

Chapter 9

Proboscidea

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Abstract Paleontological fieldwork between 1998–2005 by the Eyasi Plateau Expedition at Laetoli and nearby sites produced a large collection of proboscidean fossils from the early to mid Pliocene Lower and Upper Laetolil Beds and late Pliocene Upper Ndolanya Beds, and possibly older sediments at Endolele, that substantially enlarges the sample of proboscidean material recovered earlier by Louis Leakey in 1935, Kohl-Larsen in 1938–1939, and Mary Leakey in the 1970s and early 1980s. The present study of the combined proboscidean sample confirms the presence of deinotheres and loxodont elephants, and provides the first description of anancine gomphotheres from the area. In addition, the first stegodont from the Eyasi Plateau is identified. The study also suggests that gomphotheres and loxodont elephants evolved locally in the Eyasi Plateau during the early Pliocene. Inference from stratigraphic distribution of proboscidean taxa, isotopic analyses, and dental morphology corresponds with paleoecological reconstruction depicting the Eyasi Plateau during the early-mid Pliocene as covered with abundant shrub- and grassland, with more restricted gallery forest, and as drier during the late Pliocene. Age-grade mortality profiles of elephants and deinotheres from the Laetolil and Upper Ndolanya Beds indicate a chronic lack of standing water or cyclical incidences of drought in the region for a sustained interval of time.

Keywords Laetoli • Endolele • Pliocene • Tanzania • Deinotheres • Loxodont elephants • Anancine gomphotheres

Introduction

Pliocene fossil proboscidean remains from the Eyasi Plateau comprise an integral segment of the temporally successive record of the order from northern Tanzania, interpolated between Mio-Pliocene localities of the Manonga Valley that

have yielded fossils of the archaic elephants *Primelephas korotorensis* and *Stegotrabelodon orbus* and the primitive anancine gomphothere *Anancus kenyensis* (Sanders 1997) and Pleistocene horizons at Olduvai dominated by the more advanced elephant *Elephas recki* (Maglio 1973; Coppens et al. 1978; Beden 1980, 1985). The most productive sites of the Eyasi Plateau for proboscidean fossils are Kakesio and Laetoli, which have yielded important collections from the Lower Laetolil Beds, Upper Laetolil Beds and Upper Ndolanya Beds, respectively. Of these sites, the greatest number of proboscidean fossils derives from Laetoli. The discovery of hominin fossils at Laetoli, including the holotype specimen of *Australopithecus afarensis*, several series of bipedal trackways attributed to *A. afarensis*, possibly the oldest specimen of *Paranthropus aethiopicus*, and an archaic *Homo sapiens* cranium (Johanson et al. 1978; Leakey and Hay 1979; Day and Wickens 1980; Day et al. 1980; Leakey 1987a, b; Harrison 2002, 2011) have made it one of the most famous paleontological sites in East Africa. Although less celebrated than the hominins, the proboscideans from Laetoli and other Eyasi Plateau sites are nonetheless important for establishing a reliable chronological framework for the region, and for paleoecological reconstruction. Moreover, they provide evidence of environmental changes that may have impacted on regional succession of early hominins.

The East African Archaeological Expedition of 1934–1935, led by Louis Leakey, undertook the first paleontological collecting in the Eyasi Plateau area, and recovered a small number of proboscidean fossils from Laetoli and Endolele (or Endulele = Esere?). The Laetoli (“Vogel River”) material was briefly mentioned by Hopwood in Kent (1941), who recognized the occurrence of two elephant species and *Deinotherium bozasi*, after initially placing the elephant fossils into one species (Hopwood 1936). It is less clear whether Hopwood’s (Kent 1941: 179) “*Mastodon* from the basal beds” refers to gomphothere specimens from Endolele. Slightly later, in 1938–1939, Kohl-Larsen made a larger collection of deinotheres and elephants at Laetoli, which was subsequently described by Dietrich (1941, 1942). Given what is now understood about the elephant sample from

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the site, it is notable that Dietrich grouped the elephant specimens from the Laetolil Beds into a single species, “*Archidiskodon exoptatus*.” It was not until much later, however, that Coppens (1965) first recognized that this elephant belonged in *Loxodonta*. A return to a two-species taxonomic scheme was made by Maglio (1969, 1973), who identified *Elephas recki* and *Loxodonta adaurora* in the combined Louis Leakey and Kohl-Larsen collections. More recently, however, with the addition of a much larger proboscidean collection from the Mary Leakey expeditions to Laetoli in the 1970s and early 1980s, Beden (1987a) organized all of the Laetolil Beds elephant material again into one species, *Loxodonta exoptata*. This work was supplemented by Harris’ (1987a) detailed description of the deinotheres specimens. Although Mary Leakey’s group collected at the nearby site of Kakesio, at which the Lower Laetolil Beds is exposed, the proboscidean fossils recovered there were not described, nor was a gomphothere molar from the Upper Laetolil Beds.

Between 1998–2005, paleontological survey and collecting were resumed at Laetoli and nearby sites by the Eyasi Plateau Expedition, under the direction of Terry Harrison, in collaboration with the Tanzanian National Museums. A substantial number of proboscidean fossils with well-controlled chronostratigraphic proveniences were recovered, increasing size of the overall sample and taxonomic diversity. In addition to supporting the identification and validity of *Loxodonta exoptata* from the Laetolil Beds (and overlying Upper Ndolanya Beds), study of this material also confirms the presence of *Deinotherium bozasi*, adds the first formal record of the rare (in the eastern rift) *Stegodon* from Tanzania, and provides the first description and taxonomic interpretation of anancine gomphotheres from Endolele, Kakesio, and Laetoli. The proboscidean sample shows signs of regional evolution of the anancine gomphotheres and elephants, is consistent with early-late Pliocene dating of the Lower and Upper Units of the Laetolil Beds and Upper Ndolanya Beds, and suggests that the enigmatic site of Endolele may be older than Lower Laetolil Beds localities (particularly Kakesio) dated to ca. 4.4–3.85 Ma (Deino 2011). Furthermore, by inference from dental morphology, isotopic analyses, and stratigraphic occurrence of taxa, the proboscidean sample supports paleoecological reconstruction depicting Laetoli and the surrounding area during the mid-Pliocene as primarily covered with abundant grassland and shrubland, with more restricted patches of gallery forest, and becoming drier in the late Pliocene. In addition, the age-grade mortality profile of the proboscidean sample, particularly the elephants, indicates the periodic occurrence of drought or chronic lack of standing water. This view of ancient Laetoli is critical for understanding the ecological dynamics associated with the evolution of early hominins, including our own precursors.

Abbreviations

Geological: Loc., locality; Ma, Mega annum (10^6 years); Mb., member; Fm., formation. Skeletal: dP/dp, upper/lower deciduous premolar; ET, enamel thickness; H, height; HI, hypsodonty index ($H \times 100/W$); l., left; L, length; LF, lamellar frequency (number of plates per 100 mm); M/m, upper/lower molar; mc, metacarpal; mm, millimeters; mt, metatarsal; P/p, upper/lower premolar; r., right; W, width; x, anterior or posterior cingulum(id). Institutional: BM(NH), The Natural History Museum, London (formerly the British Museum [Natural History]); -AT, Aterir, Kenya; -BC, Chemeron Formation, Baringo Basin, Kenya; EP, specimens collected by the Eyasi Plateau Expedition; KK, Kakesio, Tanzania; KNM, Kenya National Museums; -KP, Kanapoi, Kenya; L followed by a number series, Middle Awash, Ethiopia; LAET, specimens from Laetoli collected by Mary Leakey; -LT, Lothagam, Kenya; NK, Kairo-Nkondo Area, Nyawiega, Uganda; WM, Wembere-Manonga Formation, Manonga, Tanzania.

Systematic Paleontology

Order PROBOSCIDEA Illiger, 1811
 Suborder INCERTAE SEDIS
 Superfamily DEINOTHERIOIDEA Bonaparte, 1845
 Family DEINOTHERIIDAE Bonaparte, 1845
 Subfamily DEINOTHERIINAE Bonaparte, 1845
 Genus *DEINOTHERIUM* Kaup, 1829
DEINOTHERIUM BOZASI Arambourg, 1934

Eyasi Plateau Occurrence: Upper Laetolil Beds: Loc. 2, 5–10, 10NE, 10W, and 22; Upper Ndolanya Beds: surface below Loc. 7E.

Diagnosis: Readily distinguished from elephantoid proboscideans by its low-slung cranium, absence of upper tusks, downturned mandibular symphysis and lower tusks, molar bilophodonty (except for trilophodont dP4/dp4 and M1/m1), and simultaneous presence of all cheek teeth in adult animals (no horizontal tooth replacement) (Harris 1978). Differentiated from *Chilgatherium* and *Prodeinotherium* by larger teeth, from *Prodeinotherium* by simplification of postmetaloph ornamentation of second and third molars, more retracted nasal aperture, and a shorter, narrower cranial roof, and from *D. giganteum* by narrower external nares and rostral trough (Harris 1978; Sanders et al. 2004).

Description: *Deinotherium bozasi* is represented at Laetoli by a small number of mostly isolated teeth. While there are five teeth (P3–M3) in each adult jaw quadrant, as opposed to three deciduous teeth (dP2–4) in infant and juvenile jaw quadrants, the proportion of deciduous premolars in the

combined deinother cheek tooth collection from Laetoli (13/39) indicates a substantial percentage of pre-adult individuals in the sample, especially as at least four adult teeth are from one individual.

The majority of the best specimens from the Mary Leakey expeditions have been previously well described and figured, and include LAET 75-541, r. dp2, LAET 78-5221, r. dp2, LAET 79-5452, l. dp3, LAET 81-16, r. dp4, LAET 81-77, l. dp4, LAET 75-2032, l. p3-4 and m2-3, and LAET 78-4973, l. P3 (Table 9.1; Harris 1987a).

A tooth from the Mary Leakey collection previously not described is a heavily worn left dP2, LAET 81-10 (Fig. 9.1a), from Loc. 2. This deciduous premolar is missing most of its lingual edge, and enamel is spalled off of its buccal and distal margins. The protocone and hypocone have been worn into large dentine ovals that are transversely connected to the ectoloph by ridges forming the proto- and metalophs, respectively. These lophs tightly enclose a central fovea. There is a remnant of a low mesial cingulum. Though dP2 is otherwise poorly known for *D. bozasi*, the preserved length of LAET 81-10 (Table 9.1) is typical in size for other species of *Deinotherium*.

Earlier (1938–1939), Kohl-Larsen collected a small number of deinother fossils from the Laetoli area, including 12 teeth and a third metacarpal, apparently from the Upper Laetoli Beds. The dental sample is composed of four dp3s, a p4, two P3s, a P4, two M1s, an M2, and an M3, and was briefly described by Dietrich (1942). Dimensions for these teeth are provided in Table 9.1, and fall within the range for

Deinotherium (Fig. 9.2a). The metacarpal has a greatest length of 210 mm and mid-shaft breadth of 65 mm (Dietrich 1942: 92).

Louis Leakey (together with G.T. Bell, Stanhope White, and Peter Kent, part of the East African Archaeological Expedition of 1934–1935) collected the first deinother fossils from the Laetoli area in 1935. These include two dP2s and part of a permanent molar. Each dP2 preserves enough morphology to show that the ectoloph merged with the transverse proto- and metalophs in wear (Fig. 9.1b), and that when unworn these lophs were ornamented apically by mammelons. Dimensions for these few specimens are listed in Table 9.1.

More recent collecting by the Eyasi Plateau Expedition has produced eight deinother dental specimens, from Loc. 2, 8, 9, and 10. All of these derive from the Upper Laetoli Beds. Several of these are complete enough to warrant description: EP 412/98 is a dp3 with the mesial cingulid and protolophid intact, and a remnant of the anterior cristid of the hypolophid showing. The protolophid exhibits typical deinother chisel-like wear along its distal margin, and has a height of 38.5 mm. The exposed enamel ranges from 1.5–1.7 mm in thickness. EP 4231/00, from Loc. 2, is a moderately worn right dP3, nearly complete (Fig. 9.1c). It has low mesial and distal cingula closely appressed to the main lophs, which are separated by a transverse valley. The proto- and metalophs form continuous transverse crests that expand into large dentine ovals lingually; prominent cristae project distally from the buccal margins of each crest. EP 1410/03 is a more heavily worn, left dP3

Table 9.1 Inventory and dimensions of identifiable deinother cheek teeth from Laetoli (Eyasi Plateau region), in mm. Specimens lacking accession numbers were collected by Kohl-Larsen and measured by Dietrich (1942)

Taxon/Accession #/ Specimen	Locality	Plates/Loph(id)s	L	W	H	ET	HI
<i>Deinotherium bozasi</i>							
No#		–	53.0	37.0	–	–	–
dp3		–	82.0	64.0	–	–	–
p4		–	91.0	–	–	–	–
No#		–	90.0	–	–	–	–
P3		–	90.0	–	–	–	–
No#		3	102.0	80.0	–	–	–
M1		2	98.0	–	–	–	–
No#		2	100.0	98.0	–	–	–
M2		2	100.0	98.0	–	–	–
No#		–	–	–	–	–	–
BM(NH) 14946		–	–	–	–	–	–
Permanent molar		–	–	–	–	–	–
BM(NH) 14946		2	40.7	36.7	–	–	–
dP2		–	–	–	–	–	–
LIT.AS 7-VI-35		Loph	–	40.7	–	–	–
?dP2		–	–	–	–	–	–

(continued)

Table 9.1 (continued)

Taxon/Accession #/ Specimen	Locality	Plates/Loph(id)s	L	W	H	ET	HI
LAET 75-541 dp2	10	–	34.0	21.3	32.0	–	150
LAET 78-5221 dp2	7	–	32.5	23.0	31.0	1.5	135
LAET 79-5452 dp3	6	2	55.5	40.8	–	–	–
LAET 81-16 dp4	2	3	73.5	50.5	–	–	–
LAET 81-77 dp4	10	3	76.4	49.0	–	–	–
LAET 75-2032 p3	10	–	77.6	57.9	–	–	–
LAET 75-2032 p4	10	2	81.5	67.5	53.0	–	78
LAET 75-2032 ^a m2	10	2	92.3e	81.1	–	–	–
LAET 75-2032 ^a m3	10	2	109.2e	91.7+	–	–	–
LAET 81-10 dP2	2	2	41.7+	35.5+	–	–	–
LAET 78-4973 ^a	2	2	94.5e	93.5e	–	–	–
LAET 75-621 Molar fragments	5	–	–	–	–	–	–
LAET 81-80 Parts of two loph(id)s	7 east	–	–	–	–	–	–
LAET 75-813 Protolophid of m2 or m3	7	–	–	–	–	–	–
LAET 75-156B Tooth chip	9	–	–	–	–	–	–
LAET 75-1411 Small molar fragment	9	–	–	–	–	–	–
LAET 75-2554 Molar fragment	10 northeast	–	–	–	–	–	–
LAET 75-2314 Molar fragment	10	–	–	–	–	–	–
LAET 75-635 Molar fragment	22	–	–	–	–	–	–
EP 412/98 dp3	10	2	46.9+	–	38.5	1.5–1.7	–
EP 4231/00 dP3	2	2	54.9	49.3	–	–	–
EP 1410/03 dP3	8	2	56.7	53.4	–	–	–
EP 697/00 Molar fragment	2	–	–	–	–	–	–
EP 4126/00 DP fragment	8	–	–	–	–	–	–
EP 1082/98 Adult molar fragment	9	–	–	–	–	–	–
EP 3200/00 Molar fragment	10 west	–	–	–	–	–	–
EP 3199/00 adult lower molar fragments	10 west	–	–	–	–	–	–

BM(NH) and LIT.AS specimens are from the 1935 collection of Louis Leakey. LAET specimens are from the Mary Leakey collections. EP specimens are from the collection of Eyasi Plateau expeditions

e estimated, *ET* enamel thickness, *H* height, *HI* hypsodonty index, $H \times 100/W$, *L* length, *W* width, + indicates a missing portion of a specimen, and that the dimension was greater when complete

^a Marks specimens with dimensions from Harris (1987a)

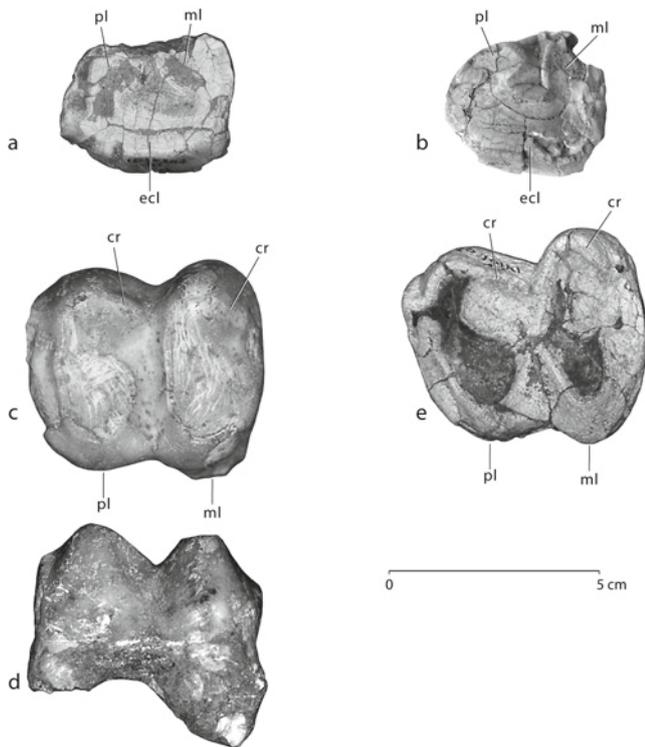


Fig. 9.1 Dental specimens of *Deinotherium bozasi* from Laetoli (*cr* crista, *ecl* ectoloph, *ml* metaloph, *pl* proto-loph). Anterior is to the left in each specimen. (a) Occlusal view, left dP2 specimen LAET 81-10 (*reversed*). (b) Occlusal view, right dP2 specimen BM(NH) 14946. (c) Occlusal view, right dP3 specimen EP 4231/00 (*reversed*). (d) Lateral view, right dP3 specimen EP 4231/00 (*reversed*). (e) Occlusal view, left dP3 specimen EP 1410/03

(Fig. 9.1d), from Loc. 8. It is similar in shape and occlusal construction to EP 4231/00, with a prominent ento- and ecto-loph demarcating the two lophs. This gives the crown a figure eight shape in occlusal view. A strong crista extends posteriorly from the buccal margin of the proto-loph to connect with a nearly indistinct, low crista extending anteriorly from the buccal margin of the metaloph. Because of the high degree of wear, the lophs converge nearly across the transverse valley in the midline. Upper deciduous third premolars are poorly known for *D. bozasi*; however, the dimensions of the Laetoli specimens (Table 9.1) are similar to those of dP3s of *D. giganteum*, and exceed the range for *Prodeinotherium* (Fig. 9.2b).

Remarks: At Laetoli, deinotheres are known for certainty from the Upper Laetoli Beds. A fragment of an upper permanent molar (LAET 81-80, not 80-81 as is listed in Harris 1987a) was thought to be of unknown provenience because it was a surface find (Harris 1987a: 295), but its collection below Loc. 7E indicates that it derives from the Upper Ndolanya Beds. Because they are very useful in distinguishing African *Deinotherium* from *Prodeinotherium*, it is unfortunate that no deinotheres crania or dentaries were recovered from Laetoli. Tusk fragments associated with LAET 75-2032 in the collection are too large to belong to a deinotheres and are clearly those of an elephant. Nonetheless, the cheek teeth in the sample are large (Fig. 9.2a, b) and distally simple enough to indicate assignment to *Deinotherium*. As pointed out by Harris (1987a), the only deinotheres identified from late Miocene-early Pleistocene sites in Africa is *D. bozasi*, so it is likely that this is the species present at Laetoli.

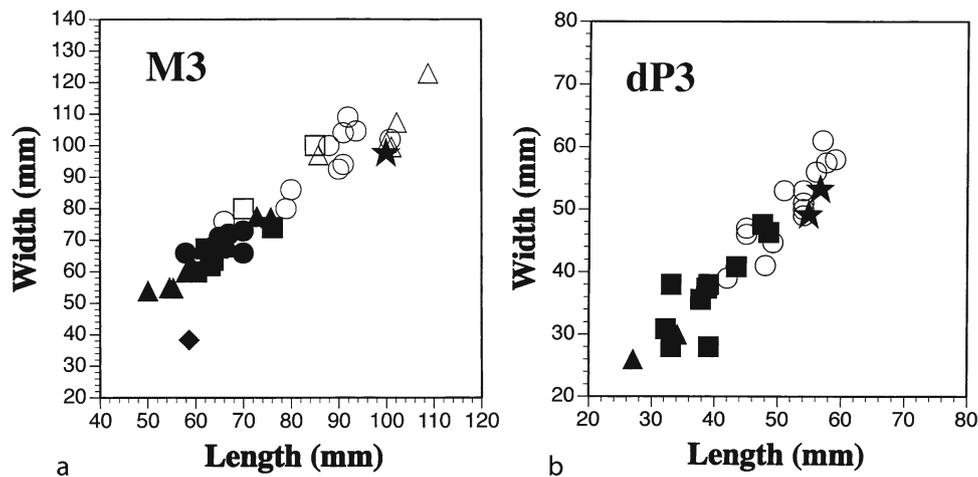


Fig. 9.2 Bivariate plots of M3 and dP3 crown length versus width in deinotheres. Comparative dimensions supplementing original measurements are from Bachmann (1875), Weinsheimer (1883), Roger (1886), Andrews (1911), Cooper (1922), Palmer (1924), Éhik (1930), MacInnes (1942), Gräf (1957), Sahni and Tripathi (1957), Symeonidis (1970), Harris (1973, 1977, 1983, 1987a), Gaziry (1976), Tobien (1988),

Tsoukala and Melentis (1994), Huttunen (2000), Sach and Heizmann (2001), Sanders (2003), and Sanders et al. (2004). Symbols: ♦, *Chilgathierium harrisi*; ▲, *Prodeinotherium hobleyi*; ■, *P. bavarium* (including “*P. hungaricum*”); ●, *P. pentapotamiae*; △, *Deinotherium bozasi*; ○, *D. giganteum* (including “*D. levius*”); □, *D. indicum*; ★, deinotheres specimens from Laetoli. (a) M3. (b) dP3

Deinotherium bozasi is the terminal species of a specialized proboscidean family that first appeared in the late Oligocene of Africa (Sanders et al. 2004) and persisted on the continent until the end of the early Pleistocene (Beden 1985; Behrensmeyer et al. 1995). Although possibly the largest terrestrial animal of the African Neogene (Christiansen 2004), it is poorly represented in the fossil record (Harris 1987a), usually by pieces of isolated teeth. The structure of its brachyodont, lophodont molars and results of dental isotopic analyses indicate that it was a dedicated browser (Harris 1975; Cerling et al. 2005). Harris (1978) interpreted its craniodental features to suggest that it occupied densely vegetated gallery forests, which has important implications for reconstructing the paleoecology of mid Pliocene Laetoli. If *D. bozasi* was as rare in the Upper Ndolanya Beds as evidence indicates (only one specimen recovered), this may signal a shift to drier conditions locally during the late Pliocene. Although deinotheres are thought to have had shorter trunks and less ability to reach the ground than elephants (Harris 1975), $\delta^{18}\text{O}$ enamel composition for deinotheres and elephants at Laetoli are equally depleted (Kingston and Harrison 2007), suggesting that they both relied on drinking meteoric water and therefore presumably were not drought resistant. This might be an important consideration for determining the cause of high pre-adult mortality of deinotheres at Laetoli.

Suborder ELEPHANTIFORMES Tassy, 1988
 Superfamily ELEPHANTOIDEA Gray, 1821
 Family GOMPHOTHERIIDAE Hay, 1922
 Subfamily ANANCINAE Hay, 1922
 Genus ANANCUS Aymard, 1855
ANANCUS KENYENSIS (MacInnes, 1942)

Eyasi Plateau Occurrence: ?Lower Laetolil Beds: Endolele (Endulele)=Esere?.

Diagnosis: African anancine gomphotheres have short, broad crania with elevated vaults and raised bases. Upper tusks are straight and lack enamel. Mandibles are brevirostrine and lack incisors. Intermediate molars (dP4/dp4-M2/m2) of *A. kenyensis* are tetralophodont. Third molars have five or six loph(id)s. Dental enamel is very thick (5.0–7.0 mm in third molars), and usually unfolded. Crown morphology is simple, with posttrite posterior accessory conules restricted to the mesial moiety of m3, and usually M3, as well. Loph(id)s are constructed of massive, low conelets. In upper molars, pretrite half-lophs are offset anteriorly, relative to their posttrite half-lophs (anancoidy), and the reverse condition occurs in lower molars; anancoidy may be weakly expressed.

Description: No crania or mandibles of this species have been recovered from the Eyasi Plateau region. Nonetheless, two molars from Endolele document the presence of *A. kenyensis* at the site. These specimens are distinctly different from anancine gomphothere molars from the Lower and

Upper Laetolil Beds at Kakesio and Laetoli. BM(NH) 32958 is a nearly complete right M3 in wear, collected in 1935 by Louis Leakey, missing only its posterior cingulum, with five lophs, accessory conules to mid-crown, moderately well-expressed anancoidy, and a trace of cementum in the transverse valleys (Fig. 9.3a). Enamel is very thick, and coarsely folded in the first loph. The lamellar frequency is 3.75, reflecting the anteroposterior massivity of the lophs.

The second specimen (Endo: LS BKE 35 is its field catalogue reference) confirms the presence of *A. kenyensis* at the site. It is a very worn, tetralophodont right M1 or M2 (Fig. 9.3b). Despite the wear, anancoid arrangement of half-lophs is perceptible. This tooth was also collected by Louis Leakey in 1935. Dimensions for these specimens are provided in Table 9.2. Comparative assessment of these specimens (Table 9.3) confirms the opinion of V. J. Maglio, in a note accessioned with them, that the specimens are “not *A. osiris*. Looks like good *kenyensis*.”

A fragmentary astragalus from Esere 1 (=Endolele?) (EP 1671/98) has a more saddle-shaped tibial articular surface than is typical for elephants, and might also belong to *A. kenyensis*. Although African anancine gomphotheres are well-represented craniodentally, little is known of their postcranials.

Remarks: *Anancus kenyensis* is the best-known anancine gomphothere species of East and Central Africa, and is also the oldest representative of the subfamily in Africa. Abundant evidence exists showing that the species underwent progressive evolution, with increases over time in occlusal complexity, crown size, loph(id) number, and degree of anancoidy (Mebrate and Kalb 1985; Kalb and Mebrate 1993; Kalb and Froehlich 1995). The East-Central African anancine lineage was subdivided into time-successive stages by Mebrate and Kalb (1985), and into primitive “*kenyensis*”- and advanced “*petrocchii*”-morphs by Tassy (1986). The use of the term “*petrocchii*-morph,” however, was unfortunate because it confused an advanced *stage* with a North African anancine *species* (*A. petrocchii*) that originally was depicted as having a simple crown morphology and weak anancoidy (Petrocchi 1943, 1954; Coppens 1965; Sanders 2008). Examination of unnumbered anancine gomphothere molars collected more recently at Sahabi (Boaz et al. 1979) reveals a more complex occlusal pattern than reported by Petrocchi or Coppens (Sanders 2008). This calls into question whether Petrocchi’s original descriptions and figure (1943, 1954: Fig. 20b) were inaccurate or, alternatively, a precise depiction of a sample from a different geological unit than the specimens more recently studied. There is some evidence that the proboscidean collections from Sahabi are representative of two time-successive intervals of late Miocene and early Pliocene age (Sanders 2008). If so, the older material may belong in *A. petrocchii*, and the younger material may be identifiable with the

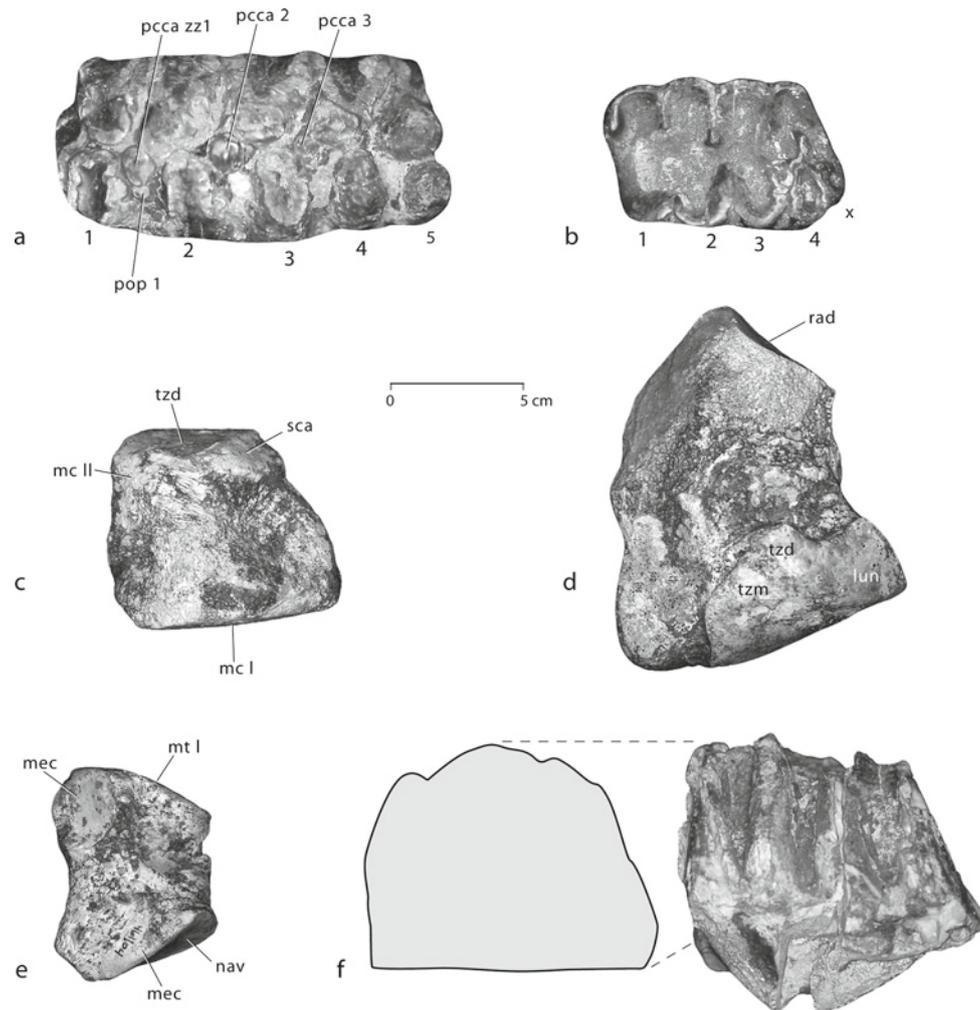


Fig. 9.3 Elephantoid dental and postcranial specimens from Endolele and Noiti 3 (*lun* lunate, *mc* metacarpal, *mec* mesocuneiform, *mt* metatarsal, *nav* navicular, *pcca*, posterior pretrite accessory conule, *pop* posterior posttrite accessory conule, *rad*, radius, *sca* scaphoid, *tzd*, trapezoid, *tzm* trapezium, *x* cingulum(id)). Anterior is to the left in each tooth. (a) Occlusal view, right M3 specimen BM(NH) 32958, *Anancus kenyensis*, from Endolele. (b) Occlusal view, right

M1 or M2 specimen Endo: LS BKE 35, *A. kenyensis*, from Endolele. (c) Lateral view, trapezium EP 461/04, *Loxodonta exoptata*, from Noiti 3. (d) Lateral view, scaphoid EP 461/04, *L. exoptata*, from Noiti 3. (e) Lateral view, entocuneiform EP 461/04, *L. exoptata*, from Noiti 3. (f) Lateral view and anterior cross-section, third molar specimen Endo: LS BKE 35, *Loxodonta* sp. cf. *Loxodonta cookei*, from Endolele

advanced morph of *A. kenyensis*. In any case, differences between the primitive and advanced anancine gomphothere morphs of East and Central Africa are substantial enough to merit formal taxonomic division. Here, the primitive morph of the lineage is retained in *A. kenyensis* with the type from Kanam, Kenya (MacInnes 1942), and the advanced morph is placed in its own species (see below).

Anancus kenyensis (as newly defined above) is a late Miocene-early Pliocene species, with an established age range of ca. 7.4–4.3 Ma (Sanders et al. 2010), occurring in the Lower and Upper Mbs. of the Nawata Fm. at Lothagam, Kenya (Tassy 2003), at Toros Menalla, Chad (Vignaud et al. 2002; Hautier et al. 2009), the Mpesida Beds and Lukeino Fm. in the Tugen Hills, Kenya (Hill et al. 1985, 1986; Tassy

1986; Hill 2002), the Adu Asa Fm. and Kuseralee and Haradaso Mbs. of the Sagantole Fm., Middle Awash, Ethiopia (Kalb and Mebrate 1993; Haile-Selassie 2001; Haile-Selassie et al. 2004), Lemundong’o, Kenya (Ambrose et al. 2003; Saegusa and Hlusko 2007), the Ibole Mb. of the Wembere-Manonga Fm., Manonga Valley, Tanzania (Sanders 1997), Kanam East and West, Kenya (MacInnes 1942; Tassy 1986), Nkondo, Uganda (Tassy 1985), Lasdanan Mb., Galili, Ethiopia (Kullmer et al. 2008), and at Kossom Bougoudi, Chad (Brunet et al. 2000; Brunet 2001). A note written by Louis Leakey in 1935 locates Endolele in the “general Laetoli area... near the ‘springs’ some 8 miles away [from the Laetoli type site] in a different formation.” The lower age assessment of 4.4 Ma for the Lower Laetoli Beds exposed at

Table 9.2 Dimensions of anancine gomphothere cheek teeth from the Eyasi Plateau region, in mm

Taxon/Accession #/Locality	Specimen	Plates/Loph(id)s	L	W	H	ET	HI
<i>Anancus kenyensis</i>							
No # (Endo: LS BK 35) (Endolele)	M2	x4x	99.1	60.9 (4)	–	3.0–3.9	–
BM(NH) 32958 (Endolele)	M3	x5+	160.0+	76.0	66.0 (4)	4.9–5.5	87
<i>Anancus ultimus</i> sp. nov.							
EP 157/00 Loc. 16, Upper Unit	dP2	x3	25.7	18.5	–	–	–
EP 1149/00 Loc. 8, Upper Unit	dp2	x2	25.1	14.4	–	–	–
EP 080/98 (Kakesio 6)	dp3	x3x	50.2	30.9 (3)	–	–	–
EP 1514/04 (Loc. 22 East, Upper Unit)	dp3	x3x	47.0	28.2 (3)	–	–	–
KK 82-57 (Kakesio)	dp3	x3x	58.1	37.4	–	1.5	–
LAET 81-75 (?Laetoli ?Upper Unit)	dp4 Distal molar frag.	5x +3x	102.5 +87.3	52.2 +76.3	– –	– 5.7–6.0	– –
KK 82-49 (Kakesio)	Molar frag.	+3+	+56.1+	56.0+	–	3.9–4.8	–
EP 073/98 (Kakesio 6)	Molar frag.	x3+	109.0+	69.8+	–	4.3–4.6	–
EP 861/04 (Kakesio 8)	Distal molar frag.	+1x	+41.0	63.5	57.0	3.3	90
KK 82-248 (Kakesio)	m1	x5x	123.6	64.0 (4)	–	5.0	–
EP 073/98 (Kakesio 6)	M2 or M3	x3+	102.0+	67.9+	–	2.7–3.5	–
KK 82-69 (Kakesio)	M3	7x	220.0	80.8 (6)	–	5.0–5.2	–
KK 82-292 (Kakesio)	M3	x7x	205.0	90.0 (3)	–	4.8–5.5	–
EP 197/05 (type) (Loc. 16, Upper Unit)	m3	x7x	160.0	79.6 (2)	–	–	–

e estimated, *ET* enamel thickness, *H* height, *HI* hypsodonty index, $H \times 100/W$, *L* length, *W* width, + indicates a missing portion of a specimen, and that the dimension was greater when complete. Numbers in parentheses indicate loph(id)s of greatest width and height

Table 9.3 Comparative distribution of traits in African anancine gomphothere molars

Taxon	Intermediate molars	Third molars	Anancoidy	Crown complexity	Enamel folding	Other
<i>Anancus kenyensis</i>	Tetralophodont	5–6 loph(id)s	Weak	Simple	None-coarse	
<i>A. ultimus</i> sp. nov.	Pentalophodont	6–7 loph(id)s	Moderate-pronounced	Complex	Moderate-strong	
<i>A. capensis</i>	Tetralophodont	6–7 loph(id)s	Pronounced	Complex	Moderate-strong	
<i>A. petrocchii</i> (type series of Petrocchi, 1943, 1954)	Pentalophodont	6 lophids (only m3 known)	Weak	Simple	Unknown	m3 very large, relatively narrow
<i>A. osiris</i>	Tetralophodont	5–6 loph(id)s	Weak-pronounced	Very simple	None-coarse	

Kakesio (Drake and Curtis 1987; Harris 1987b; Hay 1987; Deino 2011), with its more derived anancine than at Endolele, indicates that Endolele is even older, supporting Louis Leakey's assertion about the stratigraphy of the site.

ANANCUS ULTIMUS SP. NOV.

Partial Synonymy: *Trilophodon angustidens* cf. *kisumuensis* (in part), Hooijer, 1963; *Anancus osiris*, Coppens, 1965; *A. osiris*, Servant-Vildary, 1973; *A. kenyensis* (in part),

Coppens et al., 1978; *A. kenyensis* (in part; *A. kenyensis* “*petrocchii*-morph”), Tassy, 1986; *Anancus* sp. (Sagantole-type), Kalb and Mebrate, 1993; *Anancus* cf. *Anancus* sp. (Sagantole-type), Sanders, 1997; *A. kenyensis*, Harris and Leakey, 2003; *A. kenyensis* (in part), Tassy, 2003; *A. kenyensis*, Mackaye et al., 2005; *A. osiris*, Mackaye et al., 2005; *A. kenyensis*, Kingston and Harrison, 2007.

Etymology: *Ultim’us* (L., masc.), meaning “most extreme in time or sequence,” in reference to the final phase of the anancine gomphothere lineage in East-Central Africa.

Holotype: Tanzanian National Museums, Dar es Salaam, EP 197/05, l. m3 (Fig. 9.4a).

Paratypes: Laetoli, EP 157/00, ?r. dp2; EP 1149/00, l. dp2; EP 1514/04, r. dp3; LAET 81-75, molar fragment.

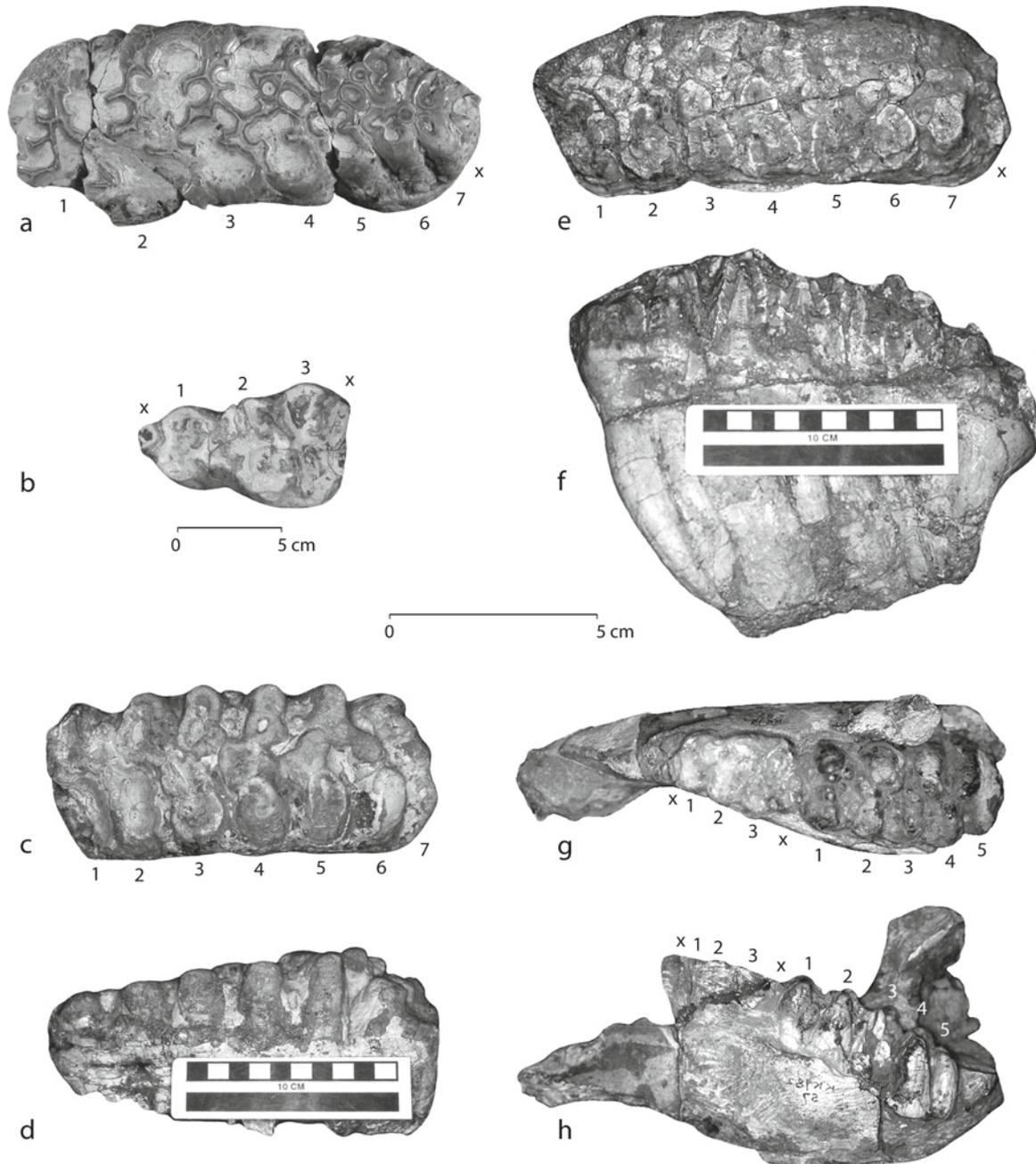


Fig. 9.4 Dental specimens of *Anancus ultim'us* sp. nov. from Kakesio and Laetoli (x cingulum(id)). (a) Occlusal view, left m3 specimen EP 197/05, holotype. (b) Occlusal view, left dp3 specimen EP 080/98. (c) Occlusal view, M3 specimen KK 82-292. (d) Lateral view, M3 specimen

KK 82-292. (e) Occlusal view, M3 specimen KK 82-69. (f) Lateral view, M3 specimen KK 82-69. (g) Occlusal view, right partial dentary with worn dp3 and emergent dp4 KK 82-57. (h) Lateral view, right partial dentary with worn dp3 and emergent dp4 KK 82-57

Type Locality: Loc. 16, Upper Laetolil Beds, Laetoli, Tanzania, ca. 3.6 Ma.

Age and Occurrence: Early-mid Pliocene, eastern, central, and ?North Africa.

Eyasi Plateau Occurrence: Lower Laetolil Beds: Kakesio 6 and 8, Kakesio South; Upper Laetolil Beds: Loc. 16 and 22E.

Referred Specimens: Kanapoi, Kenya: KNM-KP 384, l. m2; KNM-KP 410, associated l. and r. m2, l. m3. Chemeron Fm., Tugen Hills, Kenya: KNM-BC 33, l. M3; KNM-BC 380, r. dentary fragment with partial m3; KNM-BC 1627, l. M2 or M3 fragment; KNM-BC 1628, r. M1 or M2 fragment; KNM-BC 1655, l. dentary fragment with m3; KNM-TH 15591, l. M3. Aterir, Kenya: KNM-AT 20, l. M3; EP 197/05, l. m3. Lothagam, Kenya: KNM-LT 341, associated r. and l. partial m3 and l. partial M3; KNM-LT 361, r. partial m1; KNM-LT 383, r. partial M1; KNM-LT 23790, l. partial M1 or M2; KNM-LT 28567, l. partial P4. Kiloleli, Tanzania: WM 927/92, r. partial ?M3. Ngofila 1, 2, Tanzania: WM 493/94, molar fragment; WM 791/94, molar fragment. Beredi South 3, Tanzania: WM 1706/92, molar fragment. Kakesio, Tanzania: KK 82-292, r. M3 (Fig. 9.4c, d); KK 82-49, molar fragment; KK 82-57, r. dentary with dp3-dp4 (Fig. 9.4g, h); KK 82-69, l. m3 (Fig. 9.4e, f); KK 82-248, r. dentary fragment with m1 or m2; EP 073/98, l. M2 or M3 fragment; EP 080/98, l. dp3; EP 861/04, molar fragment. Middle Awash, Ethiopia: L124-1, r. partial M3; L227-1, r. M2; L337-3, l. M3; L140-1, r. partial m3; L150-1, r. m3; (Dhidnley and Shabeley Laag Mbs., Galili, Ethiopia) GAL-VP 1/002, l. M2; GLL-242, l. m1 or m2. As Duma, Gona, Ethiopia: WMS 6 P1, r. m3; WM 9 P346, r. dp4 or m1. Nkondo-Kaiso Area, Nyawiega, Uganda: NK 438'86, maxillary fragment with r. M2-M3 and pieces of a left molar; NK 2580'89, molar fragment; BM(NH) 25159, l. partial m1; BM(NH) 25166, molar fragment. Sinda River, Democratic Republic of Congo: Sinda n° 2, r. partial M3.

Diagnosis: Intermediate molars (dP4/dp4-M2/m2) pentalophodont; third molars with six or seven loph(id)s. Lower third molars smaller and relatively wider than those of *A. petrocchii*. Anancoidy well expressed. Occlusal morphology usually complex; posttrite and pretrite accessory conules often extend to the posterior moiety of molar crowns. Accessory conules may be doubled. Talonids may be crowded with many conelets. Moderately worn half-loph(id)s with coarsely to finely folded enamel. This combination of features is unique among African species of *Anancus* (Table 9.3).

Description: The type m3, from Laetoli, Tanzania is worn and some pieces are missing along its edges, but exhibits important diagnostic features. This molar has very derived anancine morphology, with seven lophids, strong anancoidy, and a complex occlusal pattern of anterior and posterior central accessory conules throughout nearly the entire extent of both the pre- and posttrite sides (Fig. 9.4a). The complexity

of the crown characteristic of *A. ultimus* sp. nov. is also exhibited by a partial upper molar that may have been derived from the Upper Laetolil Beds, LAET 81-75. If so, this is the first anancine gomphothere specimen recovered from the Upper Unit, unreported until now. The presence of anancine gomphotheres in the Upper Laetolil Beds is also marked by EP 1514/04, an extremely worn right dp3 from Loc. 22E. Even in this state of wear, the offset of pre- and posttrite half-lophids is apparent. In occlusal view, this specimen has an elongate triangular shape, and exhibits a small anterior cingulid and three lophids.

EP 1514/04 closely resembles EP 080/98, a left dp3 from an older horizon at nearby Kakesio. EP 080/98 is heavily worn, and has a diminutive anterior cingulid, three lophids, and a compressed posterior cingulid with obvious transverse offset of half-lophids (Fig. 9.4b).

In addition, two other deciduous teeth from Laetoli may also belong to *A. ultimus* sp. nov. The first is a small, narrow, sub-triangular dp2 (EP 1149/00) with a diminutive anterior cingulid formed of a single conelet, a first lophid composed of two slightly offset conelets, and a posterior lophid formed of one stout conelet. The second is a more robust, worn dP2 (EP 157/00) that is rounder in occlusal aspect. This tooth is relatively broader, and has three lophs, each formed of two conelets. The conelets in lophs 2 and 3 are slightly offset. Low anterior and posterior cingulae are apparent, though heavily worn and closely appressed to lophs. Dimensions for these specimens are given in Table 9.2. The offset of half-loph(id) conelets suggests they are from anancine gomphotheres.

Anancine gomphothere fossils are far more common in the Lower than Upper Laetolil Beds, particularly at Kakesio, and unmistakably document the presence of *Anancus ultimus* sp. nov. in the lower part of the Laetolil Beds sequence. Molars from Kanapoi, Kenya (Harris et al. 2003), dated to 4.2–4.1 Ma (Feibel 2003), are morphologically similar to those from Kakesio, helping to corroborate its age at ca. 4.4–3.85 Ma (Drake and Curtis 1987; Deino 2011). An M3 from Kakesio (KK/82 292) is strongly anancoid, with thick (4.8–5.5 mm), coarsely folded enamel, seven lophs, posterior accessory conules fused to worn pretrite half-lophs 1–5, and doubled posterior accessory conules associated with posttrite half-lophs 1–4 (Fig. 9.4c, d). Cementum is thinly distributed on loph walls and in the transverse valleys. Similarly, although crown details are not as easy to see in M3 specimen KK 82-69, it is evident that it has seven lophs and posttrite accessory conules (Fig. 9.4e, f). EP 073/98 is an incomplete M2 or M3 from Kakesio that exhibits the strong anancoidy and doubled posttrite accessory conules typical of the species.

Among the features distinguishing *A. ultimus* sp. nov. from *A. kenyensis* is pentalophodonty of intermediate molars, present in several specimens from Kakesio. Specimen KK 82-248 is a right dentary fragment with a complete, worn m1 or

m2 that has five lophids and pretrite accessory conules associated with lophids 1–3. KK 82-57 is a partial right dentary with a worn dp3 and emergent dp4. The dentary is brevirostrine, with a corpus height of 76.5 mm and width of 68.2 mm at the anterior end of dp4. The dp3 has a lophid formula of x3x, and is larger and less triangulate in occlusal shape than EP 080/98 or EP 1514/04. The dp4 has five lophids and a low posterior cingulid tightly appressed to the last lophid, distinct anancoidy, traces of cementum, and accessory conules associated with pre- and posttrite half-lophids to the middle of the crown (Fig. 9.4g, h). It is possible that Kakesio is the source area of the “*Mastodon*” from the “basal beds” mentioned by Hopwood in Kent (1941: 178–179).

Remarks: *Anancus ultimus* sp. nov. is primarily composed of specimens of the “advanced morph” of the *A. kenyensis* lineage. The species is present in the Chemeron Fm., Tugen Hills, Kenya (Hill et al. 1985, 1986), the Apak Mb. of the Nachukui Fm. at Lothagam, Kenya (Tassy 2003), at Kollé, Chad (Brunet 2001), Nyawiega, Uganda (Tassy 1995), Aterir, Kenya (Hill 1994), in the Kilolei Mb. of the Wembere-Manonga Fm., Manonga Valley, Tanzania (Sanders 1997), at Kanapoi, Kenya (Harris et al. 2003), at Ekora, Kenya (Kalb and Mebrate 1993), in the Aramis, Beidareem, and Adgantole Mbs. of the Sagantole Fm., Middle Awash, Ethiopia (Kalb and Mebrate 1993; Kalb and Froehlich 1995; Renne et al. 1999), in the Dhidnley and Shabeley Laag Mbs. of the Mount Galili Fm., Galili, Ethiopia (Kullmer et al. 2008), at As Duma, Gona, Ethiopia (Semaw et al. 2005), and in the Sinda Beds, Democratic Republic of Congo (Hooijer 1963; Yasui et al. 1992; Boaz 1994). The age of these sites suggests that evolution of tetralophodont into pentalophodont anancine gomphotheres in East-Central Africa occurred in the 5.0–4.5 Ma interval, and that tetralophodont and pentalophodont forms coexisted for at least 500,000 years. The last known occurrence of *A. ultimus* sp. nov. is at Laetoli, marking a mid-Pliocene termination of anancines in East-Central Africa. In northern and southern Africa, however, the subfamily persisted until the end of the late Pliocene (Depéret et al. 1925; Arambourg 1945, 1970; Fournet 1971; Hendey 1978, 1981; Cooke 1993; Geraads and Amani 1998; Geraads and Metz-Muller 1999; Geraads 2002; Sahnouni et al. 2002).

Considerable intra-site variation and morphological and metric overlap among temporally successive site samples complicate attempts to subdivide the *A. kenyensis*-*A. ultimus* sp. nov. lineage, particularly at sites where fossil teeth are fragmentary and intermediate molars are absent. Further taxonomic challenges may arise due to progressive changes in the morphology of early to late forms of *A. ultimus* sp. nov. For example, molars of the species from the lower Chemeron Fm., Tugen Hills, Kenya have little or no folding of enamel wear figures, thick enamel, and a maximum of six loph(id)s in third molars. Third molar specimens from the Aramis and Beidareem Mbs. of the Sagantole Fm., Middle

Awash, Ethiopia that are probably geologically younger, on the other hand, have a more complex occlusal morphology, with pre- and posttrite accessory conules distributed throughout the length of the crown, thinner enamel, greater enamel folding, and thicker cementum. Despite these complications, differences in molar occlusal organization, particularly between end members of this lineage, are more than sufficient to reliably distinguish *A. kenyensis* and *A. ultimus* sp. nov. at the species level.

Anancine gomphotheres may have differentiated regionally over time in Africa, based on different combinations of cheek tooth features (Table 9.3). For example, while the *A. kenyensis*-*A. ultimus* sp. nov. lineage of East and Central Africa evolved molars with more complex distribution of accessory conules, more folded enamel, stronger anancoidy, pentalophodonty of intermediate molars, and a greater number of third molar loph(id)s (Mebrate and Kalb 1985; Kalb and Mebrate 1993), in South Africa progressive molar crown features in *A. capensis* are accompanied by primitive retention of tetralophodonty of intermediate molars (Sanders 2006, 2007), and in North Africa, *A. osiris* primitively retained simple molar crowns with heavy, pyramidal loph(id)s, and tetralophodont intermediate molars, right to the end of the Pliocene (Arambourg 1945; Coppens 1965; Coppens et al. 1978; Tassy 1986). *Anancus petrocchii*, known only from the latest Miocene or early Pliocene of Sahabi, Libya (Coppens 1965; Coppens et al. 1978), was depicted as uniquely having massive, pyramidal molar loph(id)s, simple occlusal morphology, and weak anancoidy coupled with the more advanced trait of intermediate molar pentalophodonty (Petrocchi 1943, 1954). Examination of more recently collected anancine molars from Sahabi reveals occlusal morphology that is more complex than previously described, with small pre- and posttrite accessory conules distributed throughout molar crowns, and coarsely-folded enamel in some worn specimens (Sanders 2008). This sample is much closer morphologically to *A. ultimus* sp. nov. than to *A. osiris*, differentiated from the former primarily by larger size and relative narrowness of its third molars (Sanders 2008). Assessing whether this implies a biogeographic connection between anancine populations in East-Central and northeast Africa, or is due to convergence, will require further investigation. *Anancus ultimus* sp. nov. clearly differs morphometrically from *A. petrocchii* as described by Petrocchi (1943, 1954) and Coppens (1965). If the original diagnoses and illustration of *A. petrocchii* are incorrect, and the entire anancine sample from Sahabi is as derived as *A. ultimus*, a good argument could be made for invalidating *A. petrocchii* and placing the sample in *A. ultimus*.

Because of the low-crowned, bunodont condition of their molars, anancine gomphotheres were considered to have been browsers that inhabited forests (Smart 1976). However, stable isotope analyses on tooth enamel from a number of

East and Central African sites, including Kakesio, indicate that anancines had predominantly C_4 -plant based diets (Cerling et al. 1999, 2003; Zazzo et al. 2000; Harris et al. 2003; Semaw et al. 2005; Kingston and Harrison 2007), except at Langebaanweg, South Africa, where C_3 grasses are inferred to have been prevalent (Franz-Odenaal et al. 2002). Preference for graze and the need to feed close to the ground, and possibly greater reliance on the trunk for food acquisition, might be correlated with the loss of lower tusks in this gomphothere subfamily.

Family STEGODONTIDAE Osborn, 1918

Genus *STEGODON* Falconer and Cautley, 1847

STEGODON SP. CF. *STEGODON KAISENSIS* Hopwood, 1939

Eyasi Plateau Occurrence: Upper Laetolil Beds: Loc. 22.

Diagnosis: Convergent on elephants in having molars constructed of enamel plates, high, antero-posteriorly compressed crania with elevated parietals and occipital, and mandibles with brevisrostrine symphyses and no lower tusks (Osborn 1942; Saegusa 1987, 1996; Kalb et al. 1996). Molars are very brachyodont, with plates separated by Y-shaped transverse valleys in lateral cross-section, and formed of numerous bi-laterally compressed conelets, or “mammellons” (Osborn 1942; Coppens et al. 1978; Kalb et al. 1996; Saegusa 1996).

Description: Only one stegodont specimen has been recovered from the Laetoli area, EP 1197/98, a fragment of a left upper fourth deciduous premolar (Fig. 9.5a, b). The specimen preserves one full plate, and parts of two other plates. Its length is +30.8+ mm, width is 44.6 mm, slightly worn height is 34.6 mm, and enamel thickness is 1.8 mm. The greater width than height of the tooth shows that it was low crowned. It has abundant cementum coating the anteriormost transverse valley, and infilling the posteriormost transverse valley. There are no accessory conules. The complete plate is

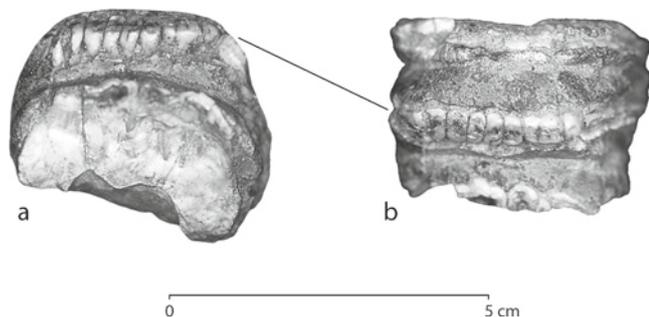


Fig. 9.5 Dental specimen of *Stegodon* sp. cf. *Stegodon kaisensis* from Laetoli. (a) Anterior oblique view, partial dP4 specimen EP 1197/98. (b) Occlusal view, partial dP4 specimen EP 1197/98. Note the transversely straight array of numerous, laterally compressed conelets, typical of stegodonts

formed of 11 laterally compressed conelets, and is transversely straight. The first two plates are apically divergent, indicating that this is an upper tooth, and the width of the specimen suggests it is a dP4.

Remarks: Elephants and stegodonts both have molars constructed of plates, rather than loph(id)s, and in both, plates of deciduous premolars may be formed of numerous conelets. The identification of EP 1197/98 as a stegodont is based on the lateral compression of the conelets, so that each has a greater mesio-distal than transverse dimension.

Stegodonts are best known in Africa from latest Miocene to mid Pliocene sites in Central Africa (Brunet et al. 1998, 2000; Zazzo et al. 2000; Brunet 2001; Fara et al. 2005) and the Western Rift (Hopwood 1939; MacInnes 1942; Cooke and Coryndon 1970; Coppens et al. 1978; Sanders 1990; Yasui et al. 1992; Pickford et al. 1993; Tassy 1995). By comparison, in East Africa stegodont occurrences are extremely rare, known only from a handful of specimens from the Tugen Hills, Kenya (Sanders 1999), Manonga Valley, Tanzania, and the Omo, Ethiopia (Beden 1975, 1976), of late Miocene to late Pliocene age (Harrison and Baker 1997; Kingston et al. 2002; Alemseged 2003). Thus, it is not surprising that only a single specimen has been recovered from the Laetoli area. Together with the Manonga specimens, the Laetoli tooth represents the southernmost extent of stegodonts in Africa.

Only one species of stegodont, *Stegodon kaisensis*, is currently recognized in Africa (Sanders et al. 2010). Tassy (1995) has divided this species into a primitive “Nkondo stage” and more derived “Warwire stage,” separated by slight differences in crown height, plate number, conelet compression, and development of cementum. Based on Tassy’s criteria, EP 1197/98 is most similar to “Warwire stage” molars from the Western Rift, Koro Toro, Chad, and the Omo, Ethiopia, of mid to late Pliocene age.

Based on their extreme brachyodonty, upper tusk morphology, body proportions, and isotopic analysis of South Asian molar specimens, stegodonts have been depicted as forest-dwelling browsers (Osborn 1921, 1942; Cerling et al. 1999). Isotopic analysis of Central African stegodonts, however, shows that during the mid to late Pliocene, their feeding habits in that region shifted from browsing to grazing (Zazzo et al. 2000). Because the East African stegodont sample, including EP 1197/98, has not been similarly isotopically sampled, it is not known if they followed the same trend.

Family ELEPHANTIDAE Gray, 1821

Subfamily ELEPHANTINAE Gray, 1821

Genus *LOXODONTA* Cuvier, 1825 (anonymous emendation 1827)

LOXODONTA SP. CF. *LOXODONTA COOKEI* Sanders, 2007

Eyasi Plateau Occurrence: ?Lower Laetolil Beds: Endolele (Endulele) = Esere 1.

Diagnosis: *Loxodonta cookei* is a primitive loxodont elephant that retained permanent third and fourth premolars. It is further distinguished from other species of *Loxodonta* by having fewer molar plates and lower hypsodonty indices, usually less than 100 (third molar width exceeds height; Sanders 2007). 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 $x6$; $P3=x3x-x4$; $M1=5x-x6$; $M2=x5x-x6x$; $M3=7-8$.

Description: A partial third molar with four preserved plates from Endolele (Endo: LS BKE 35) is wider (93.6 mm) than high (79.0 mm), with each plate composed of between four-six conelets. Lamellar frequency is 4.0. In anterior view, the plates are broadest basally and taper gradually inward toward the crown (Fig. 9.3f). In lateral view, the plates are parallel-sided and separated by U-shaped transverse valleys that are antero-posteriorly compressed and filled with cementum (Fig. 9.3f). Distribution of accessory conules suggests that they would have been incorporated into loxodont sinuses, or “<>” figures, with wear of enamel.

Other fragmentary molar specimens, collected more recently from Esere 1, may also belong to this taxon. The most substantial of these specimens is EP 117/99, a partial third molar with a greatest width of 89.4 mm, and enamel thickness reaching 3.3 mm.

Remarks: The morphology of the elephant molar from Endolele is more primitive than that of *L. exoptata* molars in anterior cross-sectional shape (Fig. 9.3f compared with Fig. 9.8) and crown height. Its closest resemblance is to molars of *L. cookei*, which are best documented at the latest Miocene-early Pliocene site of Langebaanweg, South Africa and that have also been recovered from the Chemeron Fm. (5.3–4.0 Ma; Hill et al. 1985, 1986; Deino et al. 2002) and possibly from the Lukeino Fm. (6.2–5.6 Ma; Hill et al. 1985, 1986; Tassy 1986; Hill 2002) in the Tugen Hills, Kenya, as well as from the Nkondo Fm. in the Nkondo-Kaiso region, Uganda (ca. 5.0 Ma; Pickford et al. 1993; [= *Loxodonta* sp.]. “Lukeino stage” of Tassy, 1995) (see Sanders 2007). In third molars of this species, lamellar frequencies are low (3.4–4.2), and crown height rarely exceeds width (hypsodonty indices range from 81–102). Molars are also primitive in having fewer plates than all other crown elephant species (*Mammuthus* spp., *Elephas* spp., *Loxodonta* spp.); for example, third molars have only seven-eight plates. As in molars from the *L. exoptata*-*L. africana*+*L. cyclotis* lineage, in *L. cookei* molars accessory conules are lower than plate conelets and with wear form loxodont sinuses that may touch in the midline. *Loxodonta cookei* is contrasted with the contemporaneous *L. adaurora* by the development of more prominent loxodont sinuses, and appears to have been a late Miocene-early Pliocene precursor of the *L. exoptata*-*L. africana*+*L. cyclotis* clade. The presence of a primitive loxodont elephant at Endolele supports the inference made from its anancine fossils that it is older than Kakesio and other

localities in the Eyasi Plateau that have exposures of the Lower Laetolil Beds.

LOXODONTA EXOPTATA (Dietrich, 1941)

Eyasi Plateau Occurrence: Lower Laetolil Beds: Kakesio, Kakesio 2, 6, 8, Noiti 3, and Emboremony; Upper Laetolil Beds: Loc. 1–9, 9S, 10, 10E, 10W, 10NE, 11–17, 19–22, 22E, and Garusi River southwest of Norsigidok; Upper Ndolanya Beds: Loc. 7E (=10West in Beden 1987a), 14 (=18 in Beden 1987a), 18, 22S (Nenguruk Hill), 22E, and Silal Artum.

Diagnosis: Molars slightly hypsodont with moderately thick enamel (third molar ET=2.0–4.0 mm), and plates closer spaced than in archaic elephants (third molar LF=4.1–5.5). With occlusal wear, anterior and posterior accessory central conules contribute to formation of loxodont median sinuses that occur throughout the length of molar crowns; when wear is light, sinuses may not be apparent or enamel figures may form “propeller” shapes, with the center of the figure prominently rounded and the lateral segments of the figure antero-posteriorly compressed (Kalb and Mebrate 1993; Sanders 1997). Notably, the main criterion used by Dietrich (1941) for creating the species “*exoptatus*” from Laetoli was the similarity of its occlusal enamel figures in the anterior molars to those in *Loxodonta africana*. Compared with *L. cookei*, molars of *L. exoptata* have more plates, are higher crowned, have their widest point higher on the crown, and have higher lamellar frequencies, and permanent premolars were apparently lost (Sanders 2007). Distinguished from contemporaneous *L. adaurora* by molars with narrower plates, more delicate plate construction, and more pronounced development of median sinuses.

Plate formulae: $dp2-x3x-x4x$; $dp3=x6x$; $dp4=?7$; $m1=x7x-x8$ (?); $m2=8-9x$; $m3=11-12$; $dP2=x3x=x4$; $dP3=x5x=6x$; $dP4=?x6-x7x$; $M2=8x-9x$; $M3=11-12$ (Beden 1983, 1987b; Harris et al. 2003; Sanders et al. 2010).

Description: Fossil remains of *Loxodonta exoptata* numerically dominate the proboscidean sample from the Eyasi Plateau. Specimens attributable to this species were first recovered by Louis Leakey and party in 1935, and later were added to by more significant collections made by Kohl-Larsen in 1938–1939, Mary Leakey in the 1970s and early 1980s, and the Eyasi Plateau Expedition between 1998–2005. These remains derive primarily from the Upper Laetolil Beds, and a few are also known from the Lower Laetolil Beds and the Upper Ndolanya Beds (Table 9.4). There are no crania of *L. exoptata* known from Laetoli or elsewhere, and the only parts of mandibles that exist for the species are a right dentary fragment with an m2 and crypt for m3 from Kanapoi, Kenya (KNM-KP 30611) and right dentary fragment with an m3 from the Kohl-Larsen collection from Laetoli (lectotype GADJ 2/39=IPUB 24). The Kanapoi dentary is 111.0 mm high and 102.0 mm wide at the mid-crown of m2.

Table 9.4 Inventory and dimensions of identifiable *Loxodonta exoptata* cheek teeth from the Eyasi Plateau, in mm. All specimens are from the Upper Laetolil Beds, Laetoli, unless otherwise specified

Specimen	Locality	Plates	L	W	H	ET	HI
dP2							
LAET 75-3025	9 south	x3x	26.0	21.1	10.5+	–	–
LAET 74-212	5	x4 or x3X	26.0	21.0	–	–	–
IPUB (18)		x3x	27.0	19.0	13.0	–	68
IPUB (20)		x3	25.0	22.0	–	–	–
IPUB (21)		x3x	26.0	22.0	17.0	–	77
IPUB (22)		x3+	23.0+	22.0	–	–	–
EP 268/03	16	x3x or x4	22.6	16.6	12.0+	–	–
EP 895/98	9 south	x4	22.0	18.3	11.6	–	64
		x3x	21.9	17.8	–	–	–
EP 2652/00	2	x3x	20.3	15.4	–	–	–
EP 209/99	9	x3+	17.0+	14.0	10.7+	–	–
EP 207/01	3	x4x	28.7	21.2	–	–	–
EP 265/99	9 south	x3x	–	–	–	–	–
EP 255/01	5	+2x	+15.3	18.8	14.9	–	79
EP 268/03	16	3x	22.6	16.6	+12.0	–	–
EP 878/98	10	2 plates	–	15.2	12.0	–	79
EP 3696/00	21	–	–	–	–	–	–
EP 4127/00	8	–	–	–	–	–	–
EP 280/04 ^a	18	x3+	17.4+	11/6+	–	–	–
dp2							
LAET 75-500	11	x3x	19.8	14.3	10.5	–	73
LAET 74-312	6	x3x	18.8	15.2	–	–	–
IPUB (17)		x3x	22.0	15.0	15.0	–	100
IPUB (23)		3x	20.0	16.0	13.0	–	81
EP 517/98	10	x3x	22.3	16.3	–	–	–
EP 301/00	8	+3x	21.3	17.2	17.0	–	99
EP 112/01	6	x3+	25.0	18.5	–	–	–
EP 753/00	2	x3+	28.8	20.7	14.0	–	68
EP 499/01	2	x3x	25.0	–	–	–	–
EP 792/00	10 east	x3 or 4	27.9	21.9	–	–	–
EP 1150/00	8	–	–	–	–	–	–
EP 1479/00	7 east ^a	x4 or x3X	21.0	17.0	18.0	–	106
dP3							
LAET 75-3451	21	6	55.1	38.3	33.0	1.5	86
LAET 78-4996	2	6	e 55.8	34.1	21.6+	–	–
LAET 75-3044	17	6 or x5	58.8	37.9	–	1.0–1.4	–
LAET 74-114	1	+3+	+31.3+	–	–	1.1–1.3	–
LAET 74-106	x	+4	+50.0	–	–	1.3–1.6	–
LAET 75-1249	8	+3+	–	–	–	1.3–1.5	–
LAET 75-3311	19	+4	+45.0	41.0	–	1.5	–
LAET 76-3950	18 ^a	7	53.0	50.0	36.0	1.4–1.5	90
BM(NH) 14941		x6x	59.8	31.0	–	1.2	–
BM(NH) (9)		+4x	+41.0	40.0	–	1.3–1.7	–
LIT.AS 10-VI-35		x6+	61.4+	37.2	–	–	–
IPUB (12)		6	54.0	40.0	–	1.5	–
IPUB (16)		6x	71.0	43.0	–	1.5–1.8	–
EP 1323/04	5	6x	56.2	33.4	–	–	–
EP 121/04	22	+3+	+24.5+	33.9	–	1.3	–
EP 113/01	6	+2x	+27.8	33.8	–	1.0–1.5	–
EP 681/03	2 west	–	–	–	–	–	–
EP 3695/00	8	–	–	–	–	–	–
EP 3349/00	15	x3+	–	–	–	–	–
EP 693/00	2	–	–	–	–	–	–
EP 692/00	2	–	–	–	–	–	–

(continued)

Table 9.4 (continued)

Specimen	Locality	Plates	L	W	H	ET	HI
EP 1148/00	8	–	–	–	–	–	–
EP 612/98	10 west	–	–	–	–	–	–
EP 807/98	10 west	–	–	–	–	–	–
EP 733/98	10 west	–	–	–	–	–	–
EP 734/98	10 west	–	–	–	–	–	–
EP 1081/98	9	–	–	–	–	–	–
EP 1619/98	10 west	–	–	–	–	–	–
dp3							
LAET 76-3963	9 north	6	66.8	35.8	–	1.2	–
LAET 78-5364	21	+4x	+38.3	32.0	–	1.6–1.8	–
LAET 78-5125	4	+5	e 61.5	37.1	–	–	–
LAET 75-1090	6	6x	62.3	34.1	–	1.0–1.5	–
LAET 78-4635	3	4+	41.2+	28.6+	–	–	–
LAET 75-1711	2	x6x	69.3	40.7	–	1.4–2.0	–
LAET 75-1366	12 south	x5+	45.1+	33.1+	26.0+	–	–
LAET 75-822	7	x3+	27.0+	28.4+	–	–	–
LAET 74-280	9	+4x	+38.6	33.1	–	–	–
LAET 78-5164	9	x6	82.7	38.0	32.0	–	84
LAET 75-1503	9	x2+	19.0+	–	22.0	–	–
LAET 75-1930	2	+3	+26.0	–	–	1.5	–
LAET 75-2823	6	–	–	–	–	–	–
LAET 74-236	8	–	–	–	–	–	–
BM(NH) 14942		x6x	73.3	36.2	–	1.2	–
BM(NH) (8)		?6	+62.0	38.0	–	1.6	–
BM(NH) (16)		x7	59.0+	34.0	–	1.4–1.6	–
LM.AS 7-VI-35		+5x	+55.5	33.1	–	0.8–1.0	–
IPUB (9)		+4x	+40.0	35.0	–	1.4–1.7	–
IPUB (10)		x3+	30.0+	–	–	1.2–1.5	–
IPUB (11)		6	55.0	36.0	–	1.5	–
IPUB (13)		7x	70.0	38.0	33.0	1.2–1.5	87
IPUB (14)		+4	+42.0	36.0	–	1.2–1.6	–
EP 2201/03	7	x5x or x6	66.0	–	–	–	–
EP 896/98	9 south	+4x	+43.2	34.6	–	1.6–1.9	–
EP 911/04	21	x2+ or 3+	22.0+	28.0	–	1.8	–
EP 910/04	21	x3+ or 4+	41.2+	31.2	–	–	–
EP 370/01	2	x3+	41.5+	30.2	–	–	–
EP 269/03	16	+4	56.3+	40.4	–	–	–
EP 815/01	18	–	–	–	–	–	–
EP 2362/03	13 east	–	–	–	–	–	–
EP 270/03	16	–	–	–	–	–	–
EP 1619/98	10 west	–	–	–	–	–	–
dP4							
LAET 75-2248	10 east	+4x	+63.6	47.1+	–	2.0–2.2	–
LAET 75-2180	4	x3+	46.7+	47.0	–	2.5	–
LAET 75-3043	12	3+	27.0+	–	47.0	1.8–2.0	–
LAET 74-196	5	5+	49.8+	47.1	–	–	–
LAET 75-2267	10	+1x	–	–	–	2.0	–
LAET 75-2930	4	5+	47.0+	53.0	–	1.8–2.2	–
LAET 74-212	5	–	–	–	–	–	–
BM(NH) (4)		4+	45.0+	–	–	2.0	–
BM(NH) (7)		3+	32.0+	–	–	1.8	–
LIT.AS 10-VI-35		+3x	+43.4	58.7	47.0	–	80
LIT.AS 6-VI-35		x3+	52.0+	41.0+	–	–	–
IPUB (6)		+4	+45.0	61.0	–	2.0	–
IPUB (25)		+4	–	–	–	1.8	–
EP 1887/03	1	+4x	+65.5	48.2	–	1.9–2.2	–
EP 1698/00	5	+6+	+73.8+	39.8+	–	2.2–2.5	–

(continued)

Table 9.4 (continued)

Specimen	Locality	Plates	L	W	H	ET	HI
EP 691/00	2	x3+	46.7+	50.8	45.0	2.7	89
EP 633/98	10 west	+5+	+58.5+	47.5	45.0	1.6–2.8	95
EP 808/98	10 west	x6+ (originally x7x)	76.5+	45.4	–	–	–
EP 3065/00	5	–	–	–	–	–	–
EP 516/98	10	–	–	–	–	–	–
EP 767/03	9	–	–	–	–	–	–
EP 496/05	1	–	–	–	–	–	–
EP 068/03	2 west	–	–	–	–	–	–
dp4							
LAET 76-3919	1	x4+	67.5+	47.1	–	1.2–1.6	–
LAET 78-4923	5	6+	72.5+	46.1	–	1.8–2.5	–
LAET 75-2027	10	+3x	+54.0	44.0	–	2.3–2.8	–
LAET 75-2553	10	+3x	+45.3	39.5+	–	1.8–2.2	–
LAET 75-2552	10 northeast	7+	85.8+	46.8	48.0	1.4–2.0	103
LAET 75-519	1	–	–	–	–	–	–
LAET 75-1452	9 south	Plate	–	–	–	–	–
LAET 78-5164	9	–	–	–	–	–	–
LAET 75-2240	10 east	–	–	–	–	–	–
LAET 75-3102	12	–	–	–	–	–	–
LAET 75-1969	14 ^a	9	113.0	–	–	1.8–2.2	–
?dp4?							
LIT.AS 10-VI-35		+4x	+41.1	38.9	–	1.3	–
BM(NH) no #		x3+	52.0+	41.0+	–	–	–
BM(NH) (1)		4+	35.0+	–	–	1.8	–
BM(NH) (6)		+4x	+72.0	59.0	–	2.0–2.5	–
BM(NH) (10)		4+	45.0+	–	–	1.8–2.1	–
IPUB (2)		5+	55.0+	–	–	1.8–2.0	–
IPUB (15)		5+	53.0+	–	–	1.5–1.8	–
EP 1147/00	8	+4x	+46.4	36.2	–	1.2	–
EP 2201/03	7	–	–	–	–	–	–
EP 269/03	16	–	–	–	–	–	–
EP 2995/00	–	–	–	–	–	–	–
EP 016/98	Kakesio 2 ^b	+4+	+71.7+	50.0+	–	2.5–2.7	–
EP 556/04	Silal Artum ^a	–	–	–	–	–	–
M1							
LAET 75-488	10 west	+3+	+50.0+	59.5	78.5	2.3–2.7	132
LAET 75-3101	12	6+	92.4+	–	–	3.3	–
LAET 74-302	6	+3x	+59.0	–	–	2.0–2.2	–
LOL:AS 12-VI-35		+4+	+64.1+	72.7	–	3.2–3.7	–
EP 559/00	22	+3+	44.8+	57.0	–	2.4–3.0	–
EP 695/00		–	–	–	–	–	–
EP 1617/00		–	–	–	–	–	–
EP 1957/00		–	–	–	–	–	–
m1							
LAET 75-522	4	+6x	+125.0	60.0	–	2.2–3.1	–
LAET 74-194	5	+5	+90.2	63.6	–	2.6–3.9	–
LAET 78-4829	18 ^a	+4	+67.0	+63.0	–	2.5–2.8	–
LAET 75-277	18 ^a	+2+	–	–	–	2.0–2.4	–
BM(NH) (5)=LIT.AS 6-VI-35		x4+	60.0+	–	–	2.4–2.8	–
LIT.AS 6-VI-35		+4x	+74.2	54.0	–	–	–
IPUB (5)		+5	+113.0	–	–	2.4–2.8	–
IPUB (31)		+3x	+58.0	–	–	2.5	–
IPUB (35)		+5x	+91.0	56.0	–	2.5–2.8	–
IPUB (36)		+4+	+107.0+	63.0	–	2.3–2.7	–
EP 1270/01	9 south	x7x or x8	120.5	–	–	2.4–2.6	–

(continued)

Table 9.4 (continued)

Specimen	Locality	Plates	L	W	H	ET	HI
EP 560/00	22	+3+	+77.4+	–	–	2.8–3.5	–
EP 2406/00	16	+4x	+122.2	64.6	–	3.0–3.3	–
EP 1196/98	22	+6	+118.7	67.0	–	3.0–4.0	–
EP 1605/04	11	+3+	+44.4+	60.7	–	2.2	–
KK 82-249	Kakesio ^b	7	133.7	+64.0	–	3.0	–
M2							
LAET 75-3818A	7 east (10 west in Beden, 1987a)	+6	+140.0	–	–	3.0–3.5	–
LAET 75-3818B	7 east (10 west in Beden, 1987a)	+6	+145.0	67.9	–	3.0–3.5	–
LAET 75-521	2	+5+	+107.1+	76.1	–	3.0–3.5	–
LAET 76-4117	12	+4+	+65.6+	+56.7	–	2.3–3.1	–
LAET 75-428		9x	162.0	78.0	80.0	3.0–3.6	103
LAET 75-2574B	15	–	–	–	–	–	–
LAET 75-1684	14 ^a	7+	–	–	–	–	–
LOL.AS 12-VI-35		+3+	+71.9+	+78.0	–	2.7–3.7	–
LOL.AS 12-VI-35		+3+	+88.7+	77.7+	–	2.5–3.0	–
BM(NH) 15416		+7x (x9 in Beden, 1987a)	+195.0	86.0	–	3.4–3.7	–
IPUB (7)		+4	+73.0	80.0	–	3.0–3.2	–
IPUB (28)		7+	160.0+	–	–	3.2	–
IPUB (33)		+6x	+103.0	80.0	–	3.0–3.4	–
EP 320/03	3	x2+	58.8+	73.6	–	3.0–3.2	–
EP 694/00	2	+7	+122.7	75.7	–	3.0–4.0	–
EP 519/98	10	8x or 9	+190.0	64.9	72.0	3.4–3.8	111
EP 017/98	Kakesio 2 ^b	+3x	+62.7	68.2	+61.0	2.9–3.5	–
EP 029/99	Kakesio 6 ^b	5+	107.5+	–	–	2.5–2.7	–
m2							
LAET 75-2791	5	+5	+90.0	69.8	86.0	2.4–2.6	123
LAET 75-1365	12	+4	+108.0	–	–	3.1–3.3	–
LAET 75-3361	21	–	–	–	–	–	–
IPUB (3)		+6	+109.0	75.0	–	–	–
IPUB (4)		+7	+155.0	81.0	–	3.2–3.5	–
IPUB (27)		+4x	+88.0	79.0	–	3.1	–
EP 3173/00	10 west	+3x or +4	+59.8	64.6+	–	2.4–3.6	–
EP 3559/00	12	+4x	+105.1	78.0	84.0	–	108
KK 82-290B	Kakesio ^b	x4+	87.5+	72.5+	–	3.0–3.4	–
M3							
LAET 75-3370	21	+6x	+135.0	85.0	–	3.0–3.7	–
LAET 74-325	7	3+	74.2+	88.8	99.0	3.5–3.7	111
LAET 75-2135	2	x7+	153.0+	84.0	–	3.1–3.5	–
LAET 75-3310	19	x7+	150.0+	77.1	87.0+	3.0–3.3	–
LAET 76-4558	14 ^a	11x (13 in Beden, 1987a)	250.0	93.2	100.0	3.0–4.0	107
IPUB (30)		+4x	+103.0	79.0	–	3.4–3.8	–
IPUB (32)		+5x	+118.0	84.0	–	3.5	–
EP 321/03	3	+6+	+128.7	75.4+	–	3.6–3.7	–
EP 1023/00	16	+4+	+59.0+	79.2	111.5	3.2–3.4	141
EP 1618/00	3	+12x	290.0	97.5	140.0	3.5	144
KK 82-no #	Kakesio ^b	+10x	+210.0	76.0+	55.0+	3.0–3.3	–
m3							
LAET 75-489	10 west	+3+	+40.0+	87.6	–	2.5–4.0	–
LAET 79-5458	14 ^a	+4+	+85.5+	+75.3	–	3.5–4.0	–
LAET 80-6403	18 ^a	11	260.0	82.0	–	3.0–3.5	–
IPUB (8)		+5+	+137.0+	–	–	3.2–3.5	–

(continued)

Table 9.4 (continued)

Specimen	Locality	Plates	L	W	H	ET	HI
IPUB (24)		+7x	+205.0	84.0	97.0	3.0–3.3	115
Lectotype							
IPUB (26)		+3+	+73.0+	–	–	3.0–3.3	–
IPUB (29)		+4+	+85.0+	84.0	+80.0	3.5	–
IPUB (34)		+7x	+165.0	93.0	–	3.4–3.7	–
IPUB (37)		+8	+184.0	82.0	–	3.2–3.6	–
EP 2295/00	7	+5+	+98.5+	85.7	–	3.0–4.0	–
EP 696/00	2	–	–	–	–	–	–
EP 1650/04	4	–	–	–	–	–	–
EP 029/99	Kakesio 6 ^b	–	–	–	–	–	–

BM(NH), LIT.AS, and LM.AS specimens are from the 1935 collection of Louis Leakey. IPUB specimens are from the Kohl-Larsen collection and their measurements are from Beden (1987a). KK and LAET specimens are from the Mary Leakey collection. EP specimens are from the collection of Eyasi Plateau expeditions

e estimated, *ET* enamel thickness, *H* height, *HI* hypsodonty index, $H \times 100/\text{width}$, *L* length, *W* width, *x* indicates an anterior or posterior cingulum (id), *X* indicates a very large cingulum (id), or incipient plate, + indicates a missing portion of a specimen, and that the dimension was greater when complete

^a specimen from the Upper Ndolanya Beds, Laetoli

^b specimen from the Lower Member of the Laetolil Beds

Most of the Eyasi Plateau specimens consist of isolated teeth and tusk fragments. Dietrich (1942: 73) reported a total of 108 elephant teeth from Laetoli, of which 42, or 39%, are deciduous, and the remainder permanent molars. Beden (1987a: 263) sorted these into categories of “very young” (dP2/dp2–dP3/dp3), 24%; “young” (dP4/dp4–M1/m1), 34%; and “adult” (M2/m2–M3/m3), 42%. Unfortunately, many of these teeth did not survive the ravages of World War II. From the combined Louis Leakey, Kohl-Larsen, and Mary Leakey collections, Beden (1987a) estimated that more than 100 individuals were represented, and that more than half of these individuals were infants or young juveniles at death. The recovery of a substantial number of teeth by the Eyasi Plateau Expedition skews the distribution towards infants and young juveniles even more (Table 9.4): 65% (138/213) of identifiable specimens are deciduous teeth (deciduous second premolars, 14%; deciduous third premolars, 29%; and deciduous fourth premolars 22%), and 35% (75/213) are permanent molars (first molars, 11%; second molars, 13%, and third molars 11%). Extant African elephants with only deciduous teeth in occlusion are calves and juveniles; puberty is reached as the first molar starts to emerge, and animals become mature coincident with the first molar being completely in place and well worn (Laws 1966; Sikes 1967). The small percentage of second and third molars in the Eyasi Plateau collections indicates that few prime adults or senior elephants are represented.

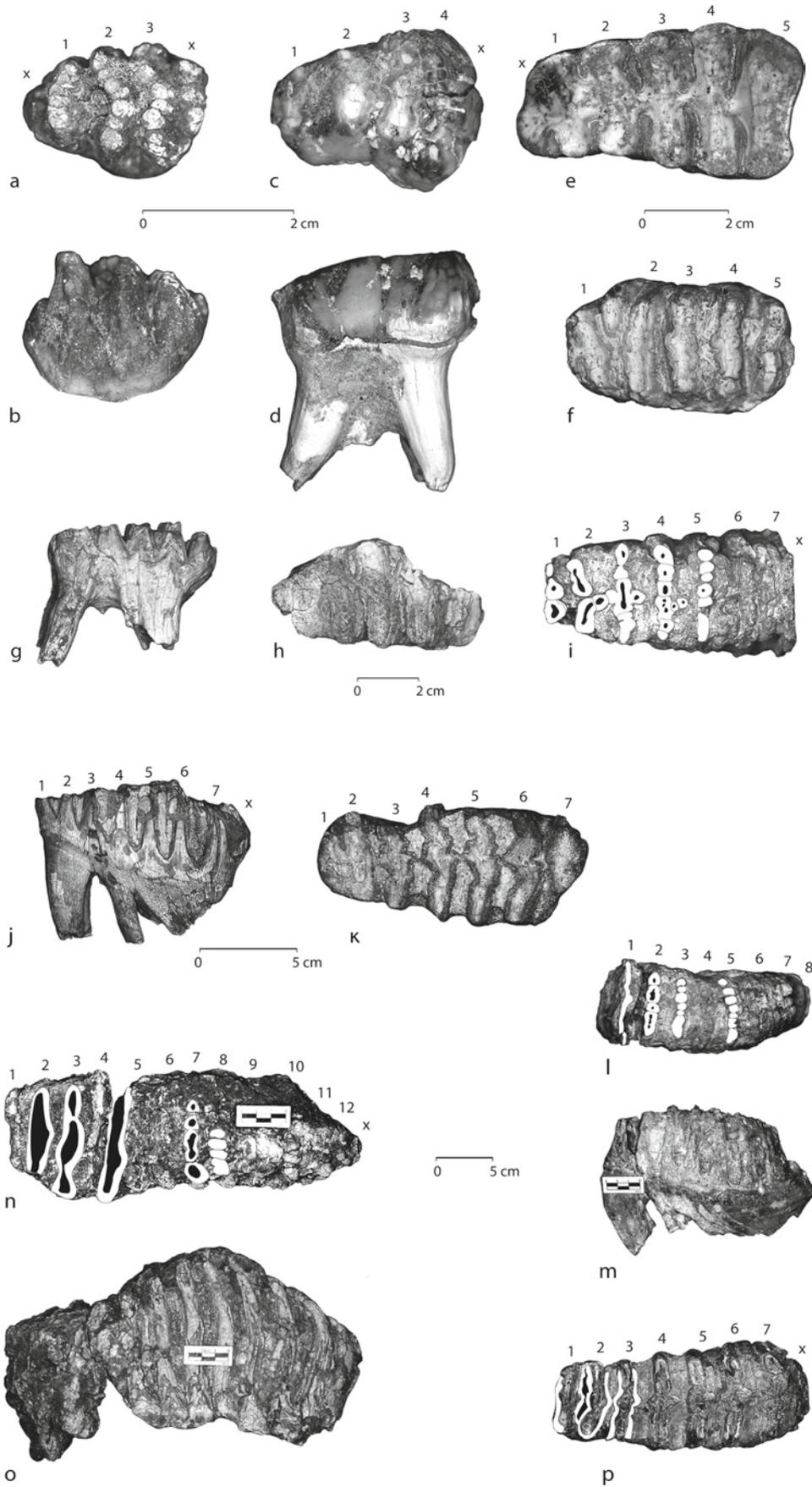
The increased ratio of deciduous-to-adult teeth in the sample between 1935 and 2005 can be explained as a collecting phenomenon, that is, larger, adult teeth were easily discovered early on, leaving smaller, deciduous teeth to be recovered by more recent intensive collecting episodes, with little fossil “turnover” from erosion in the interim. Because of the large number of fragmentary, unidentifiable specimens (not listed in Table 9.4), and because proveniences are poorly known for most of the Kohl-Larsen and Louis Leakey specimens, however, it is impossible to precisely calculate the minimum number of individuals for the combined *L. exoptata* sample.

Deciduous second premolars are relatively very small and sub-triangular in shape in occlusal view, with the narrower end anterior (Fig. 9.6a–d). They usually have three plates and anterior and posterior cingulae(id)s, or more rarely four plates. dP2 tends to be much broader posteriorly than dp2. Plates exhibit five or six apical digitations, but are not accompanied by accessory central conules.

Deciduous third premolars are approximately twice the size of the diminutive dP2/dp2s, and vary in occlusal shape from rectangular to sub-triangular, with the narrowest end anterior (Fig. 9.6e–g). Uppers are relatively broader and shorter than lowers. Small anterior and posterior swellings may project from moderately worn plates in the midline, but true loxodont sinuses are not generally formed. Depending on how anterior and posterior cingulae(id)s are counted, these teeth appear to

Fig. 9.6 Cheek tooth specimens of *Loxodonta exoptata* from Kanapoi, Kenya and the Eyasi Plateau, Tanzania. Anterior is to the left (x cingulum(id)). (a) Occlusal view, dp2 specimen EP 1479/00. (b) Lateral view, dp2 specimen EP 1479/00. (c) Occlusal view, dP2 specimen EP 207/01. (d) Lateral view, dP2 specimen EP 207/01. (e) Occlusal view, dp3 specimen LAET 76-3963. (f) Occlusal view, dP3 specimen EP 1323/04. (g) Lateral view, dP3 specimen EP 1323/04. (h) Occlusal

view, dP4 specimen EP 1698/00. (i) Occlusal view, dp4 specimen LAET 75-2552. (j) Lateral view, m1 specimen EP 1270/01 (reversed). (k) Occlusal view, m1 specimen KK 82-249. (l) Occlusal view, M2 specimen EP 519/98 (reversed). (m) Lateral view, M2 specimen EP 519/98 (reversed). (n) Occlusal view, M3 specimen EP 1618/00 (reversed). (o) Lateral view, M3 specimen EP 1618/00 (reversed). (p) Occlusal view m2 specimen KNM-KP 30611



have six-seven plates (or a lamellar formula as low as $x4x$), each formed of numerous (eight-nine) rounded conelets.

Deciduous fourth premolars tend to have at least six-seven plates, formed of stouter, rounded conelets. In each plate, the central conelet is larger than the lateral ones. As with all other cheek teeth, uppers are relatively wider and shorter than lowers. In occlusal view, these teeth are rectangular (Fig. 9.6h, i). Accessory central conules, particularly posterior ones, are more prominent than in other deciduous premolars, and with moderate wear enamel figures are propeller-shaped. With additional wear, loxodont sinuses may be formed, but when heavily worn enamel figures are rectilinear. LAET 75-1969, from the Upper Ndolanya Beds, has nine plates, but its length (113.0 mm) and enamel thickness (1.8–2.2) are undersized for a permanent molar, and consequently it has been interpreted as a dp4 (Beden 1987a). If so, it is the only complete deciduous fourth premolar known for the species, and indicates that either an estimate of six-seven plates for dP4/dp4 is too low, or that later demes of *L. exoptata* are more progressive in plate number. However, the resemblance of LAET 75-1969 to m1 specimen EP

1270/01 in length, plate number, and overall structure suggests that it is more likely to be a delicate m1 than a dp4.

Permanent molars from M1/m1 to M3/m3 (Figs. 9.6j–p and 9.7a–e) are similar in occlusal morphology, but increase serially in length, width, height, enamel thickness, and number of plates (see above; Table 9.4). Plates are formed of a modest number of conelets (usually five-seven, with the central conelet the most prominent), and in lateral view are parallel-sided and separated by U-shaped transverse valleys that are filled with cementum. Cementum covers plates in unworn specimens. Enamel is coarsely to moderately folded in worn specimens. Greatest width of plates is usually slightly above their bases (Fig. 9.8), and in transverse view plates taper gently towards their apices. Anterior and larger posterior accessory central conules are present throughout the crown, and are lower than plates. In unworn specimens or sections of molars, accessory conules may not be visible, and molars may appear to lack these structures and loxodont sinuses in light wear stages (Figs. 9.7a and 9.9a, b). Accessory conules are intimately attached to plates (Fig. 9.9d) and have their greatest girth at their mid-height (Fig. 9.9c), so it is only with moderate

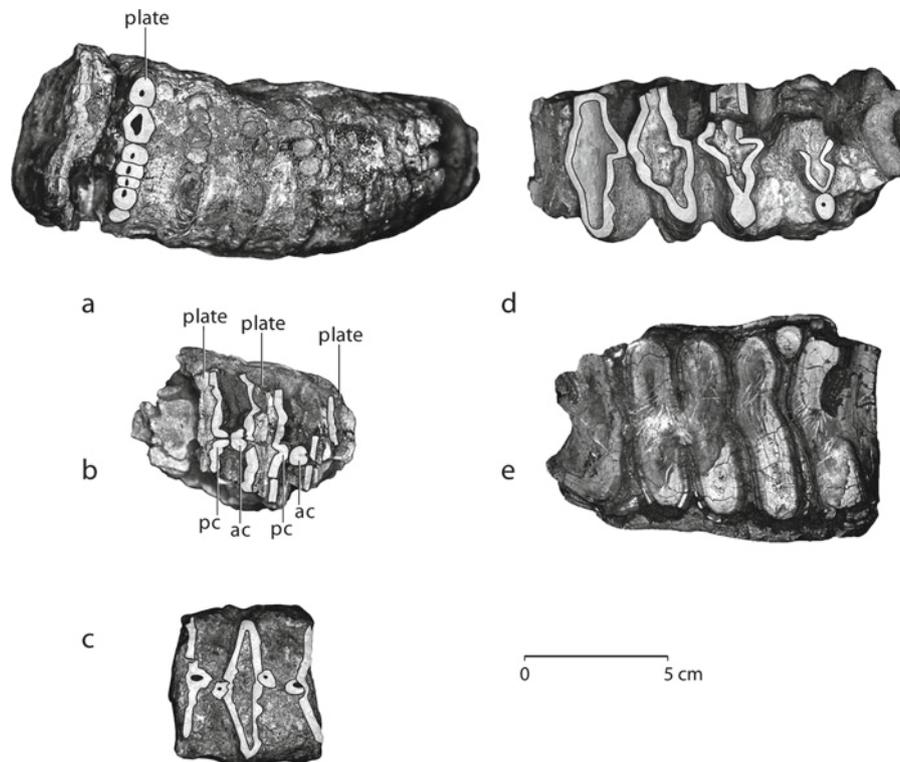


Fig. 9.7 Occlusal view, molar specimens of *Loxodonta exoptata* in different stages of wear (*ac* anterior accessory conule, *pc* posterior accessory conule). (a) Occlusal view, M2 specimen EP 519/98, with little or no wear on plates 3–8. No accessory conules are evident in association with plates 3–8, as they are still covered over with cementum. A small accessory conule is present posterior to and fused with plate 2. (b) Occlusal view, partial m1 specimen EP 560/00, in moderate wear. Accessory conules are evident anterior and posterior to plates, and were in the process of being incorporated into the enamel wear

figures. (c) Occlusal view, partial M1 specimen LAET 75-488, in medium wear. Angulation of plate arms and position of accessory conules contribute to the formation of antero-posterior “loxodont sinus” enamel wear figures. (d) Occlusal view, M2 specimen LAET 75-3818B, in medium-heavy wear. Accessory conules are completely incorporated into *L. africana*-like loxodont sinus enamel wear figures. (e) Occlusal view, ?M2 specimen EP 694/00, in heavy wear. The crown has been worn nearly to the level of the cervix, and the accessory conules and loxodont sinuses have been obliterated (see Fig. 9.9)

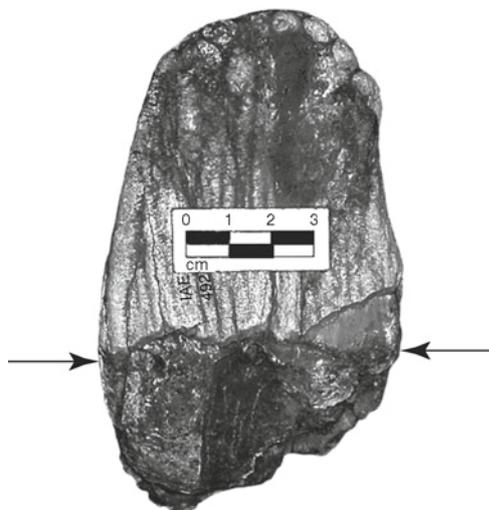


Fig. 9.8 Anterior view, molar plate, LAET 78-4927, *Loxodonta exoptata*. Note that the plate is higher than wide, gently tapered towards the apex, and the greatest width occurs about one-third of the total height of the specimen above its base (which is partially broken). Superficial apical digitations (“conelets”) are evident superiorly

wear that they begin to contribute to the formation of propeller shapes and loxodont sinuses, or “< >” enamel wear figures (Figs. 9.7b–d and 9.9e). In heavy wear, accessory conules taper away, and plates assume more rectilinear occlusal shapes with the obliteration of the midline sinuses (Figs. 9.7e and 9.9f). For this reason, molars of *L. exoptata* exhibit a high degree of variation in occlusal morphology, which has almost certainly contributed to the contentious taxonomic history of this taxon (see below). Even individual molars have plates worn differentially to a variety of different occlusal shapes, as, for example, in KNM-KP 30611, a complete right m2 from Kanapoi, Kenya (Fig. 9.6p).

There are also a number of largely isolated postcranial elements in the combined *L. exoptata* sample, primarily dense, compact podials that survive weathering well. Many of these are from the Upper Ndolanya Beds. The most complete elements are described here, and include LAET 75-1017 (Fig. 9.10a), a right astragalus from Loc. 7E that was listed by Beden (1987a) as a juvenile left astragalus. The dimensions of this podial are L=109.1 mm, W=127.1 mm, and H=80.2 mm. As noted by Beden, it differs from astragali of *Elephas* and is similar to those of *Loxodonta africana* in having a medial tuberosity that does not extend posterior to the tibial articular surface, and by the absence of a tuberosity on its neck. Another podial from the Upper Ndolanya Beds is LAET 76-18-263 (listed as 74-263 in Beden 1987a, but not described), a right navicular from Loc. 18. This podial is anteroposteriorly flattened and arcuate in anterior view (Fig. 9.10b), and measures 120.0 mm in width and 79.0 mm in height. Its dimensions make it a good fit for an astragalus the size of LAET 75-1017. Proximally, its astragalus surface

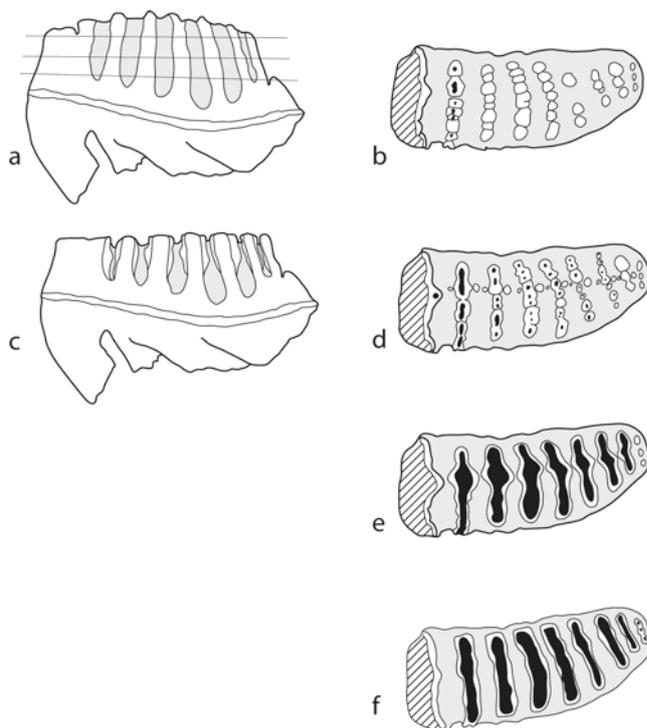


Fig. 9.9 Stages of molar wear and associated patterns of occlusal enamel wear figures, based on M2 specimen EP 519/98, *Loxodonta exoptata*. (a) Lateral view, unworn or lightly worn from plates 3–8. Note the tall, U-shaped transverse valleys, filled with cementum, and the parallel arrangement of the plates. Lines placed over the specimen indicate hypothetical areas of transverse cross-sectioning, reflected in occlusal diagrams c–f. (b) Occlusal view, plates 3–8 unworn or lightly worn. In this stage, individual apical digitations, or conelets, can be seen, but accessory conules are not evident, and plates are approximately rectilinear in shape transversely. (c) Lateral view, in light wear (*uppermost line*). Cementum is cut away, and the anterior and posterior accessory conules can be seen. Note that the greatest diameter of the accessory conules is at their mid-height or slightly below, occlusally producing the greatest development of loxodont sinuses throughout the crown. (d) Occlusal view, light wear on the plates (*uppermost line*). Conelets have not worn together to form enamel loops yet, but accessory conules are evident anterior and posterior to the plates. (e) Occlusal view, medium wear on the plates (*middle line*). Conelets have combined to form complete enamel loops, which incorporate anterior and posterior accessory conules to form “loxodont sinuses” that may touch in the midline. (f) Occlusal view, heavy wear on the plates (*lowermost line*). Accessory conules and loxodont sinuses are obliterated, and enamel wear figures are transversely rectilinear in shape

is modestly concave, and distally it presents flattened facets for ento-, meso-, and ectocuneiforms and cuboid. A third podial from the Upper Ndolanya Beds is LAET 75-1033, a right ectocuneiform from Loc. 7E. This small bone is subtriangular in shape (Fig. 9.10c), and is 79.4 mm in its longest dimension and 46.7 mm in width. Also from Loc. 18 in the Upper Ndolanya Beds is a left unciform, LAET 76-18-308 (listed as 74–308 by Beden 1987a, but not described). This blocky, trapezoidal-shaped element has a greatest length of 133.7 mm, width of 112.4 mm, and thickness of 102.7 mm. Distally, it has distinct, confluent facets for metacarpals III–V,

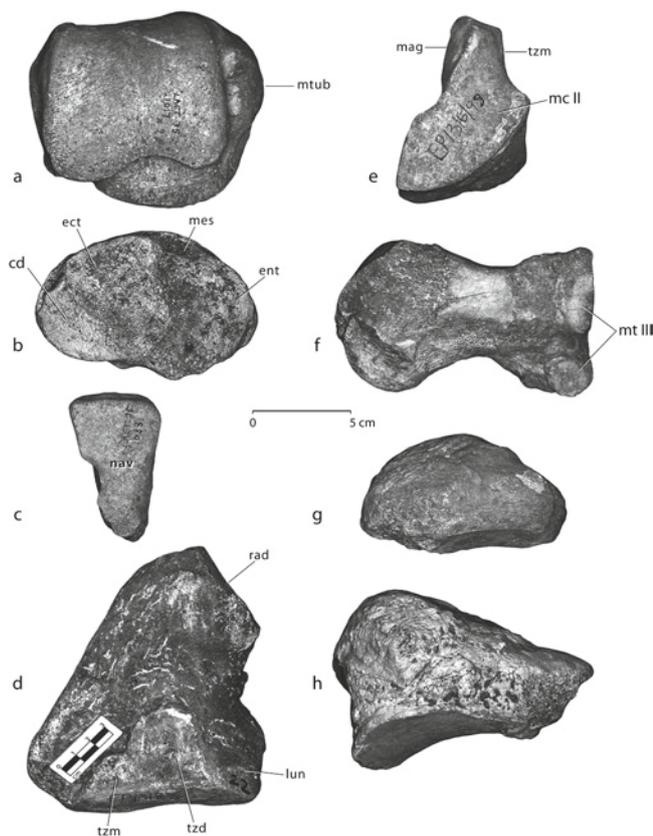


Fig. 9.10 Postcranial specimens of *Loxodonta exoptata* from Laetoli (*cd* cuboid, *ect* ectocuneiform, *ent* entocuneiform, *lun* lunate, *mag* magnum, *mc II* metacarpal II, *mes* mesocuneiform, *mt III* metatarsal III, *mtub* medial tuberosity, *nav* navicular, *rad*, radius, *tzd*, trapezoid, *tzm* trapezium). (a) Superior view, right astragalus LAET 75-1017. (b) Distal view, right astragalus LAET 76-18-263. (c) Proximal view, right ectocuneiform LAET 75-1033. (d) Lateral view, right scaphoid EP 1318/98. (e) Distal view, left trapezoid EP 1316/98. (f) Lateral view, left mt IV LAET 78-4909. (g) Lateral view, patella EP 1422/04. (h) Lateral view, patella EP 402/04

two elongate articular facets for the os magnum medially, and a large squared surface proximally for articulation with the triquetrum (cuneiform). The elephant postcranial collection of Mary Leakey from the Upper Ndolanya Beds is supplemented by the more fragmentary LAET 75-1068, distal radius, LAET 76-18-177 (74-177 in Beden 1987a), femoral head, and LAET 75-2981, vertebral fragments.

Collecting by Eyasi Plateau expeditions have contributed to the elephant postcranial sample from the Upper Ndolanya Beds. EP 4023/00, from Loc. 7E, is a manual sesamoid that measures 63.8 mm in height, 37.8 mm in width, and has a thickness of 36.1 mm. A thoracic vertebral body, EP 3031/00, was recovered from Loc. 1. A fragmentary os magnum, EP 1227/00, was also collected from Loc. 22 S. EP 1317/98, from Loc. 22 S, is a mostly complete sacrum missing its caudalmost extreme; its dimensions are $L=210.0+$ mm, $W=280.0$ mm, and thickness=100.0 mm. The discrete

nature of the bone scatter at Loc. 22 S makes it possible that several other elephant postcranials from the locality are from the same individual. EP 1318/98 is a right scaphoid in good preservation, and closely resembles the scaphoid from Noiti 3 (EP 461/04) (Fig. 9.10d; compare with Fig. 9.3d). EP1318/98 measures 142.7 in length and 116.0 mm in width. The manus is further represented at Loc. 22S by EP 1316/98, a left trapezoid. This element laterally has two curved facets for the os magnum, a large curved facet medially for the os trapezium, and flattened, keyhole shaped articular surfaces proximally and distally for the os lunate and mc II, respectively (Fig. 9.10e). Dimensions of the facet for mc II are $L=86.2$ and $W=78.5$; dimensions of the facet for the os lunate are $L=78.0$ mm and $W=56.3$ mm; and overall length of the specimen is 105.6 mm.

Postcranials from the Upper Laetoli Beds include LAET 75-1250, probably a proximal phalanx for mt II, which measures 50.7 mm in length and is 52.2 mm wide at the base and 42.8 mm wide distally. A right patella, EP 1422/04 (Fig. 9.10g), derives from Loc. 6, and may be from a female individual, with its small dimensions of $L=118.0$ mm, $W=86.3$ mm, and thickness=68.2 mm. A larger, presumably male left patella, EP 402/04 (Fig. 9.10h), from Loc. 16, measures 137.6 mm in length, 99.3 mm in width, and has a thickness of 95.7 mm, due in large part to its robust proximal end. Earlier, Mary Leakey collected LAET 78-4909, a left mt IV (Fig. 9.10f), from Loc. 22 south. This metapodial is robust, with a length of 131.3 mm and basal, midshaft, and head widths of 72.8 mm, 53.5 mm, and 77.5 mm, respectively. This is an important specimen because it exhibits a number of loxodont elephant features, enumerated by Beden (1987a), such as double facets for mt III that do not touch the cuboid articulation.

Other proboscidean postcranials were collected from the Lower Laetoli Beds. These include an abraded left mc II, EP 210/03, from Kakesio 8, with a length of 140 mm and width across the base of 54.6 mm and across the head of 65.0 mm. In size and morphology, it appears to belong in the elephant sample. Collecting in 2004 at Noiti 3 yielded an elephant maxillary fragment with alveoli for M2-3 associated with postcranial specimens. Each postcranial element carries the same accession number, EP 461/04. Among these are a first cervical vertebra fragment, two thoracic vertebrae, right trapezium, right scaphoid, and a left entocuneiform, most likely from the same individual. The trapezium is a blocky, trapezoidal-shaped specimen (Fig. 9.3c), with a distal articular surface for the first metacarpal (mc I) that is broader (86.0 mm) than its proximal end (61.6 mm) and greater than overall length (85.1 mm). Three distinct articular surfaces are confluent at the proximal end: a large, flat articulation for the adjacent trapezoid, a smaller articulation for the scaphoid, and a diminutive surface for mc II.

The scaphoid measures 136.7 mm in greatest length, and is 110.4 mm in distal width and 85.0 mm across its mid-section. Part of its medio-proximal surface is missing, but otherwise the specimen retains its original elongate trapezoidal shape (Fig. 9.3d). At the proximal end, the articular surface for the radius is flattened and acutely angled relative to the long axis of the bone. The articulation for the lunate at the proximal end of the scaphoid is broken away, but the distal articular surface for the lunate is preserved and is confluent with the small trapezoid articulation and larger, more distally facing surface for the trapezium. Together, the articular surfaces for the trapezoid and lunate are 85.3 mm long. A large tuberosity is located along the disto-lateral portion of the scaphoid.

The third podial from Noiti 3 is a left medial, or ento-, cuneiform (Fig. 9.3e), measuring 86.6 mm in length, 66.5 mm in proximal width, and 62.9 mm across its distal end. Proximally, the articular surface for the navicular is slightly concave and is continuous at a right angle to a smaller, flat surface for the middle, or meso-, cuneiform. A round, flat additional articulation for the mesocuneiform is located at the distal end of the specimen, set at a right angle to the large, distally facing articulation for the first metatarsal. Both the navicular and metatarsal articular surfaces slope toward each other at their ventral extents.

Remarks: *Loxodonta exoptata* is best documented at Laetoli in the Upper Laetolil Beds, and is also known from a few specimens in the Lower Laetolil Beds and Upper Ndolanya Beds. Along with its Eyasi Plateau occurrences (Beden 1987a; Harris 1987b; Sanders 2005), *L. exoptata* has also been documented in the Kilolele Mb. of the Wembere-Manonga Fm. in the Manonga Valley, Tanzania (Sanders 1997), at Kanapoi, Kenya (Harris et al. 2003), in the Chiwondo Beds, Malawi (Bromage et al. 1995), at Allia Bay, Kenya (Beden 1983), Koro Toro, Chad (Brunet et al. 1995; Brunet 2001), in the Nachukui Fm. at West Turkana, Kenya (Harris et al. 1988), the Warwire and Nyakabingo Fms., Nkondo and Nyabusosi Areas, Uganda (Tassy 1995), Mb. A of the Shungura Fm., Omo, Ethiopia (Beden 1987b), the Denen Dora Mb. of the Hadar Fm., Hadar, Ethiopia (White et al. 1984), and apparently in the Matabaietu Fm. of the Middle Awash, Ethiopia (Kalb and Mebrate 1993; Kalb 1995), giving it an estimated temporal range of ca. 4.5 to 2.0 Ma (de Heinzelin 1983; Drake and Curtis 1987; Hay 1987; Brown 1994; Harrison and Baker 1997; Harrison 2002; Alemseged 2003; Feibel 2003; Bonnefille et al. 2004).

The elephant fossils from the Laetolil and Ndolanya Beds have a long and colorful taxonomic history, which has been recounted in detail by Beden (1983, 1987a). The material recovered by the Leakey expedition in 1935 was initially placed by Hopwood (1936) in *Palaeoloxodon antiquus recki*, though he soon (in Kent 1941) transferred these fossils into two species, *Elephas recki* and *E. aff. planifrons*. The interpretation

of multiple elephant species at Laetoli was followed in a number of subsequent studies, including those of Dietrich (1941, 1942), who had a larger sample at hand with the addition of the Kohl-Larsen 1938–1939 fossils and identified, from different levels, *Archidiskodon exoptatus*, *Palaeoloxodon antiquus*, and a subspecies of *Loxodonta africana*. Most importantly, however, Dietrich (1941, 1942) placed all of the elephant remains from the Laetolil Beds in a single species (his “A.” *exoptatus*), hence providing the species nomen used today for this material. Nonetheless, for most of the interval since their first discovery, the Laetoli fossils have been placed in various lineages or species of *Elephas* (e.g., Arambourg 1943, 1947; Cooke 1960), and it was not until 1965 that Coppens finally recognized the presence of true loxodont elephants in the Laetolil Beds (“*Loxodonta africanavus exoptata*”). Cooke’s (1960) identification of some elephant teeth from Laetoli with *Archidiskodon subplanifrons* from the Vaal River, South Africa inadvertently proved prescient, because the Vaal River specimens in fact belong in *Loxodonta* (Sanders 2007; Sanders et al. 2010).

Subsequently, Maglio (1969) undertook taxonomic revision of the Louis Leakey and Kohl-Larsen elephant collections, and also assigned the specimens to two species. After designating IPUB 24, a right dentary fragment with its m3, as the lectotype of *Archidiskodon exoptatus* Dietrich, 1941, he sank the taxon into *Elephas recki*, and placed other specimens into *Loxodonta* sp. Largely on the basis of differential preservation, he believed that the occurrences of these taxa at Laetoli were separated stratigraphically and temporally, with the loxodont elephant being older. In subsequent publications (e.g., Maglio 1970, 1973; Cooke and Maglio 1972), he refined his identifications and assigned the Laetoli elephants to *Elephas recki* stage 2 and *Loxodonta adaurora*, using morphometric criteria such as degree of enamel folding, hypsodonty indices, expression of accessory conules, and enamel thickness to distinguish them.

More recently, Beden (1987a) restudied these fossils, and with the advantage of having a much larger elephant sample from the Mary Leakey collections, reached the very different conclusion that all of the elephant specimens from the Laetolil Beds belong in a single loxodont species which can be distinguished from both *E. recki* and *L. adaurora*. In doing so, Beden (1987a) resurrected Dietrich’s (1941) species, giving it the more proper nomen “*Loxodonta exoptata*.” In addition, he also recognized the affinity of the few elephant fossils from the Ndolanya Beds to *Loxodonta exoptata*.

The addition of a wealth of fossil elephant teeth to the sample by the Eyasi Plateau Expedition helps to confirm that the morphometric variation of the combined dental sample can be accommodated within a single loxodont species of elephant. While there is evidence for *Elephas recki* from younger horizons at Laetoli, such as LAET-87-L16-1, an incomplete right m1 collected by the IHO 1987 Expedition

that probably derives from the Olpiro Beds, and a broken right M1 (S 88) illustrated by Dietrich (1942: fig. VI, 60) that is likely also from the Olpiro Beds, the rest of the elephant sample, from the Laetolil and Ndolanya Beds, belongs in *L. exoptata*. Metric variation for the combined sample is normal for a species (Table 9.4), and, taking into account wear (Figs. 9.7 and 9.9) and weathering, the morphology for each tooth type (e.g., m1, m2) is consistent within its set. Thus, the present study supports Beden's (1987a) assessment and is in agreement with his explanation that the incomplete condition of many of the molars, and varying states of occlusal wear, particularly as it impacted on expression of loxodont sinuses, complicated previous taxonomic efforts. *Loxodonta exoptata* is distinguishable from the penecontemporaneous *L. adaurora*, and appears from its more pronounced development of loxodont molar sinuses to be phylogenetically closer (and possibly ancestral) to the extant *Loxodonta africana* (Beden 1983; Kalb and Mebrate 1993; Kalb et al. 1996; Tassy 2003; Sanders et al. 2010).

Beden (1987a) reasoned that the presumed displacement of loxodont elephants by *Elephas recki* throughout East Africa for much of the Pleistocene was due to preference of loxodonts for humid or wet wooded savannas and disappearance of those habitats at the end of the Pliocene. Based in part on that assumption, he used the absence of *Elephas recki* (which was otherwise widely prevalent throughout East Africa during the time of deposition of the Laetolil and Ndolanya Beds [Maglio 1973; Sanders et al. 2010]) at Laetoli to reconstruct the Pliocene environment of the area as a wet wooded savanna (Beden 1987a: 276). However, carbon isotope analysis of elephant tooth enamel from Eyasi Plateau sites indicates that these animals were mixed feeders or grazers; their $\delta^{13}\text{C}_{\text{enamel}}$ signal does not reveal any evidence of being specialists for a unique dietary niche (Kingston and Harrison 2007). Moreover, paleoecological reconstruction of the Upper Laetolil Beds using diverse covariables (including faunal composition) reveals an ecosystem with a mosaic of habitat types that remained stable over the entire interval of deposition (3.8–3.5 Ma), with grassland, savanna, and open woodland, but not specifically humid savanna, as important components of that ecosystem (Su and Harrison 2007). In addition, faunal analysis of the suprajacent Ndolanya Beds indicates the dominance of semi-arid scrub or bushland, but certainly not wet wooded savanna, at Laetoli around 2.7–2.6 Ma (Kovarovic et al. 2002). Perhaps, as speculated by Beden (1987a), the absence of *E. recki* at Pliocene Laetoli had more to do with the availability of drinking water.

The most interesting aspect of the *L. exoptata* collection from the Eyasi Plateau is its large number of deciduous premolars, suggesting a disproportionate representation of calves and juveniles in the sample. Although the anancine gomphothere sample, particularly from the Upper Laetolil Beds, is too small to similarly assess its mortality profile,

juveniles are also well represented in the modest deinothere sample. Dietrich (1942) believed that this ratio of elephant juveniles to adults was possibly due to a catastrophic volcanic explosion, but the stratigraphic distribution of these specimens shows that the die off was not a singular event (Beden 1987a).

A more likely explanation is that the age-grade mortality profile of Eyasi Plateau elephants indicates attritional mortality due to repeated drought conditions, in which young individuals too small to reach into holes dug into the lower water table are far more vulnerable to die offs than mature elephants (Dudley et al. 2001; Wittemeyer et al. 2005; Woolley et al. 2008). The oxygen isotope data for elephants from the Laetolil and Ndolanya Beds indicates that these animals relied on meteoric water for hydration (Kingston and Harrison 2007). African elephants are weaned around the age of 4–5 years (Moss 1992), by which time they have shed their deciduous second premolars (at about two years of age) and their deciduous fourth premolars are fully erupted (Sikes 1967). Nursing calves hydrating from milk have more protection from arid conditions than older juveniles, particularly if their mothers are experienced (Dudley et al. 2001; Foley et al. 2008; Woolley et al. 2008), which is consistent with the higher percentage of third and fourth than second deciduous premolars in the Eyasi Plateau elephant sample (see above).

A more even representation of all age groups would indicate time-averaged, cumulative single mortalities (Niven 2005), and die off due to disease would also cause mortality in all age classes (Lindeque and Turnbull 1994). An alternative explanation for the high occurrence of juvenile mortality in the Eyasi Plateau elephants is cumulative predation by lions, especially of weaned juveniles whose maternal bonds are weaker than those of nursing calves (Woolley et al. 2008 and references therein); attritional mortality of ungulate populations caused by carnivores usually yields high numbers of juveniles in death assemblages (Palmqvist et al. 1996). Lion predation on elephant calves is documented to increase during times of drought (Loveridge et al. 2006). However, predation of modern elephant populations accounts for only a small percentage of total juvenile mortality (e.g., Wittemeyer et al. 2005). It is also possible that the ratio of deciduous-to-adult teeth in the elephant sample is, at least in part, a taphonomic effect: small deciduous molars that accumulated on the surface at Laetoli are far more compact than adult molars and probably better survived weathering and trampling. Indeed, few complete permanent molars from Laetoli have been recovered, and approximately 75 unidentifiable dental specimens (from the Mary Leakey and Eyasi Plateau Expedition collections, but not included in Table 9.4) may be fragments of adult teeth. Even if these specimens were accounted for in the calculation of deciduous-to-adult tooth ratio, however, deciduous premolars would still comprise nearly half of all teeth in the sample, continuing to indicate a

disproportionate mortality of calves and older juveniles in successive populations of *L. exoptata* (and possibly other proboscideans) from the Eyasi Plateau. Thus, drought (or at least seasonally inadequate supply of standing water) cannot be ruled out as a factor contributing to the skewed mortality profile of fossil elephants from this region.

Discussion

The proboscidean sample from the Eyasi Plateau region derives from the Lower and Upper Laetolil Beds (ca. 4.4–3.85 Ma and 3.85–3.6 Ma, respectively; Deino 2011) and the Upper Ndolanya Beds (2.66 Ma; Deino 2011), principally exposed at Kakesio and Laetoli. In addition, proboscidean remains that have been recovered from Endolele (=Esere?) may be from older deposits. The taxa represented are taxonomically diverse and include deinotheres, a stegodont, anancine gomphotheres, and elephants. They are stratigraphically distributed as follows: from Endolele, *Anancus kenyensis* and *Loxodonta* sp. cf. *L. cookei*; from the Lower Laetolil Beds, *Anancus ultimus* sp. nov. and *Loxodonta exoptata*; from the Upper Laetolil Beds, *Deinotherium bozasi*, *A. ultimus* sp. nov. (including the holotype), *Stegodon* sp. cf. *S. kaisensis*, and *L. exoptata* (including the lectotype); and from the Upper Ndolanya Beds, *L. exoptata* and a single specimen of *D. bozasi*. Also, several elephant molars attributable to *Elephas recki*, but not detailed in the present study, appear to be from the Olpiro Beds (ca. 1.2 Ma, Hay 1987; 2.1–2.0 Ma, Deino 2011).

The Eyasi Plateau sample is important for the study of proboscidean evolution because anancine gomphotheres made their last East African appearance in the Upper Laetolil Beds at Laetoli; the elephant fossils were the first recovered of *Loxodonta exoptata* and constitute the most substantial collection of the species; and it documents regional evolution of anancine gomphotheres and elephants over much of the Pliocene. In Africa, the early-mid Pliocene interval was a particularly dynamic one for proboscidean evolution, as archaic elephant genera such as *Stegotetrabelodon*, *Stegodibelodon*, and *Primelephas* disappeared and were replaced by an adaptive radiation of cranio-dentally more advanced crown elephant species (*Loxodonta adaurora*, *L. cookei*, *L. exoptata*, *Elephas ekorensis*, *E. recki*, *M. africanavus*). As all Mio-Pliocene elephants and most anancine gomphotheres relied heavily on C₄ plants in their diets (Cerling et al. 1999, 2003; Zazzo et al. 2000; Harris et al. 2003; Semaw et al. 2005), it can be inferred that progressive changes in molar crown morphology that occurred independently within the *Anancus kenyensis*-*A. ultimus* sp. nov. succession and among crown elephant lineages, such as increased hypsodonty and number of plates (or loph(id)s), were associated

with ecological changes that favored enhanced efficiency in grazing adaptations during the early-mid Pliocene. The paleoenvironment of mid Pliocene Laetoli has been reconstructed as including open woodland, shrubland, grassland, and more limited gallery forest (Andrews and Bamford 2008; Su and Harrison 2007, 2008), and may have become considerably drier during the late Pliocene time of deposition of the Upper Ndolanya Beds (Kovarovic et al. 2002). This fits well with the ecologically diverse presence of grazers, such as *L. exoptata* and *A. ultimus* alongside committed browsers, such as *Deinotherium bozasi* (which may not have been ultimately sustainable locally during the time of deposition of the Upper Ndolanya Beds). The absence from Laetoli of *Elephas recki* and the large elephant *Loxodonta adaurora*, which contemporaneously occurred elsewhere in East Africa, and the high proportion of calves and juveniles in the proboscidean assemblage from the site indicate that these habitats may have periodically been subject to drought, seasonally low rainfall, a poor supply of standing water, or some combination of these factors.

Taxonomically, the identification of deinotheres and a stegodont at Laetoli is straightforward, because their dental morphology is so distinct. As well, there is little question that the anancine gomphothere specimens from Endolele, and Kakesio and Laetoli respectively belong to what has been considered primitive and advanced morphs, or different stages, of the East-Central African species *Anancus kenyensis* (Tassy 1986; Kalb and Mebrate 1993; Kalb 1995). Because the differences between these morphs are consistent, especially in the number of loph(id)s in intermediate molars and complexity of distribution of accessory conules throughout molar crowns, and are typical for paleo-sister species, these morphs or stages are elevated here to species level, with the primitive forms (including the type from Kanam, Kenya [MacInnes 1942]) retained in the original species, *A. kenyensis*, and the advanced forms in a new species, *A. ultimus* sp. nov. The molar chosen for the type of *A. ultimus* sp. nov., m3 specimen EP 197/05, was selected because of its extreme occlusal complexity, high number of lophids, and because it is the youngest known anancine gomphothere specimen of the lineage (ca. 3.5 Ma). Anancine gomphotheres in this lineage paralleled elephants in their commitment to a C₄-plant based diet (Cerling et al. 1999, 2003; Zazzo et al. 2000; Harris et al. 2003; Semaw et al. 2005; Kingston and Harrison 2007), and associated evolutionary progression of molar hypsodonty and addition of loph(id)s to cheek teeth (Kalb and Mebrate 1993; Kalb 1995). It appears, however, that they were outcompeted for grazing resources, or ecologically swamped by expanding adaptive radiations to C₄ diets of other large-bodied mammals, including elephants, bovids, rhinos, equids, suids, and hippos (see Cerling et al. 2003), likely contributing to their mid Pliocene demise in East Africa.

By contrast, the elephant fossils from the region, particularly the most substantive sub-sample from the Upper Laetoli Beds, escaped proper taxonomic assignment for so long because of several confounding factors: first, the nomenclature initially chosen for the Louis Leakey collection (and later for the Kohl-Larsen assemblage) followed a now-outdated systematic scheme based heavily on ideas of Eurasian elephant phylogeny, and was evidently typological in approach, given the low amount of occlusal variation among those few molars; second, and rather surprisingly, it was not until relatively late that paleontologists recognized the presence of fossil *Loxodonta* in African Plio-Pleistocene deposits (e.g., Coppens 1965); third, early representatives of the African *Elephas* lineage have molars with accessory conules throughout much of their crowns, particularly on the posterior side of plates (but do not develop loxodont sinuses), and, depending on wear stage, this can make it difficult to differentiate partial molars of *Loxodonta* and early *Elephas*; and last, with a much more comprehensive sample of teeth of *L. exoptata* now available, it is evident that molars of the species underwent substantial morphological transformation as they wore down (Figs. 9.7 and 9.9).

The identification by Beden (1987a) of a single, loxodont elephant species, *L. exoptata*, at Laetoli, supported here, has implications for the reconstruction of African elephant phylogeny. *Loxodonta exoptata* is documented at other sites by only a handful of specimens, and its existence might be questionable if not for the evidence from Laetoli. The development of true loxodont sinuses throughout the molar crowns of this species is shared morphologically by older, more primitive, Mio-Pliocene loxodont elephants (*L. cookei*; see Sanders 2006, 2007), and by the extant African savanna and forest elephants *L. africana* and *L. cyclotis*. Thus, *L. exoptata* appears to provide an important link that extends the phylogeny of modern African elephants back into the late Miocene, consistent with genomic estimates of elephant lineage divergence dates (Rohland et al. 2007). Conversely, the loxodont contemporary of *L. exoptata*, *L. adaurora*, which existed from the earliest Pliocene until the start of the Pleistocene in East Africa (Sanders et al. 2010; Maglio 1973), has little development of median sinuses in its molars, and is therefore less likely to have been ancestral to modern African elephants.

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References

- Alemseged, Z. (2003). An integrated approach to taphonomy and faunal change in the Shungura Formation (Ethiopia) and its implication for hominid evolution. *Journal of Human Evolution*, 44, 451–478.
- Ambrose, S. H., Hlusko, L. J., Kyule, D., Deino, A., & Williams, M. (2003). Lemudong'o: A new 6 Ma paleontological site near Narok, Kenya rift valley. *Journal of Human Evolution*, 44, 737–742.
- Andrews, C. W. (1911). On a new species of *Dinotherium* from British East Africa. *Proceedings of the Zoological Society of London*, 1911, 943–945.
- Andrews, P., & Bamford, M. (2008). Past and present vegetation ecology of Laetoli, Tanzania. *Journal of Human Evolution*, 54, 78–98.
- Anonymous. (1827). A review of Frédéric Cuvier and Étienne Geoffroy Saint-Hilaire Histoire Naturelle des Mammifères. *The Zoological Journal (London)*, 3, 140–143.
- Arambourg, C. (1934). Le *Dinotherium* des gisements de l'Omo (Abyssinie). *Bulletin de la Societe Geologique de France*, 4, 305–309.
- Arambourg, C. (1943). Mission scientifique de l'Omo 1932–1933. *Museum National Histoire naturelle, Géologique. Anthropologie, Paris I*, 157–230.
- Arambourg, C. (1945). *Anancus osiris*, un mastodonte nouveau du Pliocène inférieur d'Égypte. *Bulletin de la Societe Geologique de France*, 15, 479–495.
- Arambourg, C. (1947). Mission scientifique de l'Omo 1932–1933. *Museum National Histoire naturelle, Géologique. Anthropologie, Paris I*, 231–562.
- Arambourg, C. (1970). Les Vertébrés du Pléistocène de l'Afrique du Nord. *Archives du Muséum National d'Histoire Naturelle, Paris, 7e Serie*, 10, 1–126.
- Aymard, A. (1855). *Anancus* Aymard. *Anancus macroplis* Aymard. In M.J. Dorlhac, (Ed.), Notice géologique sur le cratère de Coupet et sur son gisement de gemmes et d'ossements fossiles. *Annales de la Société d'Agriculture. Sciences, Arts et Commerce du Puy (Procès-Verbaux, Janvier)*, 19, 497–517.
- Bachmann, I. (1875). Beschreibung eines Unterkiefers von *Dinotherium bavaricum* H. v. Meyer. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, 2, 1–20.
- Beden, M. (1975). A propos des Proboscidiens Plio-Quaternaires des Gisements de l'Omo (Ethiopie). Colloque international

- CNRS n° 218 (Paris 4–9 juin 1973). Problèmes Actuels de Paléontologie-Évolution des Vertébrés (pp. 693–705).
- Beden, M. (1976). Proboscideans from Omo Group Formations. In Y. Coppens, F. C. Howell, G. L. Isaac, & R. E. F. Leakey (Eds.), *Earliest man and environments in the Lake Rudolf Basin* (pp. 193–208). Chicago: The University of Chicago Press.
- Beden, M. (1980). *Elephas recki* Dietrich, 1915 (Proboscidea, Elephantidae). Évolution au cours du Plio-Pléistocène en Afrique orientale. *Geobios*, 13, 891–901.
- Beden, M. (1983). Family Elephantidae. In J. M. Harris (Ed.), *Koobi Fora research project* (Vol. 2, pp. 40–129). Oxford: Clarendon.
- Beden, M. (1985). Les Proboscidiens des grands gisements à Hominidés Plio-Pléistocènes d'Afrique Orientale. In M. Beden, A. K. Behrensmeyer, N. T. Boaz, R. Bonnefille, C. K. Brain, H. B. S. Cooke, Y. Coppens, R. Dechamps, V. Eisenmann, A. Gentry, D. Geraads, R. Geze, C. Guerin, J. Harris, J.-C. Koeniguer, R. Letouzey, G. Petter, A. Vincens, & E. Vrba (Eds.), *L'Environnement des Hominidés au Plio-Pléistocène* (pp. 21–44). Paris: Masson.
- Beden, M. (1987a). Fossil Elephantidae from Laetoli. In M. D. Leakey & J. M. Harris (Eds.), *Laetoli: A Pliocene site in northern Tanzania* (pp. 259–294). Oxford: Clarendon.
- Beden, M. (1987b). *Les Faunes Plio-Pléistocènes de la Vallée de l'Omo (Éthiopie). Tome 2. Les Elephantidés (Mammalia, Proboscidea)*. Paris, CNRS.
- Behrensmeyer, A. K., Potts, R., Plummer, T., Tauxe, L., Opdyke, N., & Jorstad, T. (1995). The Pleistocene locality of Kanjera, western Kenya: Stratigraphy, chronology and paleoenvironments. *Journal of Human Evolution*, 29, 247–274.
- Boaz, N. T. (1994). Significance of the western rift for hominid evolution. In R. S. Corruccini & R. L. Ciochon (Eds.), *Integrative paths to the past. Paleoanthropological advances in honor of F. Clark Howell* (pp. 321–343). Englewood Cliffs: Prentice Hall.
- Boaz, N. T., Gaziry, A. W., & El-Arnauti, A. (1979). New fossil finds from the Libyan upper Neogene site of Sahabi. *Nature*, 280, 137–140.
- Bonaparte, C.L. (1845). *Catalogo Metodico dei Mammiferi Europei*. Milan: Valenciennes.
- Bonnefille, R., Potts, R., Chalié, F., Jolly, D., & Peyron, O. (2004). High resolution vegetation and climate change associated with Pliocene *Australopithecus afarensis*. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 12125–12129.
- Bromage, T. G., Schrenk, F., & Juwayeyi, Y. M. (1995). Paleobiogeography of the Malawi rift: Age and vertebrate paleontology of the Chiwondo beds, northern Malawi. *Journal of Human Evolution*, 28, 37–57.
- Brown, F. H. (1994). Development of Pliocene and Pleistocene chronology of the Turkana basin, east Africa, and its relation to other sites. In R. S. Corruccini & R. L. Ciochon (Eds.), *Integrative paths to the past. Paleoanthropological advances in honor of F. Clark Howell* (pp. 285–312). Englewood Cliffs: Prentice Hall.
- Brunet, M. (2001). Chadian australopithecines: Biochronology and environmental context. In P. V. Tobias, M. A. Raath, J. Moggi-Cecchi, & G. A. Doyle (Eds.), *Humanity from African naissance to coming Millennia* (pp. 103–106). Florence: Firenze University Press.
- Brunet, M., Beauvilain, A., Billiou, D., Bocherens, H., Boisserie, J.-R., de Bonis, L., Branger, P., Brunet, A., Coppens, Y., Daams, R., Dejax, J., Denys, C., Düringer, P., Eisenmann, V., Fanoné, F., Fronty, P., Gayet, M., Geraads, D., Guy, F., Kasser, M., Koufos, G., Likius, A., Lopez-Martinez, N., Louchart, A., Maclatchy, L., Mackaye, H. T., Marandat, B., Mouchelin, G., Mourer-Chauviré, C., Otero, O., Peigné, S., Campomanes, P. P., Pilbeam, D., Rage, J. C., de Ruyter, D., Schuster, M., Sudre, J., Tassy, P., Vignaud, P., Viriot, L., & Zazzo, A. (2000). Chad: Discovery of a vertebrate fauna close to the Mio-Pliocene boundary. *Journal of Vertebrate Paleontology*, 20, 205–209.
- Brunet, M., Beauvilain, A., Coppens, Y., Heintz, E., Moutaye, A. H. E., & Pilbeam, D. (1995). The first australopithecine 2,500 kilometres west of the rift valley (Chad). *Nature*, 378, 273–275.
- Brunet, M., Beauvilain, A., Geraads, D., Guy, F., Kasser, M., Mackaye, H. T., MacLatchy, L. M., Mouchelin, G., Sudre, J., & Vignand, P. (1998). Tchad: Découverte d'une faune de mammifères du Pliocène inférieur. *Comptes Rendus de l'Académie des Sciences, Paris. Sciences de la Terre et des Planètes*, 326, 153–158.
- Cerling, T. E., Harris, J. M., & Leakey, M. G. (1999). Browsing and grazing in elephants: The isotope record of modern and fossil proboscideans. *Oecologia*, 120, 364–374.
- Cerling, T. E., Harris, J. M., & Leakey, M. G. (2003). Isotope paleoecology of the Nawata and Nachukui Formations at Lothagam, Turkana Basin, Kenya. In M. G. Leakey & J. M. Harris (Eds.), *Lothagam: The dawn of humanity in eastern Africa* (pp. 605–624). New York: Columbia University Press.
- Cerling, T. E., Harris, J. M., & Leakey, M. G. (2005). Environmentally driven dietary adaptations in African mammals. In J. R. Ehleringer, M. D. Dearing, & T. E. Cerling (Eds.), *History of atmospheric CO₂ and its effects on plants, animals, and ecosystems* (pp. 258–272). New York: Springer.
- Christiansen, P. (2004). Body size in proboscideans, with notes on elephant metabolism. *Zoological Journal of the Linnean Society*, 140, 523–549.
- Cooke, H. B. S. (1960). Further revision of the fossil Elephantidae of southern Africa. *Palaeontologia Africana*, 5, 46–58.
- Cooke, H. B. S. (1993). Fossil proboscidean remains from Bolt's Farm and other Transvaal cave breccias. *Palaeontologia Africana*, 30, 25–34.
- Cooke, H. B. S., & Coryndon, S. (1970). Fossil mammals from the Kaiso Formation and other related deposits in Uganda. In L. S. B. Leakey & R. J. G. Savage (Eds.), *Fossil vertebrates of Africa* (pp. 107–224). Edinburgh: Academic.
- Cooke, H. B. S., & Maglio, V. J. (1972). Plio-Pleistocene stratigraphy in East Africa in relation to proboscidean and suid evolution. In W. W. Bishop & J. A. Miller (Eds.), *Calibration of hominoid evolution. Recent advances in isotopic and other dating methods applicable to the origin of man* (pp. 303–329). New York: Scottish Academic.
- Cooper, C. F. (1922). Miocene Proboscidea [sic] from Baluchistan. *Proceedings of the Zoological Society of London*, 42, 606–626.
- Coppens, Y. (1965). Les Proboscidiens du Tchad. *Actes du Ve Congrès Panafricain de Préhistoire et de l'Étude du Quaternaire (Santa Cruz de Tenerife)*, 1(5), 331–387.
- Coppens, Y., Maglio, V. J., Madden, C. T., & Beden, M. (1978). Proboscidea. In V. J. Maglio & H. B. S. Cooke (Eds.), *Evolution of African mammals* (pp. 336–367). Cambridge: Harvard University Press.
- Cuvier, F. (1825). Eléphant d'Afrique. In E. Geoffroy Saint-Hilaire & F. Cuvier (Eds.), *Histoire naturelle des Mammifères* (Vol. 3, pp. 1–2). Paris: Muséum d'Histoire Naturelle.
- Day, M. H., & Wickens, E. H. (1980). Laetoli Pliocene hominid footprints and bipedalism. *Nature*, 286, 385–387.
- Day, M. H., Leakey, M. D., & Magori, C. (1980). A new hominid fossil skull (L.H.18) from the Ngaloba Beds, Laetoli, northern Tanzania. *Nature*, 284, 55–56.
- de Heinzelin, J. (1983). The Omo Group. Volume One – Text. Archives of the International Omo Research Expedition. Musée Royal de l'Afrique Centrale, Tervuren, Belgique, *Annales Série in-8°, Sciences Géologiques n° 85*, 1–365.
- Deino, A. L. (2011). ⁴⁰Ar/³⁹Ar dating of Laetoli, Tanzania. In T. Harrison (Ed.), *Paleontology and geology of Laetoli: Human evolution in context* (Geology, geochronology, paleoecology and paleoenvironment, Vol. 1, pp. 77–97). Dordrecht: Springer.
- Deino, A. L., Tauxe, L., Monaghan, M., & Hill, A. (2002). ⁴⁰Ar/³⁹Ar geochronology and paleomagnetic stratigraphy of the Lukeino and lower Chemeron Formations at Tabarin and Kapcherek, Tugen Hills, Kenya. *Journal of Human Evolution*, 42, 117–140.
- Depéret, C., Lavauden, L., & Solignag, M. (1925). Sur la découverte du *Mastodon arvernensis* dans le Pliocène de Ferryville (Tunisie). *Comptes Rendus Sommaire des Séances, Société Géologique de France*, 1–2, 21–22.

- Dietrich, W. O. (1941). Die Säugetierpaläontologischen Ergebnisse der Kohl-Larsen'shen expedition 1937–1939 im nördlichen Deutsch-Ostafrika. *Zentralblatt für Mineralogie, Geologie und Paläontologie, Stuttgart, B*, 1941, 217–223.
- Dietrich, W. O. (1942). Ältestquartäre Säugetiere aus der südlichen Serengeti, Deutsch-Ostafrika. *Palaeontographica*, 94, 43–133.
- Drake, R., & Curtis, G. H. (1987). K-Ar geochronology of the Laetoli fossil localities. In M. D. Leakey & J. M. Harris (Eds.), *Laetoli: A Pliocene site in northern Tanzania* (pp. 48–61). Oxford: Clarendon.
- Dudley, J. P., Craig, G. C., St, C., Gibson, D., Haynes, G., & Klimowicz, J. (2001). Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *African Journal of Ecology*, 39, 187–194.
- Éhik, J. (1930). *Prodinotherium hungaricum* n. g., n. sp. *Geological Hungarica. Series Palaeontologica*, 6, 1–24.
- Falconer, H., & Cautley, P. T. (1847). *Fauna Antiqua Sivalensis, being the fossil zoology of the Sewalik hills, in the north of India. Part II*. London: Smith, Elder.
- Fara, E., Likius, A., Mackaye, H. T., Vignaud, P., & Brunet, M. (2005). Pliocene large-mammal assemblages from northern Chad: Sampling and ecological structure. *Die Naturwissenschaften*, 92, 537–541.
- Feibel, C. S. (2003). Stratigraphy and depositional setting of the Pliocene Kanapoi Formation, lower Kerio Valley, Kenya. In J. M. Harris & M. G. Leakey (Eds.), *Geology and vertebrate paleontology of the early Pliocene site of Kanapoi, northern Kenya* (Contributions in science, Vol. 498, pp. 9–20). Los Angeles: Natural History Museum of Los Angeles County.
- Foley, C., Petteorelli, N., & Foley, L. (2008). Severe drought and calf survival in elephants. *Biology Letters*, 4, 541–544.
- Fournet, A. (1971). Les gisements a faune Villafranchienne de Tunisie. *Notes Service Geologique Tunisie*, 34, 53–69.
- Franz-Odendaal, T. A., Lee-Thorp, J. A., & Chinsamy, A. (2002). New evidence for the lack of C₄ grassland expansions during the early Pliocene at Langebaanweg, South Africa. *Paleobiology*, 28, 378–388.
- Gaziry, A. W. (1976). Jungtertiäre Mastodonten aus Anatolien (Türkei). *Geologisches Jahrbuch*, 22, 3–143.
- Geraads, D. (2002). Plio-Pleistocene mammalian biostratigraphy of Atlantic Morocco. *Quaternaire*, 13, 43–53.
- Geraads, D., & Amani, F. (1998). Bovidae (Mammalia) du Pliocène final d'Ahl al Oughlam, Casablanca, Maroc. *Paläontologische Zeitschrift*, 72, 191–205.
- Geraads, D., & Metz-Muller, F. (1999). Proboscidea (Mammalia) du Pliocène final d'Ahl al Oughlam (Casablanca, Maroc). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1999(1), 52–64.
- Gräf, I. E. (1957). Die prinzipien der Arbestimmung bei *Deinotherium*. *Palaeontographica*, 180(A), 131–185.
- Gray, J. E. (1821). On the natural arrangements of vertebrate animals. *London Medical Repository*, 15, 296–310.
- Haile-Selassie, Y. (2001). Late Miocene mammalian fauna from the Middle Awash Valley, Ethiopia. Ph.D. dissertation, University of California, Berkeley.
- Haile-Selassie, Y., WoldeGabriel, G., White, T. D., Bernor, R. L., Degusta, D., Renne, P. R., Hart, W. K., Vrba, E., Ambrose, S., & Howell, F. C. (2004). Mio-Pliocene mammals from the middle Awash, Ethiopia. *Geobios*, 37, 536–552.
- Harris, J. M. (1973). *Prodeinotherium* from Gebel Zelten, Libya. Ph.D. dissertation, University of Bristol, Bristol.
- Harris, J. M. (1975). Evolution of feeding mechanisms in the family Deinotheriidae. *Zoological Journal of the Linnean Society*, 56, 332–362.
- Harris, J. M. (1977). Deinotheres from southern Africa. *South African Journal of Science*, 73, 282–282.
- Harris, J. M. (1978). Deinotherioidea and Barytherioidea. In V. J. Maglio & H. B. S. Cooke (Eds.), *Evolution of African Mammals* (pp. 315–332). Cambridge: Harvard University Press.
- Harris, J. M. (1983). Background to the study of the Koobi Fora fossil faunas. In J. M. Harris (Ed.), *Koobi Fora Research Project* (The Fossil ungulates: Proboscidea, Perissodactyla, and Suidae, Vol. 2, pp. 1–21). Oxford: Clarendon.
- Harris, J. M. (1987a). Fossil Deinotheriidae from Laetoli. In M. D. Leakey & J. M. Harris (Eds.), *Laetoli: A Pliocene site in northern Tanzania* (pp. 294–297). Oxford: Clarendon.
- Harris, J. M. (1987b). Summary. In M. D. Leakey & J. M. Harris (Eds.), *Laetoli: A Pliocene site in northern Tanzania* (pp. 524–531). Oxford: Clarendon.
- Harris, J.M., & Leakey, M.G. (2003). Geology and vertebrate paleontology of the early Pliocene site of Kanapoi, northern Kenya. *Contributions in Science, Natural History Museum of Los Angeles County*, 498, 1–132.
- Harris, J. M., Brown, F. H., & Leakey, M. G. (1988). Geology and palaeontology of Plio-Pleistocene localities west of Lake Turkana, Kenya. *Contributions in Science*, 399, 1–128.
- Harris, J. M., Leakey, M. G., & Cerling, T. E. (2003). Early Pliocene tetrapod remains from Kanapoi, Lake Turkana Basin, Kenya. In J. M. Harris & M. G. Leakey (Eds.), *Geology and vertebrate paleontology of the early Pliocene site of Kanapoi, northern Kenya* (Contributions in science, Vol. 498, pp. 39–113). Los Angeles: Natural History Museum of Los Angeles County.
- Harrison, T. (2002). The first record of fossil hominins from the Ndolanya Beds, Laetoli, Tanzania. *American Journal of Physical Anthropology*, 119, 83.
- Harrison, T. (2011). Hominins from the Upper Laetoli and Upper Ndolanya Beds, Laetoli. In T. Harrison (Ed.), *Paleontology and geology of Laetoli: Human evolution in context* (Fossil hominins and the associated fauna, Vol. 2, pp. 141–188). Dordrecht: Springer.
- Harrison, T., & Baker, E. (1997). Paleontology and biochronology of fossil localities in the Manonga Valley, Tanzania. In T. Harrison (Ed.), *Neogene paleontology of the Manonga Valley, Tanzania* (pp. 361–393). New York: Plenum.
- Hautier, L., Mackaye, H. T., Lihoreau, F., Tassy, P., Vignaud, P., & Brunet, M. (2009). New material of *Anancus kenyensis* (Proboscidea, Mammalia) from Toros-Menalla (late Miocene, Chad): Contribution to the systematics of African anancines. *Journal of African Earth Sciences*, 53, 171–176.
- Hay, O. P. (1922). Further observations on some extinct elephants. *Proceedings of the Biological Society of Washington*, 35, 97–101.
- Hay, R. L. (1987). Geology of the Laetoli area. In M. D. Leakey & J. M. Harris (Eds.), *Laetoli: A Pliocene site in northern Tanzania* (pp. 23–47). Oxford: Clarendon.
- Hendey, Q. B. (1978). The age of the fossils from Baard's Quarry, Langebaanweg, South Africa. *Annals of the South African Museum*, 75, 1–24.
- Hendey, Q. B. (1981). Palaeoecology of the late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. *Annals of the South African Museum*, 84, 1–104.
- Hill, A. (1994). Late Miocene and early Pliocene hominoids from Africa. In R. S. Corruccini & R. L. Ciochon (Eds.), *Integrative paths to the past: Paleoanthropological advances in honor of F. Clark Howell* (pp. 123–145). Englewood Cliffs: Prentice Hall.
- Hill, A. (2002). Paleoanthropological research in the Tugen Hills, Kenya. *Journal of Human Evolution*, 42, 1–10.
- Hill, A., Drake, R., Tauxe, L., Monaghan, M., Barry, J. C., Behrensmeyer, A. K., Curtis, G., Fine Jacobs, B., Jacobs, L., Johnson, N., & Pilbeam, D. (1985). Neogene palaeontology and geochronology of the Baringo Basin, Kenya. *Journal of Human Evolution*, 14, 759–773.
- Hill, A., Curtis, G., & Drake, R. (1986). Sedimentary stratigraphy of the Tugen Hills, Baringo, Kenya. In L. E. Frostick, R. W. Renaut, I. Reid, & J.-J. Tiercelin (Eds.), *Sedimentation in the African rifts* (pp. 285–295). Oxford: Blackwell & Geological Society of London Special Publication 25.
- Hooijer, D. A. (1963). Miocene Mammalia of Congo. Koninklijk museum voor Midden-Afrika, Tervuren, Belgie, *Annalen, Reeks IN-8°*. *Geologische Wetenschappen*, 46, 1–77.

- Hopwood, A. T. (1936). New and little-known fossil mammals from the Pleistocene of Kenya colony and Tanganyika Territory. *The Annals and Magazine of Natural History, London*, 17, 636–641.
- Hopwood, A. T. (1939). The mammalian fossils. In T. P. O'Brien (Ed.), *The prehistory of Uganda Protectorate* (pp. 308–316). Cambridge: Cambridge University Press.
- Huttunen, K. J. (2000). Deinotheriidae (Proboscidea, Mammalia) of the Miocene of lower Austria, Burgenland and Franzensbad, Czech Republic: Systematics, odontology and osteology. Dr. Rer. Nat. thesis, University of Vienna, Vienna.
- Illiger, C. D. (1811). *Prodromus systematis mammalium et avium additis terminis zoographicis attrisusque classis*. Berlin: Salfeld.
- Johanson, D. C., White, T. D., & Coppens, Y. (1978). A new species of the genus *Australopithecus* (Primates: Hominidae) from the Pliocene of eastern Africa. *Kirtlandia*, 28, 1–11.
- Kalb, J. E. (1995). Fossil elephantoids, Awash paleolake basins, and the Afar triple junction, Ethiopia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 114, 357–368.
- Kalb, J. E., & Froehlich, D. J. (1995). Interrelationships of late Neogene elephantoids: New evidence from the Middle Awash Valley, Ethiopia. *Geobios*, 28, 727–736.
- Kalb, J. E., & Mebrate, A. (1993). Fossil elephantoids from the hominid-bearing Awash group, Middle Awash Valley, Afar depression, Ethiopia. *Transactions of the American Philosophical Society*, 83, 1–114.
- Kalb, J. E., Froehlich, D. J., & Bell, G. L. (1996). Phylogeny of African and Eurasian Elephantoida of the late Neogene. In J. Shoshani & P. Tassy (Eds.), *The Proboscidea: Evolution and Palaeoecology of elephants and their relatives* (pp. 101–116). Oxford: Oxford University Press.
- Kaup, J. J. (1829). *Deinotherium giganteum*. *Isis*, 22, 401–404.
- Kent, P. E. (1941). The recent history and Pleistocene deposits of the plateau north of lake Eyasi, Tanganyika. *Geological Magazine*, 78, 173–184.
- Kingston, J. D., & Harrison, T. (2007). Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: Implications for early hominin paleoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 243, 272–306.
- Kingston, J., Jacobs, B. F., Hill, A., & Deino, A. (2002). Stratigraphy, age and environments of the late Miocene Mpesida Beds, Tugen Hills, Kenya. *Journal of Human Evolution*, 42, 95–116.
- Kovarovic, K., Andrews, P., & Aiello, L. (2002). The palaeoecology of the Upper Ndolanya Beds at Laetoli, Tanzania. *Journal of Human Evolution*, 43, 395–418.
- Kullmer, O., Sandrock, O., Viola, T. B., Hujer, W., Said, H., & Seidler, H. (2008). Suids, elephantoids, paleochronology, and paleoecology of the Pliocene hominid site Galili, Somali region, Ethiopia. *Palaios*, 23, 452–464.
- Laws, R. M. (1966). Age criteria for the African elephant. *East African Wildlife Journal*, 4, 1–37.
- Leakey, M. D. (1987a). Introduction. In M. D. Leakey & J. M. Harris (Eds.), *Laetoli: A Pliocene site in northern Tanzania* (pp. 1–22). Oxford: Clarendon.
- Leakey, M. D. (1987b). The hominid footprints. In M. D. Leakey & J. M. Harris (Eds.), *Laetoli: A Pliocene site in northern Tanzania* (pp. 490–495). Oxford: Clarendon.
- Leakey, M. D., & Hay, R. L. (1979). Pliocene footprints in the Laetoli beds at Laetoli, northern Tanzania. *Nature*, 278, 317–323.
- Lindeque, P. M., & Turnbull, P. C. B. (1994). Ecology and epidemiology of anthrax in the Ethosha National Park, Namibia. *The Onderstepoort Journal of Veterinary Research*, 61, 71–83.
- Loveridge, A. J., Hunt, J. E., Murindagomo, F., & Macdonald, D. W. (2006). Influence of drought on predation of elephant calves by lions in an African wooded savannah. *Journal of Zoology*, 270, 523–530.
- MacInnes, D. G. (1942). Miocene and post-Miocene Proboscidea [sic] from East Africa. *Transactions of the Zoological Society of London*, 25, 33–106.
- Mackaye, H. T., Brunet, M., & Tassy, P. (2005). *Selenetherium kolleenensis* nov. gen. nov. sp.: un nouveau Proboscidea (Mammalia) dans le Pliocène Tchadien. *Geobios*, 38, 765–777.
- Maglio, V. J. (1969). The status of the East African elephant “*Archidiskodon exoptatus*” Dietrich 1942. *Breviora*, 336, 1–24.
- Maglio, V. J. (1970). Four new species of Elephantidae from the Plio-Pleistocene of northwestern Kenya. *Breviora*, 341, 1–43.
- Maglio, V. J. (1973). Origin and evolution of the Elephantidae. *Transactions of the American Philosophical Society*, 63, 1–149.
- Mebrate, A., & Kalb, J. E. (1985). Anancinae (Proboscidea: Gomphotheriidae) from the Middle Awash Valley, Afar, Ethiopia. *Journal of Vertebrate Paleontology*, 5, 93–102.
- Moss, C. (1992). Elephant calves: The story of two sexes. In J. Shoshani (Ed.), *Elephants* (pp. 106–115). New York: Simon and Schuster.
- Niven, L. (2005). The role of mammoths in Upper Palaeolithic economies of southern Germany. In G. Cavarretta, P. Gioia, M. Mussi, & M. R. Palambo (Eds.), *Proceedings of the First International Congress of La Terra degli Elefanti, The World of Elephants* (pp. 323–327). Rome: Consiglio Nazionale delle Ricerche.
- Osborn, H. F. (1918). A long-jawed mastodon skeleton from South Dakota and phylogeny of the Proboscidea. *Bulletin of the Geological Society of America*, 29, 133–137.
- Osborn, H. F. (1921). The evolution, phylogeny and classification of the Proboscidea. *American Museum Novitates*, 1, 1–15.
- Osborn, H. F. (1942). *Proboscidea. A monograph of the discovery, evolution, migration and extinction of the Mastodonts and Elephants of the World. Stegodontoidea, Elephantoida* (Vol. II). New York: American Museum Press.
- Palmer, R. W. (1924). An incomplete skull of *Dinotherium*, with notes on the Indian forms. *Palaeontologia Indica*, 7, 1–14.
- Palmqvist, P., Martinez-Navarro, B., & Arribas, A. (1996). Prey selection by terrestrial carnivores in a lower Pleistocene paleocommunity. *Paleobiology*, 22, 514–534.
- Petrocchi, C. (1943). Il giacimento fossilifero di Sahabi. Collezione Scientifica e documentaria a cura del Ministero dell' Africa Italiana, Verbania, 12.
- Petrocchi, C. (1954). Paleontologia di Sahabi. Parte I. Probosidati di Sahabi. Rendiconti Accademia nazionale dei XL 4–5, 8–74.
- Pickford, M., Senut, B., & Hadoto, D. (1993). *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Volume I: Geology*. Occasional Publication 24, Centre International pour la Formation et les Echanges Géologiques, Orleans.
- Renne, P. R., WoldeGabriel, G., Hart, W. K., Heiken, G., & White, T. D. (1999). Chronostratigraphy of the Miocene-Pliocene Sagantole Formation, Middle Awash Valley, Afar rift, Ethiopia. *Geological Society of America Bulletin*, 111, 869–885.
- Roger, O. (1886). Ueber *Dinotherium bavaricum*, H. v. Meyer. *Palaeontographica*, 32, 215–225.
- Rohland, N., Malaspina, A. S., Pollack, J. L., Slatkin, M., Matheus, P., & Hofreiter, M. (2007). Proboscidean mitogenomics: Chronology and mode of elephant evolution using mastodon as outgroup. *PLoS Biology*, 5(8), e207. doi:10.1371/journal.pbio.0050207.
- Sach, V. V. J., & Heizmann, E. P. J. (2001). Stratigraphie und Säugetierfaunen der Brackwassermolasse in der Umgebung von Ulm (Südwestdeutschland). *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)*, 310, 1–95.
- Saegusa, H. (1987). Cranial morphology and phylogeny of the stegodonts. *The Compass*, 64, 221–243.
- Saegusa, H. (1996). Stegodontidae: Evolutionary relationships. In J. Shoshani & P. Tassy (Eds.), *The Proboscidea: Evolution and palaeoecology of elephants and their relatives* (pp. 178–190). Oxford: Oxford University Press.
- Saegusa, H., & Hlusko, L. J. (2007). New late Miocene elephantoid (Mammalia: Proboscidea) fossils from Lemudong'o, Kenya. *Kirtlandia*, 56, 140–147.
- Sahni, M. R., & Tripathi, C. (1957). A new classification of the Indian deinotheres and description of *D. orlovii* sp. nov. Memoirs of the geological society of India. *Paleontologia India*, 33, 1–33.
- Sahnouni, M., Hadjouis, D., van der Made, J., Derradji, A., Canals, A., Medig, M., Belahrech, H., Harichane, Z., & Rabhi, M. (2002).

- Further research at the Oldowan site of Ain Hanech, north-eastern Algeria. *Journal of Human Evolution*, 43, 925–937.
- Sanders, W. J. (1990). Fossil Proboscidea from the Pliocene Lusso Beds of the Western Rift, Zaïre. In N. T. Boaz (Ed.), *Evolution of environments and Hominidae in the African Western Rift Valley* (Virginia Museum of Natural History Memoir, Vol. 1, pp. 171–187). Martinsville: Virginia Museum of Natural History.
- Sanders, W. J. (1997). Fossil Proboscidea from the Wembere-Manonga formation, Manonga Valley, Tanzania. In T. Harrison (Ed.), *Neogene paleontology of the Manonga Valley, Tanzania* (pp. 265–310). New York: Plenum.
- Sanders, W. J. (1999). Oldest record of *Stegodon* (Mammalia: Proboscidea). *Journal of Vertebrate Paleontology*, 19, 793–797.
- Sanders, W. J. (2003). Proboscidea. In M. Fortelius, J. Kappelman, S. Sen, & R. L. Bernor (Eds.), *Geology and Paleontology of the Miocene Sinap Formation, Turkey* (pp. 202–219). New York: Columbia University Press.
- Sanders, W. J. (2005). New Pliocene fossil proboscidean specimens from Laetoli, Tanzania. *Journal of Vertebrate Paleontology*, 25(Suppl. 3), 109A.
- Sanders, W. J. (2006). Comparative description and taxonomy of proboscidean fossils from Langebaanweg, South Africa. *African Natural History*, 2, 196–197.
- Sanders, W. J. (2007). Taxonomic review of fossil Proboscidea (Mammalia) from Langebaanweg, South Africa. *Transactions of the Royal Society of South Africa*, 62, 1–16.
- Sanders, W. J. (2008). Review of fossil Proboscidea from the late Miocene-early Pliocene site of As Sahabi, Libya. *Garyounis Scientific Bulletin, Special Issue No. 5*, 245–260.
- Sanders, W. J., Kappelman, J., & Rasmussen, D. T. (2004). New large-bodied mammals from the late Oligocene site of Chilga, Ethiopia. *Acta Palaeontologica Polonica*, 49, 365–392.
- Sanders, W. J., Gheerbrant, E., Harris, J., Saegusa, H., & Delmer, C. (2010). Proboscidea. In L. Werdelin & W. J. Sanders (Eds.), *Cenozoic mammals of Africa* (pp. 161–251). Berkeley: University of California Press.
- Semaw, S., Simpson, S. W., Quade, J., Renne, P. R., Butler, R. F., McIntosh, W. C., Levin, N., Dominguez-Rodrigo, M., & Roger, M. J. (2005). Early Pliocene hominids from Gona, Ethiopia. *Nature*, 433, 301–304.
- Servant-Vildary, S. (1973). Stratigraphie et néotectonique du Pliocène-Pléistocène ancien du Tchad d'après l'étude des Diatomées. *Comptes Rendus de l'Académie des Sciences, Série D*, 276, 2633–2636.
- Sikes, S. K. (1967). The African elephant, *Loxodonta africana*: A field method for the estimation of age. *Journal of Zoology, London*, 154, 235–248.
- Smart, C. (1976). The Lothagam I fauna: Its phylogenetic, ecological, and biogeographic significance. In Y. Coppens, F. C. Howell, G. L. Isaac, & R. E. Leakey (Eds.), *Earliest man and environments in the Lake Rudolf Basin* (pp. 361–369). Chicago: The University of Chicago Press.
- Su, D. F., & Harrison, T. (2007). The paleoecology of the Upper Laetolil Beds at Laetoli. In R. Bobe, Z. Alemseged, & A. K. Behrensmeyer (Eds.), *Hominin environments in the East African Pliocene: An assessment of the faunal evidence* (pp. 273–313). Dordrecht: Springer.
- Su, D. F., & Harrison, T. (2008). Ecological implications of the relative rarity of fossil hominins at Laetoli. *Journal of Human Evolution*, 55, 672–681.
- Symeonidis, N. K. (1970). Ein *Dinotherium*-Fund in Zentralmakedonien (Griechenland). *Annales Géologiques des Pays Helléniques*, 3, 1153–1165.
- Tassy, P. (1985). La place des mastodontes miocènes de l'ancien monde dans la phylogénie des Proboscidea (Mammalia): Hypothèses et conjectures. Thèse Doctorat de Etat ès Sciences Naturelles, Université Pierre et Marie Curie, Paris, Volumes I–III.
- Tassy, P. (1986). *Nouveaux Elephantoidea (Mammalia) dans le Miocène du Kenya. Cahiers de Paleontologie*. Paris: CNRS.
- Tassy, P. (1988). The classification of Proboscidea: How many cladistic classifications? *Cladistics*, 4, 43–57.
- Tassy, P. (1995). Les Proboscidiens (Mammalia) fossiles du Rift Occidental, Ouganda. *Geology and palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. II: Palaeobiology*. CIFEG Occasional Publications, 1994/29 (pp. 217–257). Orléans: CIFEG.
- Tassy, P. (2003). Elephantoidea from Lothagam. In M. G. Leakey & J. M. Harris (Eds.), *Lothagam: The dawn of humanity in eastern Africa* (pp. 331–358). New York: Columbia University Press.
- Tobien, H. (1988). Les Proboscidiens Deinotheriidae. *Palaeovertebrata, Mémoire extraordinaire*, 1988, 135–175.
- Tsoukala, E. S., & Melentis, J. K. (1994). *Deinotherium giganteum* Kaup (Proboscidea) from Kassandra Peninsula (Chalkidiki), Macedonia, Greece. *Geobios*, 27, 633–640.
- Vignaud, P., Düringer, P., Mackaye, H. T., Likius, A., Blondel, C., Boisserie, J.-R., de Bonis, L., Eisenmann, V., Etienne, M.-E., Geraads, D., Guy, F., Lehmann, T., Lihoureau, F., Lopez-Martinez, N., Mourer-Chauviré, C., Otero, O., Rage, J.-C., Schuster, M., Viriot, L., Zazzo, A., & Brunet, M. (2002). Geology and palaeontology of the upper Miocene Toros-Menalla hominid locality, Chad. *Nature*, 418, 152–155.
- Weinsheimer, O. (1883). Über *Dinotherium giganteum* Kaup. *Palaeontologische Abhandlungen*, 1, 205–282.
- White, T. D., Moore, R. V., & Suwa, G. (1984). Hadar biostratigraphy and hominid evolution. *Journal of Vertebrate Paleontology*, 4, 575–583.
- Wittemeyer, G., Daballen, D., Rasmussen, H., Kahindi, O., & Douglas-Hamilton, I. (2005). Demographic status of elephants in the Samburu and Buffalo Springs National Reserves, Kenya. *African Journal of Ecology*, 43, 44–47.
- Woolley, L.-A., Mackey, R. L., Page, B. R., & Slotow, R. (2008). Modelling the effect of age-specific mortality on elephant *Loxodonta africana* populations: Can natural mortality provide regulation? *Oryx*, 42, 49–57.
- Yasui, K., Kunimatsu, Y., Kuga, N., Bajope, B., & Ishida, H. (1992). Fossil mammals from the Neogene strata in the Sinda basin, Eastern Zaire. *African Study Monographs, Suppl. 17*, 87–107.
- Zazzo, A., Bocherens, H., Brunet, M., Beauvilain, A., Billiou, D., Mackaye, H. T., Vignand, P., & Mariotti, A. (2000). Herbivore paleodiet and paleoenvironmental changes in Chad during the Pliocene using stable isotope ratios of tooth enamel carbonate. *Paleobiology*, 26, 294–309.