'86, l. M2; NK 373'86, partial ?M3; NK 439'86, NK 532'86, partial ?M3; partial l. M3; NK 62'89, r. M3; NK 496'89, partial r. m3; NK 566'89, isolated molar plate; NK 787'89, r. M2; NK 2500'89, isolated molar plate; NK 2501'89, isolated molar plate; NK 2609'89, isolated molar plate (Table 1; Tassy, 1995); (Tugen Hills, Kenya) KNM-LU 67, mandibular fragment with r. m3 (Table 1; Tassy, 1986); KNM-BC 32, r. M3 fragment; KNM-BC 189, r. M3; KNM-BC 917, l. m3 fragment; KNM-BC 1761, l. M1 (Table 1);

Description

Skull unknown. The type specimen was in crypt at time of death, and cementum had not yet developed. Morphological details of this specimen and its probable antimer are typical of the entire sample: plates are formed of five–eight conelets and converge antero-posteriorly and laterally towards the apex, and are not very closely spaced (LF = 4.0); crown height (left = 85.0 mm; right = 83.0 mm) is less than width (left = 93.8 mm; right = 92.0 mm), and transverse valleys are U-shaped (Figure 4A–B). In more worn specimens, enamel is thick (m3 ET = 4.9–6.2 mm) and unfolded or coarsely folded, and wear figures form median loxodont sinuses that may touch in the midline. Cementum usually nearly fills transverse valleys. Accessory conules are lower than unworn plates, apically free (Figure 4B,G), and only become incorporated into plates with moderate wear. Molar plates are primitive in having their greatest width very low, near the cervix of the crown (Figure 4G). The transformation of the ancient gomphothere occlusal pattern into the loxodont condition (formation of median loxodont sinuses) can be seen in left m3 specimen -PQ-L 45788, where the median longitudinal sulcus divides the crown into unequal-sized pre- and posttrite halves and is only obliterated by wear, and the 'gomphothere trefoil' is buccally extended and incorporates the anterior and posterior accessory central conules to form median sinuses (Figure 4H). Deciduous premolars are miniature versions of adult molars,

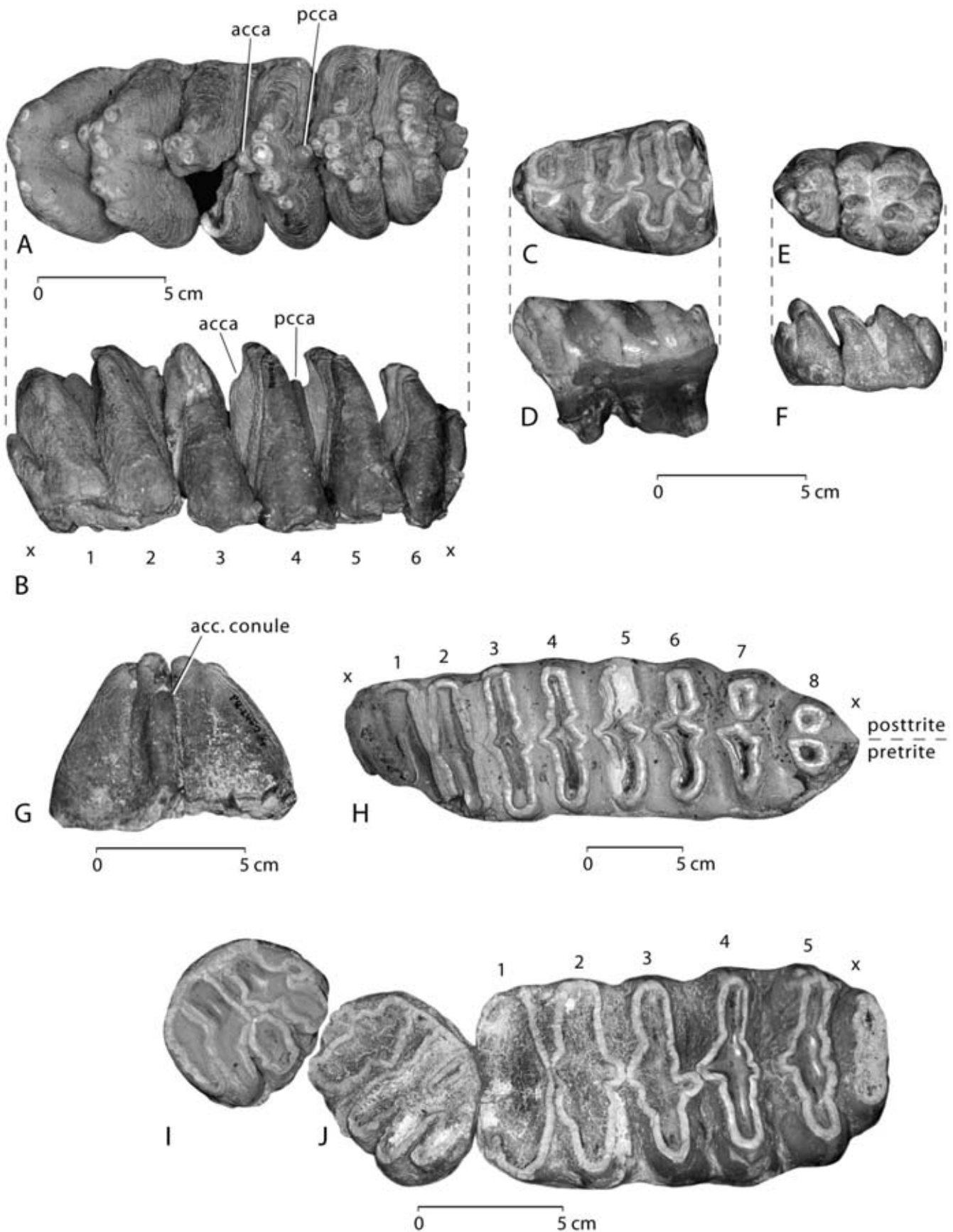


Figure 4. Cheek tooth specimens of *Loxodonta cookei* sp. nov. from Langebaanweg, South Africa. Anterior is to the left, except for (G). Abbreviations: acca, anterior accessory central conule; pcca, posterior accessory central conule. **A**, Occlusal view, SAM-PQ-L 45627, r. M2 (type). **B**, Buccal view, SAM-PQ-L 45627, r. M2 (type). **C**, Occlusal view, SAM-PQ-L 45608, l. p4. **D**, Buccal view, SAM-PQ-L 45608, l. p4. **E**, Occlusal view, SAM-PQ-L 60967, ?r. p3. **F**, ?Lingual view, SAM-PQ-L 60967, ?r. p3. **G**, Anterior view, SAM-PQ-L 45784, isolated molar plate. **H**, Occlusal view, SAM-PQ-L 45788, l. m3. **I**, Occlusal view, SAM-PQ-L 45616, r. P3. **J**, Occlusal view, SAM-PQ-L 45616, r. P4-M1 (note misalignment of P3-M1).

Table 3. Comparative data for third molars of Mio-Pliocene African elephants. Abbreviations: ac, anterior accessory central conule(s); ET, enamel thickness (in mm); LF, lamellar frequency (average number of plates per 100 mm); pc, posterior accessory central conule(s). Hypsodonty index (HI) is calculated as height \times 100/width; brachyodont = 0–79 (very brachyodont \leq 65), mesodont = 80–99, and hypsodont \geq 100. Supplemental data are from Coppens (1965, 1972), Arambourg (1970), Maglio (1973), Beden (1980, 1983, 1987a,b), Gaziry (1987), Kalb & Mebrate (1993), Tassy (1995), Haile-Selassie (2001), Sanders (1997, 2004, 2005) and Mackaye *et al.* (2005).

Species	Molar	No. plates	HI	ET	LF	Accessory conules
<i>Stegotetrabelodon orbus</i>	M3	6	66–71	4.5–7.0	3.0	pc plates 1–4
	m3	6–7	66–68	3.5–8.0	3.2	pc plates 1–5
<i>S. syrticus</i>	M3	6	51–64	6.0–7.1	3.0	pc plates 1–5
	m3	7	63	4.0–6.0	2.7	pc plates 1–7
<i>Primelephas gomphotheroides</i>	M3	7	58–68	3.4–6.0	3.3	pc plates 1–2
	m3	7–8	61–67	3.0–6.3	3.6	pc plates 1–3
<i>Stegodibelodon schneideri</i>	M3	7	71–79	5.0–6.0	2.5	–
	m3	7	–	5.0–6.0	3.0	–
<i>Mammuthus subplanifrons</i> Middle Awash	M3	8–9	89	4.0–5.8	3.5	pc plates 1–2
	m3	8	76	4.0–4.5	3.5	pc plate 1
Langebaanweg	M3	–	–	4.4–5.5	–	–
	m3	9	67–69	4.8–5.4	3.8	pc plates 1–3
Tugen Hills, Kenya	m3	9	–	–	3.1	–
<i>Mammuthus africanavus</i>	M3	9	98	3.2–4.6	3.0–4.4	ac (variable), pc anterior half of crown
	m3	10–12	109	2.6–4.3	3.6–5.2	ac (variable), pc anterior half of crown
<i>Loxodonta adaurora adaurora</i>	M3	9–10	95	3.5–4.3	4.0–4.7	ac, pc throughout crown
	m3	10–11	91	3.0–4.5	3.2–4.3	
<i>L. exoptata</i>	M3	11–12	98–107	3.0–4.0	4.1–5.5	ac, pc throughout crown
	m3	11–12	115	3.0–3.8	3.8–5.1	ac, pc throughout crown
<i>Loxodonta cookei</i> sp. nov. Langebaanweg, South Africa Western Rift, Uganda Tugen Hills, Kenya	m3	8	81–84	4.9–6.2	3.5–4.0	ac, pc throughout crown
	M3	7 or 8	91–102	4.1–4.5	3.4–4.2	ac, pc throughout crown
	M3	7	81	3.3–5.2	4.0	ac, pc throughout crown
	m3	8	–	3.8	4.0	ac, pc throughout crown
Endolele, Tanzania	third molar	–	84	–	4.0	ac, pc throughout crown
<i>Elephas ekorensis</i>	M3	11	102–110	3.5–4.2	3.4–4.8	ac, pc variable, throughout much of the crown
	m3	12	106	3.5	5.2	
<i>Elephas recki brumpti</i>	m3	11–14	102–114	2.8–4.0	4.2–5.5	ac, pc variable, throughout mesial 2/3 of crown

except for dp2s, which are tiny, triangulate teeth with three closely appressed plates.

This is the only known crown elephant (*Loxodonta*, *Elephas*, *Mammuthus*) with permanent premolars. In occlusal view, P3 is rounded, of nearly equal length and width, and p3 is more ovoid, longer than wide (Figure 4E–F,I). Fourth permanent premolars are larger, relatively more elongate, and may have better expression of accessory central conules (Figure 4C–D,J). Cementum is well developed in these teeth. Specimen -PQ-L 45616 demonstrates that third and fourth permanent premolars were in occlusion simultaneously with the first molar, without a strong wear gradient between them (Figure 4I–J).

Plate formulae: dp2 = 3x; dp3 = x4x; dp4 = x6x; p3 = x3x–x4x; p4 = x4x; m1 = x5x; m2 = x7x; m3 = x7x–x8x; DP3 = x4; DP4 = x5x or x6; P3 = x3x–x4; P4 = x4; M1 = 5x–x6; M2 = x5x–x6x; M3 = 7–8.

Remarks

This species, best represented at Langebaanweg, South Africa, encompasses late Miocene–early Pliocene specimens that exhibit strong development of antero-posterior median enamel expansions ('loxodont sinuses'), and which are characterised by mesodont–slightly hypsodont molar crowns with a low number of plates (Table 3; Sanders, 2006). The morphology of these specimens suggests close affinity with a subsequent *L. exoptata*–*L. africana* lineage (see Tassy, 1995), and is distinguished from molars of the penecontemporaneous East African species *L. adaurora* (see Maglio, 1970b, 1973; Beden, 1987a; Kalb & Mebrate, 1993) in part by the more pronounced development of its median sinuses.

Possibly the oldest representative of *L. cookei* sp. nov. is an m3 reportedly from the Lukeino Fm., Tugen Hills, Kenya (KNM-LU 67; Tassy, 1986), dated to between 6.2–5.6 Ma (Hill

et al., 1985, 1986; Hill, 2002). The actual provenance of this specimen is uncertain (Meave Leakey, pers. comm.), however, and its preservation and morphology are a better match for other specimens referable to *L. cookei* sp. nov. from the younger Chemeron Fm. (Tugen Hills, Kenya), with an age between 5.3–4.0 Ma (Hill *et al.*, 1985, 1986; Deino *et al.*, 2002).

Morphometrically, loxodont elephant molars from the Nkondo-Kaiso region of the Western Rift in Uganda and assigned to *Loxodonta* sp. 'Lukeino stage' (Tassy, 1995) are very similar to the Langebaanweg and Chemeron specimens. Although these have been dated to as old as *ca.* 6.0 Ma, they are probably closer in age to *ca.* 5.0 Ma (Pickford *et al.*, 1993; Tassy, 1995). The dimensions and morphology of an elephant molar fragment from Endolele, Tanzania indicate that it should be placed in *L. cookei*, as well. The transverse outline of its plates is identical to that in the Langebaanweg molars, crown height is low (HI = 84), and plates are well spaced (LF = 4.0). Although this site has been considered to represent the Lower Unit of the Laetoli Beds, Tanzania, which dates to *ca.* 4.3–3.8 Ma (Drake & Curtis, 1987; Harris, 1987; Hay, 1987), the elephant and accompanying anancine gomphothere specimens from Endolele are more primitive than those from known horizons of the Lower Unit at Kakesio, Tanzania (Sanders, 2005). Unfortunately, despite exhaustive search, it has proven impossible to relocate the outcrops from Endolele, making it impossible to independently assess its age.

Archival information associated with the loxodont elephant specimens from Langebaanweg indicates their derivation from the Pelletal Phosphate Mb. of the Varswater Fm., but there is no definitive indication that they were also found in the Quartzose Mb. This could have important implications for reconstruction of local habitats during the time of deposition of these members. There is some indication of significant differences in other aspects of the mammalian faunas from these geological units (e.g., carnivores; Werdelin, 2006), and in their depositional circumstances (Hendey, 1981); however, chronostratigraphic and climatic contexts of the Varswater Fm. require further investigation before it can be established if faunal contrasts are taphonomic, temporal, or ecological.

Because of the apparent absence of C_4 grasses at ancient Langebaanweg (Franz-Odenaal *et al.*, 2002), it is difficult to ascertain grazing adaptations among its mammalian taxa, including *L. cookei* sp. nov. However, since basal elephants and other Mio-Pliocene species of *Loxodonta* from East-Central Africa sampled for isotopes all appear to have been grazers or mixed feeders with a high proportion of C_4 plants in their diets (Cerling *et al.*, 1999, 2003; Zazzo *et al.*, 2000; Harris *et al.*, 2003; Schoeninger *et al.*, 2003; Kingston & Harrison, 2007), it is not unreasonable to conjecture that *L. cookei* sp. nov. had similar dietary preferences.

Genus *MAMMUTHUS* Burnett, 1830

Mammuthus subplanifrons (Osborn, 1928), Figure 5E

Archidiskodon subplanifrons Osborn, 1928: 672, figure 1.

Archidiskodon andrewsi Dart, 1929: 711, figure 14.

Archidiskodon proplanifrons Osborn, 1934: 10, figure 2.

Mammuthus (*Archidiskodon*) *scotti* Meiring, 1955: 189, pl. 1, figures 2–4.

Stegolophodon sp. Singer & Hooijer, 1958: 1–3, figures 1–4.

Mammuthus (*Archidiskodon*) *subplanifrons* Cooke & Coryndon, 1970: 123, pls 4–5.

Mammuthus subplanifrons Maglio & Hendey, 1970: 85–87; pls 1–2.

Mammuthus subplanifrons Maglio, 1973: 51, pls 14–15.

Primelephas gomphotheroides Tassy, 1986: 109, pl. 12, figure 3.

Holotype

McGregor Museum, Kimberley, South Africa, MMK 3920, partial r. m3 (Figure 5E; Table 1).

Referred specimens

(Vaal River, South Africa) MMK 435, partial ?r. lower molar; MMK 4334, partial r. m3, l. m3 (Table 1; Osborn, 1928, 1934; Dart, 1929); (Virginia, South Africa) A2882, l. I2, l. m3, l. ulna (Table 1; Meiring, 1955); (Langebaanweg, South Africa) SAM-PQ-L 12723 mandible with partial r. m3 and l. m3 (Figure 5A–B; Table 1; Maglio & Hendey, 1970); -PQ-L 20192, partial r. M3 (Figure 5C); -PQ-L 40430, ?l. I2 (Figure 5D); -PQ-L 69078, partial l. M3; (Middle Awash, Ethiopia), AME-VP-1/93, partial M2; ASK-VP-3/16 l. M2, l. M3; L 27-1a, l. m3; L 27-1b, partial l. M3 (Table 1; Kalb & Mebrate, 1993; Haile-Selassie, 2001); (Western Rift, Uganda) M 25160, partial l. M3; NK 689/86, molar fragment (Table 1; Cooke & Coryndon, 1970; Tassy, 1986); (Ishasha, Virunga National Park, Democratic Republic of Congo) unnumbered partial l. m3 (Table 1; Vanoverstraeten *et al.*, 1990); (Tugen Hills, Kenya) KNM-LU 7597, l. m3 (Table 1 and Figure 5G; Tassy, 1986).

Type locality

Middle Terrace, Vaal River, Sydney-on-Vaal, South Africa.

Age and occurrence

Latest Miocene–early Pliocene, eastern and southern Africa.

Original diagnosis

Molar crowns very broad, with plates comprised of four–six conelets. Enamel very thick. V-shaped, cementum-covered transverse valleys. Loxodont sinus foldings double, irregular, less prominent than in *Loxodonta* (Osborn, 1928, 1934).

Emended diagnosis

Large elephant with broad, brachyodont to mesodont molars with a low number of thick plates (LF = 3.2–3.75); moderately thick (ET = 4.0–5.8 mm), unfolded enamel; and accessory conules limited to the posterior side of plates in the mesial half of the crown. There are no loxodont sinuses formed by the enamel loops with wear. Molars morphologically similar to those of *Primelephas gomphotheroides*, but wider, slightly higher crowned, and with more plates.

Description

Cranial remains have not been recovered for this species. An isolated upper tusk from Langebaanweg (Figure 5D; Table 1) may belong to this species. Although postdepositionally flattened throughout, it retains a strong longitudinal torque and curves upward at its distal tip. Such torque is typical of mammoth tusks, but not of I2s of the other proboscideans represented at the site (Maglio, 1973; Coppens *et al.*, 1978). This spiral twisting is reminiscent of a very large tusk from Virginia, South Africa, which is associated with a molar morphologically comparable with those from Langebaanweg assigned to *M. subplanifrons* (Meiring, 1955).

The best preserved specimen of *M. subplanifrons* from Langebaanweg is a mandible with left and right m3s (SAM-PQ-L 12723; Maglio & Hendey, 1970). The corpus is relatively long and slender, with a high ramus that has a more restricted masseteric fossa than is usually found in loxodont elephants. Symphyseal length cannot be determined because of anterior breakage, but evidently was long compared with Recent elephants. Anterior chambers of the mandibular canal open externally via mandibular foramina; however, contrary

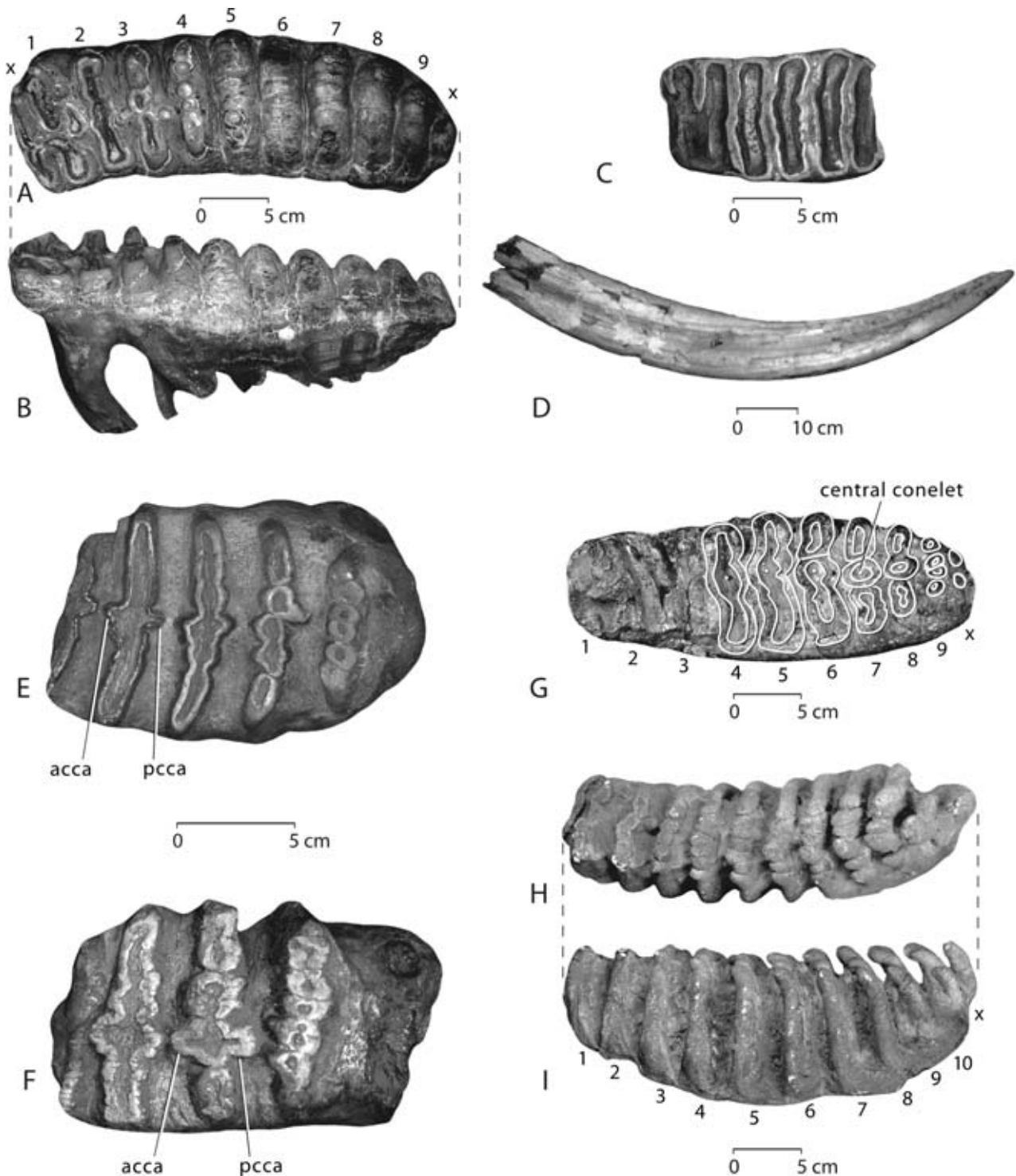


Figure 5. Dental specimens of *Mammuthus subplanifrons* and comparative elephant species. Anterior is to the left, except for (D). Abbreviations: acca, anterior accessory central conule; pcca, posterior accessory central conule. **A**, Occlusal view, SAM-PQ-L 12723, *M. subplanifrons*, Langebaanweg, South Africa, l. m3. **B**, Buccal view, SAM-PQ-L 12723, *M. subplanifrons*, Langebaanweg, South Africa, l. m3. **C**, Occlusal view, SAM-PQ-L 20192, *M. subplanifrons*, Langebaanweg, South Africa, r. partial M3. **D**, ?Lateral view, SAM-PQ-L 40430, ?*M. subplanifrons*, Langebaanweg, South Africa, ?l. l2. Anterior is to the right. **E**, Occlusal view, MMK 3920 (cast), *M. subplanifrons*, Vaal River, South Africa, r. partial m3 (type). **F**, Occlusal view, MMK 4087 (cast), '*Archidiskodon loxodontoides*', Vaal River, South Africa, left partial M3 (type). **G**, Occlusal view, KNM-LU 7597, ?*M. subplanifrons*, Tugen Hills, Kenya, l. m3. Note the dominance of the central conelets highlighted in plates 4–8. **H**, Occlusal view, 1950-1: 12, *Mammuthus africanavus*, Lac Ichkeul, Tunisia, r. m3. **I**, Lingual view, 1950-1: 12, *M. africanavus*, Lac Ichkeul, Tunisia, r. m3.

to Maglio & Hendey (1970), these never house tooth buds in proboscideans with i2s, so there is no reason to speculate that they once contained vestigial lower incisors in *M. subplanifrons*. There is no sign of incisive alveoli antero-medial to these chambers.

The third molars of the Langebaanweg mandible are low

crowned (Tables 1 and 3), with nine robustly constructed plates formed of three–five conelets (Figure 5A–B). Anterior and posterior cingulids are prominent. Accessory central conules are limited to the posterior sides of the first three plates. Plates are transversely straight with a dominant central conelet. The plates are less pyramidal in lateral cross-section than in

Primelephas gomphotheroides, and the transverse valleys are sub-U shaped. Cementum thickly covers the plates, but does not fill the transverse valleys. A few molars from the Middle Awash, Ethiopia (Table 1) are similar morphologically (Mebrate, 1983; Kalb & Mebrate, 1993), as is a large, heavily worn m3 with a dominant central conelet in each plate from the Lukeino Fm., Tugen Hills, Kenya (KNM-LU 7597; Figure 5G and Table 1), originally attributed to *P. gomphotheroides* (Tassy, 1986).

Remarks

The Langebaanweg specimens assigned to *M. subplanifrons* are apparently all from the Quartzose Mb. of the Varswater Fm., in contrast to the depositional provenance of the loxodont elephants from the site. This occurrence is among the earliest known for mammoths, perhaps exceeded in age only by the specimens from the Kuseralee Mb. of the Sagantole Fm., Middle Awash, Ethiopia (Mebrate, 1983; Kalb & Mebrate, 1993; Haile-Selassie, 2001), dated to 5.77–5.18 Ma (Renne *et al.*, 1999), and the isolated m3 from the Lukeino Fm., Tugen Hills, Kenya (Tassy, 1986), dated to 6.2–5.6 Ma (Hill, 2002).

As traditionally composed, this species is quite morphologically heterogeneous (Maglio, 1973), and is likely a wastebasket taxon. The holotype and molars of other, synonymised taxa from the Vaal River ('*Archidiskodon proplanifrons*', '*A. andrewsi*'; Dart, 1929; Osborn, 1934; Maglio, 1973) differ in important occlusal details from the Middle Awash and Langebaanweg sample, particularly in displaying modest median occlusal sinuses formed of anterior and posterior accessory central conules (Figure 5E). In this feature, they resemble other Vaal River molars (e.g., Figure 5E, the type of '*Archidiskodon loxodontoides*', Dart, 1929) that appear to belong in *Loxodonta* (see Maglio, 1973). If this interpretation is valid, *M. subplanifrons* would become a junior synonym of a species of *Loxodonta*. However, the Middle Awash and Langebaanweg sample cannot be morphologically accommodated by any other existing proboscidean taxon, and in occlusal simplicity anticipates at least part of the younger, more hypsodont mid-late Pliocene *Mammuthus africanavus* hypodigm (compare Figure 5A–B with Figure 5H–I). While in the absence of associated crania there is no certainty that *M. subplanifrons* is truly a mammoth, the spiral twisting of the tusks from Virginia and Langebaanweg, South Africa are typical mammoth features (Maglio, 1973; Lister & Bahn, 1994), providing some justification for the generic assignment of the species. For these reasons, the species *M. subplanifrons* should be maintained, at least until the Vaal River specimens can be more definitively identified.

DISCUSSION

Taxonomy and phylogeny

Comparative morphological and metrical analyses of proboscidean dental remains reveal the occurrence of three taxa in the Varswater Formation at Langebaanweg, South Africa, including an anancine gomphother and two species of elephant. The gomphother is clearly identifiable as *Anancus* by its distinctive pattern of antero-posteriorly alternating molar half-loph(id)s. This genus is represented in North Africa by *A. petrocchii* and *A. osiris*, and in East-Central Africa by *A. kenyensis*. *Anancus kenyensis* was divided into primitive and advanced morphs by Tassy (1986). Unfortunately, he referred to the advanced morph as "*A. kenyensis* '*petrocchii* morph'", which is confusing because *A. petrocchii* is advanced only in the pentalophodonty of its intermediate molars, but otherwise possesses molars with simple occlusal morphology and primi-

tive, heavily constructed loph(id)s, whereas molar specimens attributable to the advanced morph of *A. kenyensis*, in addition to being pentalophodont, exhibit more complex distribution of accessory conules throughout their crowns. The transformation of *A. kenyensis* 'primitive morph' into *A. kenyensis* '-advanced morph' can be well traced in the East African fossil record, particularly in the Middle Awash late Miocene–mid Pliocene sequence (Mebrate & Kalb, 1985; Kalb & Mebrate, 1993), without invoking any special phylogenetic connection between the advanced East African form and *A. petrocchii*. The anancine gomphother dental material from Langebaanweg exhibits a combination of primitive and advanced features not observed in other African species of *Anancus*, and therefore is placed in *Anancus capensis* sp. nov. Except for the tetralophodonty of their intermediate molars, they are morphologically similar to early Pliocene cheek teeth of *A. kenyensis* 'advanced morph' from Aterir, Kenya (Bishop *et al.*, 1971; Hill 1994) and Kakesio, Tanzania (Drake & Curtis, 1987; Harris, 1987; Hay, 1987; Sanders, 2005). It seems reasonable to posit the derivation of the Langebaanweg anancine gomphotheres from a form like *A. kenyensis* 'primitive morph'; however, the difference in intermediate molar loph(id) number from the 'advanced morph' of *A. kenyensis* suggests regionally separate evolutionary trajectories between East-Central and southern African anancine gomphother lineages.

Elephant molars from the Pelletal Phosphate Member of the Varswater Formation are also readily identifiable, as *Loxodonta*. These exhibit the characteristic loxodont elephant trait of strong anterior and posterior accessory central conules throughout their crowns, forming median sinuses in wear. In this feature, they are similar to molars of the extant African elephant, *L. africana* and the early–late Pliocene East-Central species *L. exoptata*, though the Langebaanweg taxon is more primitive in plate number, crown height, and retention of permanent premolars. It is also differentiated morphometrically in a number of ways from the Pliocene loxodont elephant *L. adaurora*, particularly in having more pronounced median sinuses. For this reason, the Langebaanweg loxodont elephant is placed in a new species, *Loxodonta cookei* sp. nov., into which are also placed unnamed elephant specimens from a number of sites in eastern Africa (including the Western Rift; Table 1). This new species may have been ancestral to the *L. exoptata*–*L. africana* lineage, and is only slightly more derived in crown height and plate construction than undescribed molars of loxodont elephants from the late Miocene localities at Toros Menalla, Chad (Brunet *et al.*, 2002) and from the Lukeino Formation, Tugen Hills, Kenya (Sanders, 2004; Sanders *et al.*, in prep.). The recognition of the morphometric distinctness of *L. cookei* sp. nov. helps to bridge a conspicuous phylogenetic gap between the first appearance of loxodont elephants and the modern African species.

The third proboscidean, from the Quartzose Member of the Varswater Formation, belongs in a more problematic, wastebasket taxon, *Mammuthus subplanifrons*. Although there are unresolved questions about the heterogeneity of this species as presently composed, the *M. subplanifrons* dental material from Langebaanweg, along with some specimens from the Middle Awash, Ethiopia and Virginia, South Africa, cannot be accommodated in other elephant species, and exhibits features consistent with identification as a mammoth, notably strong central conelets in molar plates and spirally-twisted tusks. Although taxonomic convention may force the species to be renamed (as the type specimen appears to belong in *Loxodonta*), that issue is beyond the scope of this paper. For now, *M. subplanifrons* is retained because of its usefulness for representing

the most basal stage of mammoths. The Langebaanweg material provides important evidence for an African origin for *Mammuthus*: morphometrically, *M. subplanifrons* is the most primitive known mammoth, with more brachyodont, heavily constructed molars than those of chronologically successive, mid-late Pliocene European and African mammoths (see Coppens, 1965; Arambourg, 1970; Maglio, 1973; Lister & van Essen, 2003).

Biochronology

The Quartzose (QSM) and Pelletal Phosphate (PPM) Members of the Varswater Formation at Langebaanweg which have produced the proboscidean assemblage have been treated as essentially contemporaneous horizons with an age of ~5.0 Ma, estimated from biochronological correlation and marine transgression-regression sequence stratigraphy (Hendey, 1981). More recent work on the site has emphasised age contrasts between the younger PPM and QSM, without specifying the magnitude of their temporal difference, and considered them to represent the latest Miocene–early Pliocene (e.g., Matthews, 2006). The proboscideans found in the QSM are *Anancus capensis* sp. nov. and *Mammuthus subplanifrons*. Although the utility of the anancine gomphothere for biochronological correlation is hindered by the fact that it only occurs at Langebaanweg, its grade of dental development provides some hint of geological age. The presence of folded enamel, six–seven loph(id)s in the third molars, pronounced anancoidy, and complex distribution of accessory conules on the pre- and posttrite sides of molar crowns indicate that this species is more advanced than late Miocene congeners. These features have their greatest similarity in early Pliocene specimens of *A. kenyensis* ‘advanced morph’ from eastern Africa that are dated to approximately 5.0–4.0 Ma (e.g., Hill *et al.*, 1985, 1986; Mebrate & Kalb, 1985; Kalb & Mebrate, 1993; Renne *et al.*, 1999). *Mammuthus subplanifrons* appears to have been a more widely distributed species, but absolutely dated late Miocene material from the Middle Awash, Ethiopia (5.77–5.18 Ma; Kalb & Mebrate, 1993; Haile-Selassie, 2001) and the Lukeino Formation in the Tugen Hills, Kenya (6.2–5.6 Ma; Hill *et al.*, 1985, 1986; Tassy, 1986; Hill, 2002) are slightly more primitive than Langebaanweg specimens in features such as plate number and/or lamellar frequency (Table 3), indicating that they may be older representatives of the species. *Mammuthus subplanifrons* is not known from sites younger than the early Pliocene, so its occurrence at Langebaanweg also indicates a date for the QSM of approximately 5.0–4.0 Ma.

The loxodont elephant from the PPM, *Loxodonta cookei* sp. nov., is more primitive than its putative descendant species *L. exoptata* in plate number, crown height (Table 3), and retention of permanent premolars. *Loxodonta exoptata* is firmly dated no earlier than 4.3 Ma (Beden, 1983, 1987a,b; White *et al.*, 1984; Drake & Curtis, 1987; Harris, 1987; Hay, 1987; Harris *et al.*, 1988; 2003; Kalb & Mebrate, 1993; Sanders, 2005), providing a possible terminal date for *L. cookei* sp. nov. In addition, loxodont elephant specimens from the Tugen Hills and Western Rift that are assigned to the same species (Tables 1 and 3) are dated to the interval 5.3–4.0 Ma (Hill *et al.*, 1985, 1986; Pickford *et al.*, 1993; Tassy, 1995; Deino *et al.*, 2002), essentially constraining *L. cookei* sp. nov. to an age in the same range (5.3–4.3 Ma) as that of the QSM. There are no signs of morphological or metric heterogeneity in the anancine gomphotheres from the site, which occur in the PPM as well as the QSM. This agrees with the interpretation that little time separated the deposition of the QSM and PPM (Matthews, 2006). Faunal differences between these members (Matthews, 2006; Werdelin, 2006) are more likely to

be caused by taphonomic factors (depositional and preservational biases; habitat sampling) than by temporal succession.

Palaeoecology

The Quartzose Member (QSM) of the Varswater Formation at Langebaanweg depositionally represents an estuarine complex with floodplain, salt marsh, and tidal flat facies, while the Pelletal Phosphate Member (PPM) is a fluvial and marine littoral complex (Hendey, 1981). These geological units have produced diverse mammalian herbivore cohorts that are particularly useful for palaeoecological reconstruction. The suids, giraffids, and tragelaphine bovids present in both the QSM and PPM indicate the availability of woodland habitats and browsing-to-mixed feeding adaptations (Hendey, 1981). Other taxa, including rhinos, hypsodont equids, and antelope and reduncine bovids, are suggestive of more open conditions at Langebaanweg during the time of deposition of the QSM and PPM (Hendey, 1981; Franz-Odenaal *et al.*, 2002; Bernor, 2006). This ecological heterogeneity is supported by dental microwear analysis of the Langebaanweg bovid assemblage (Ungar *et al.*, 2006). The ca. 5.0 Ma Langebaanweg environment appears to have been more lushly foliated than the semi-arid sclerophyllous vegetation present there now, with riverine woodlands flanked by grasslands, moderated by seasonal rainfall (Hendey, 1973, 1976; Tankard & Roger, 1978). Although grazing is inferred for many of the Langebaanweg herbivores, isotopic analysis of mammalian dental specimens from the site indicates that C₄ grasslands were not supported by the ecosystem and climatic regime, and instead that a Mediterranean climate with a C₃ grassland-dominated environment prevailed (Franz-Odenaal *et al.*, 2002). Prevalence of C₃ grasses implies a climatic seasonal alternation of wet winters and dry summers, and mesowear analysis of and dental pathologies in some herbivores indicate that dry periods may have cycled into periods of drought and increasing aridity during PPM times (Franz-Odenaal *et al.*, 2003; Franz-Odenaal, 2006).

The proboscidean assemblage from Langebaanweg is consistent with habitat reconstructions that include substantial distribution of grasses, necessary to provide adequate graze for multiple species of their immense size. Despite the fact that none of the proboscideans from Langebaanweg were particularly hypsodont or have especially derived dental adaptations for grazing, stable isotope analysis of *Anancus* and all early elephants sampled indicate that, at least in East-Central Africa, these animals were predominantly grazers with C₄-plant based diets (Cerling *et al.*, 1999, 2003; Zazzo *et al.*, 2000; Harris *et al.*, 2003; Schoeninger *et al.*, 2003; Semaw *et al.*, 2005; Kingston & Harrison, 2007). *Mammuthus subplanifrons* has substantially lower-crowned teeth than molars of latest Miocene–early Pliocene loxodont elephants (Table 3), but there does not appear to have been a correlation among proboscideans during this time period between crown height and diet, and therefore no reason to posit a shift in proboscidean QSM-PPM palaeoecology. The origin and subsequent adaptive radiation of elephants during the late Miocene–early Pliocene fundamentally involved a reconfiguration of craniodental anatomy (e.g., formation of molar plates; elevated, antero-posteriorly compressed crania) for fore-aft power shearing during mastication as an adaptation for grazing (Maglio, 1972, 1973; Coppens *et al.*, 1978), making it likely that this dietary emphasis was shared by all early members of the Elephantidae, including *M. subplanifrons*. For these reasons, the most rational interpretation of the Langebaanweg proboscideans is that they were all grazers feeding in open country conditions.

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