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DENTAL AND SKELETAL MORPHOLOGY OF THE EARLIEST ELEPHANTS

BY

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ABSTRACT

Recent discoveries of Mio-Pliocene Elephantidae in Africa have provided the first data on early stages in the origin of the family. The abundant cranial and post-cranial materials now available allow a standard of comparison for other less complete collections of similar age, and have made possible analysis of evolutionary phenomena within the group. The present paper provides detailed supplementary morphological descriptions of the four most primitive species known in the family.

INTRODUCTION

Until recent years the earliest stages in the evolution of Elephantidae remained virtually unknown. Elephants fulfilling our concepts of "primitive" were long recognized from early Pleistocene deposits in Europe and Asia where their "sudden" appearance was used as an index for determination of the Tertiary-Quaternary boundary. On this evidence, it was assumed that elephants (*sensu stricto*) originated in Asia from a stegodont ancestor and then rapidly expanded into Europe. Although a number of morphological problems made such a view less than satisfactory, at that time geographic and stratigraphic considerations favored such an interpretation.

It now seems more likely that early in their history stegodonts paralleled the horizontal shearing-type of dentition so characteristic of the Elephantidae. Associated with this, certain osteological and myological modifications related to the utilization of this type of dentition were also achieved by the stegodonts. Nevertheless, details of molar and cranial evolution in this group strongly point to an independent specialization, quite unrelated to that of elephants (see Maglio and Hendey, 1970).

Until recent years only one really primitive species of elephant was known in Africa. This led Osborn (1942) to favor an African origin for the family, but little direct evidence in support of this view was available at that time. One species of the genus *Stegodon* did occur in Africa during the late Pliocene (Cooke & Coryndon, 1970), but this was clearly an immigrant from Asia and could not have been the ancestral group from which elephants derived in Africa.

Attention was then turned to *Stegolophodon*, an earlier stage in the evolution of the stegodonts. This group had been reported in Africa (Petrocchi, 1941; Singer & Hooijer, 1958), and seemed a likely candidate for elephant ancestry in spite of the fact that none of the reported species were adequately known (Aguirre, 1969). It has since been suggested that the supposed *Stegolophodon* species in Africa are actually very primitive elephants and that true members of the genus probably did not occur outside Eurasia.

Recently, new field studies in Africa have added significantly to the investigation of these problems. During the past five years, faunal resolution and radiometric dating techniques have improved, greatly altering our concepts of Pliocene and Pleistocene time and of spatial and temporal distributions of faunas (Van Couvering, 1972; Brown & Lajoie, 1970; Bishop *et al.*, 1971; Cooke & Maglio, 1972). As a result, the record of elephantid evolution has now been extended back to at least 6.0 million years B.P., into the latest Miocene of Africa where the earliest known

stages appear to grade backward into ancestral Gomphotheriidae, clearly demonstrating a non-stegodont origin for the family (Maglio, 1973). A new gomphothere-like species (*Gomphotherium ngorora*) showing some intermediate trends toward the elephant type of dental adaptation has recently been described from Ngorora in Kenya, and is dated at about 9 m.y. old (Maglio, 1974).

Four species of Elephantidae from late Miocene and Pliocene deposits at Lothagam Hill and Kanapoi, Kenya, have previously been diagnosed and their relationships discussed (Maglio, 1970). These taxa represent the earliest true elephants known, and as such are crucial to interpretation of the origin and early phases in adaptive radiation that was later to result in a nearly world-wide distribution of the family during Pleistocene times. The data presented below are intended as detailed descriptions of these four taxa, based on all of the fossils presently available, and should serve as the basis for comparison of other less complete materials. Where possible collective descriptions are given rather than those of individual specimens. This material also shows some interesting features in the evolution of elephant dentitions and these are presented with the morphology.

ACKNOWLEDGEMENTS

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ABBREVIATIONS

C1, C2, etc.	Intravalley columns, numbered from front
EK	Ekora, Kenya
ET	Enamel thickness
H	Unworn height of molar crown
HI	Hypsodonty index
KNM	National Museums of Kenya, Nairobi
KP	Kanapoi Formation, Kenya
L	Maximum length of molar crown
LF	Lamellar frequency
LT	Lothagam Hill, Kenya
P	Number of molar plates
P1, P2, etc.	Plate number on molar teeth, numbered from front
W	Maximum width of molar crown

SYSTEMATIC DESCRIPTIONS

Family Elephantidae
Subfamily Stegotetrabelodontinae Aguirre, 1969

Stegotetrabelodon orbus Maglio, 1970

Orginal Reference: Maglio, 1970: 5, pls. I, II.
Holotype: KNM LT-354, complete left lower mandible with unworn left M_3, worn left M_2 and left and right lower incisors *in situ*, incomplete left and right M^3, complete right M^2 and associated skeletal fragments.
Horizon and locality: Late middle Pliocene, Lothagam 1, Lothagam Hill, Turkana, Kenya.
Material: The holotype mandible and nearly the complete dental series; isolated post-cranial elements.

SUPPLEMENTARY DESCRIPTION:

M^3

This molar is known from complete and three fragmentary specimens and consists of six plates and a small but complex anterior enamel ridge. On KNM LT-359 this anterior ridge bears a centrally placed pillar that is closely appressed to the first plate (*P1*) and fully incorporated into it at the base. On the buccal side of this central pillar is an elongated enamel fold with four very weak digitations. Other specimens show a similar fold on the lingual side, indicating that the anterior ridge may have extended across the entire width of the molar in some individuals.

P1 is divided into two laterally elongated demi-plates separated by a tightly compressed, deep, longitudinal furrow lying just to the buccal side of the midline. This furrow corresponds to and represents the vestige of the median cleft in gomphothere molars (see Maglio, 1973, pp. 93–94). Shallower apical clefts divide each of the demi-plates into two parts so that the entire plate consists of four closely appressed pillar-like structures. The median and lateral clefts effectively divide the crown so that four separate rings of enamel are formed on the occlusal surface during early stages of wear. With further wear, first the two buccal pillars, then the lingual ones, become confluent forming two elliptical loops separated by the median cleft. A complete enamel figure across the entire width of the plate appears only when the plate is worn down to about half or one-third of its original height. The position of the median cleft is marked even in late stages of wear by a prominent median constriction on the enamel figure.

In the valley behind *P1* is a strong column, *C1*, free for most of its height and arising from the base of *P1* just lingual to the median cleft. A weak

vertical groove is often present on the side of this column suggesting either incipient formation of a secondary accessory column or former fusion of two columns.

P2 also bears a deep median cleft that is marked along the plate faces by prominent grooves. As in *P1*, two laterally placed clefts subdivide the crown into four rounded pillars, the more centrally-placed of the lingual pair tending to be further subdivided. In KNM LT-359 there are three of these minor subdivisions, but on other specimens there are none. As in *P1*, a free column, *C2*, arises from the posterior face of the plate just to the lingual side of the median cleft. This column may bear an accessory ridge as in KNM LT-316, or it may be small and simple in structure. A remnant of the median constriction remains on the plate face until worn to within about 20 mm. of the crown base. A strong vertical ridge extends along the lower two-thirds of the anterior face of *P2*. This ridge contacts *C1* for most of its height and with wear the latter would form a prominent median sinus or loop.

P3 and *P4* are similar to *P2*. The central pillars may be subdivided into two or three digitations, but this is highly variable. There are no free columns behind these plates, but prominent vertical ridges just lingual to the median cleft represent columns that have been partially fused into the plate faces, a process typical in elephant evolution. As in *P2*, a small vertical ridge is also present on the anterior face of the plate.

There is a strong tendency for one of the two central pillars to be higher and more subdivided than the others, its apex spreading medially to assume a more central position. This gives the plate a superficially symmetrical appearance with a strong central column. This "overtopping" of one pillar can be so prominent as to displace the median cleft to one side, thus establishing the typical symmetry of elephant molar plates.

P5 consists of a strong central pillar flanked on either side by elongated plates, each subdivided into two pillars by an apical cleft. There are thus five pillars in all, with a tendency toward further subdivision in some specimens. The cleft on the buccal side of the central pillar is the deepest and assumes a more median position toward the base of the crown in some individuals. It probably represents the original median cleft, having been displaced buccally by the budding and enlargement of the overtopping mediolingual pillar. By early stages of wear the lateral clefts are obliterated and a three-looped enamel figure is formed – a central circular loop and two lateral elliptical ones. A strong posterior ridge marks the position of the fused *C5*.

The structure of *P6* is variable. It may consist of three massive pillars, each separated from its neighbor by very deep furrows as in KNM LT-316, or it may be a small replica of the more anterior plates. A posterior heel is very variable, being absent in some specimens. In others it may be a single large triangular pillar arising from the base of *P6*, or it may be more complex, consisting of two or three prominent pillars.

The molar as a whole is broad throughout, attaining its maximum width at *P3* or *P4*. Except for the last plate, the tapering in width from front to back of the tooth is not as great as in the lower M_3. Transverse valleys between adjacent plates are V-shaped in cross-section and not compressed at the base. The lateral sides of the plates taper toward the apex of the crown, being about one-third to one-half as narrow at the apex as at the base.

Lamellar frequency (number of plates per 10 centimeters of molar length) is 2.4 to 2.8 for complete or partially worn specimens, but may be as high as 3.3. for severely worn molars. This is due to the apical divergence of plates on upper molars.

The crown is relatively short; the hypsodonty index is 68 to 72. Enamel is unfolded and varies from 4.0 to 7.5 mm. in thickness. Its external surface is rugose and pitted. Around the base of the crown the limit of enamel is emarginated in the region of transverse valleys so that the ventral enamel border is strongly undulating.

In several specimens, small accessory cusps are present in valley floors on the buccal and lingual sides of the molar, but only in one specimen (KNM LT-316) are these present in every transverse valley. These cusps rise to a height of about 20 to 25 mm. from the crown base and contact the plates in front and behind.

A strong, broad anterior root, triangular in cross-section, supports the buccal half of *P1*. Two intermediate roots are present, one underlying the lingual half of *P4*, the other underlying *P4–P5*. A confluent posterior root system supports *P5* and *P6* for the entire width of the molar.

M_3

There are six specimens of this molar from the type locality, three unworn and virtually complete, and three worn or otherwise fragmentary. There are seven plates, an anterior ridge and a posterior heel. The anterior ridge is variable in structure; it may be absent or complexly developed consisting of up to three small pillars.

A broadly open and deep median cleft vertically divides *P1*. This persists for about half of the plate height. On the lingual side of the cleft the crown is divided into two equal pillars by a prominent but shallow lateral cleft demarcated more strongly on the posterior face of the plate by a deep vertical furrow. The buccal side of the plate may be a single pillar, or it may be subdivided into two more or less equal parts.

A prominent intermediate column, *C1*, is present in the valley between *P1* and *P2*, free for its apical one-third, and becoming incorporated into the posterior face of *P1* toward the base of the crown. Even when well worn, *C1* forms a prominent posterior sinus or loop on the occlusal surface. The column may be simple or subdivided.

P2 consists of four pillars separated by a deep median, and shallower lateral clefts. Smaller subdivisions may be present on some of the pillars,

but the exact pattern of apical budding is variable. A strong vertical fold is often present on the anterior face of the plate, forming a strong loop with wear. *C2* is strong and located just to the buccal side of the median cleft.

P3 to *P5* are essentially like *P2* in structure, but the vertical, anterior folds are usually absent. Free intermediate columns behind the plates may be present or absent. When absent, vestigial vertical folds indicate that they have been fused into the plate faces. Minor subdivisions of the crown by apical budding may result in up to seven digitations on the apex of each plate. However, the essential four-pillared nature of the plate is retained by the presence of three major clefts.

The last two pillars, *P6* and *P7*, show considerable variation in structure. They may be essentially like the anterior plates, but lacking accessory folds, or they may consist of only three rounded pillars.

The posterior heel is highly variable as is usual in Proboscidea, but it is always rather prominent. In some specimens the heel has a large base and may be considered as an eighth plate. In others, it clearly arises out of *P7*.

The molar broadens rapidly in its mid-length, attaining its maximum width at *P3* to *P5*. Here the width is up to 20 percent greater than at *P1*. The plates are strongly triangular in longitudinal-section, being nearly twice as thick at the base as at the apex. As a result, the transverse valleys between them are V-shaped, but not compressed or Y-shaped as in stegodonts. The sides of the plates taper distally, the apical width being only one-third to one-half of the basal width.

The plates are widely separated from each other; lamellar frequency is 2.8 to 3.0. In very worn specimens this value may be as high as 3.3, but this inflated figure results from the wider plate separation at the base of lower molars. The crown height is relatively low – the hyposdonty index is 68 to 83. Enamel is generally rough externally with more or less horizontally-oriented ridges giving an oyster-shell appearance.

A strong anterior root underlies *P1*. A stout intermediate root underlies the lingual half of *P3*, while a posterior root system supports the remainder of the crown.

M^2

There are three specimens of this molar, two nearly complete and the other complete. In all three, *P1* is worn or lacking, but it is clear that the total number of plates was only five. *P2* is well worn on all specimens, but a posterior enamel constriction indicates the presence of a deep median cleft. A prominent enamel loop to the lingual side of this constriction represents *C2*, but it is not possible to determine whether it was free at the apex.

P3 is not divided by a median cleft, but a deep anterior and posterior vertical groove marks the position of the cleft. A strong anterior fold on the lingual side of this groove forms an anterior sinus when worn, making contact for its entire height with *C2* in front of it. An isolated column behind *P3* is about one-third lower than the plate.

As in the other plates, *P4* is well consolidated, lacking prominent vertical furrows demarcating individual pillars. There are five apical digitations, one central in position with the weak median cleft passing to the buccal side of it. A very strong anterior vertical ridge makes contact with *C3* and is one-fourth lower than *P4*. *C4* is free only for a few millimeters at the apex and becomes completely fused into the plate at about 20 mm. from the base.

P5 is simple, consisting of four closely appressed pillars separated by vertical furrows. There is no associated intermediate column. A prominent posterior heel consists of three to five pillars arising from the base of *P5* and closely appressed to it, usually without an intervening valley.

The molar attains its greatest width at *P3* or *P4*. Transverse valleys are V-shaped but not compressed at the base. All the specimens are too worn for a determination of the maximum crown height. From the estimated height of *P5*, the hypsodonty index for this plate was about 70. Enamel is unfolded and varies from 3.7 to 6.4 mm. in thickness.

A strongly triangular anterior root underlies the lingual half of *P1* and part of *P2*. A flat intermediate root supports *P2* and the posterior root system begins at the *P3–P4* valley.

M_2

There are five examples of this molar, all complete. Six plates are present, the last somewhat variable in size, but usually too large to be considered a posterior heel. The anterior ridge, arising from *P1*, is a thin fold of enamel with a posterior swelling pressed into the median cleft of *P1*.

P1 is completely divided by a median cleft, the latter persisting to within 10 mm. of the crown base. On the buccal side of the cleft, a free column arises vertically from the posterior face of *P1*. A shallow furrow divides the lingual half of the plate into two weak pillars.

A prominent median cleft also divides *P2*, but it is not as deep as in *P1*, persisting to within 33 mm. of the crown base. In one specimen, the median cleft has been displaced lingually and a median pillar has developed through overtopping from the buccal side. A furrow is present on either side of this central pillar and other weaker furrows divide the plate face into five vague pillars. However, the plates are much more consolidated in structure than in M3. A prominent *C2* is present.

In structure, *P3* to *P6* are like *P2*. *C5* and *C6* are lacking. The apices of the last two plates may be further subdivided by minor budding.

The molar is very broad posteriorly, attaining its greatest width at *P5*. The plates are somewhat triangular in cross-section, but not as strikingly as in M3. Transverse valleys are V-shaped, but the bases are more open and less pointed than in M3.

The sides of the plates taper apically where the width is only 45 to 50 percent of that at the base. The lamellar frequency is 3.1 to 3.6. Crown height is very low; the height/width index is 52 to 63. The enamel is not

folded and measures 3.3 to 3.8 mm. in thickness. Cement is abundant, but is thin and follows the contours of the plates.

M^1

Only one incomplete specimen is known, but it appears to have had only five plates. The median cleft was not deep on *P1* and the dentine is confluent across the plate even in early stages of wear. *C1* is not free at the apex and appears as a strong posterior fold on the posterior face of *P1*. Remaining plates are like *P1* in structure, with four weakly demarcated pillars and a posterior fold. Enamel is very thick, proportionately more so than in M2 or M3. It measures 5.6 to 5.9 mm. in thickness. The plates are triangular in cross-section, but not as strongly as in M3.

The molar is widest at about *P2* or *P3*, and the greatest height is at *P3*. Hypsodonty index is 49, and the lamellar frequency is 4.4.

M_1

Only the last three plates and heel of one specimen are preserved. It is narrower throughout than the corresponding upper molar. Plates are divided by a deep median cleft for about half their height. Valleys are V-shaped, but broadly open as in M2. The lateral sides of the plates taper strongly toward the apex.

The first preserved plate (probably *P4*) consistst of four pillars, each separated by a deep apical cleft. Further subdivision of the crown is present on some of the pillars. The next posterior plate (*P5*?) has only three simple pillars, as does the last plate. The posterior heel is simple, consisting of a single pillar arising from the base of the molar just behind *P6*.

Height and width can be taken on the first preserved plate, giving a hypsodonty index of 61. As in M^1, the enamel is extremely thick for the size of the tooth, 5.5 to 6.7 mm. The lamellar frequency is 4.3, based on the preserved portion of the molar.

dM_3

This milk molar has three full plates, and a prominent anterior ridge and posterior heel. *P1* is worn to about half of its height, and the dentine is already confluent from side to side within the complete enamel figure. A strong median constriction marks the former presence of a median cleft. On the buccal side of the constriction is a very prominent, but partially fused column, *C1*, which must have been free at the apex in the unworn state. This column rises vertically from the backward-sloping posterior face of *P1* so that it becomes incorporated into it with wear.

Closely appressed to the anterior face of *P1* is a very prominent anterior ridge, as wide as a true plate, but lacking a base; it arises out of the base of *P1*.

P2 is worn for about a third of its original height. Although a strong

median constriction is present, the enamel figure is complete. A vertical fold on the lingual side of the constriction wears as a small anterior sinus. A larger posterior sinus is located just buccal to the median constriction and represents the partially fused *C2*.

P3 is only slightly worn but already forms a complete enamel figure with small anterior and posterior sinuses. The posterior heel is a massive structure composed of three main pillars, the central one higher and wider than the others.

The molar is broadest posteriorly, attaining its maximum width at *P3*. Although worn, the original height of *P3* could not have been more than about 35 mm., giving a maximum hypsodonty index at *P3* of 94.

Transverse valleys are strongly V-shaped, and constricted in their median portions where the sinuses meet in the midline. The plates are very thick and rather closely spaced; the lamellar frequency is 6.2. As is usual in Proboscidea generally, the enamel of milk molars is folded, even when enamel of the permanent molars is not. Here the enamel is only very weakly and broadly folded and is 1.7 to 1.9 mm. in thickness.

A single anterior root underlies the anterior ridge and the front half of *P1*. A large posterior root supports *P2*, *P3* and the heel.

dM_2

This milk molar is not known at present, but its alveolus is present in a mandibular fragment referred to this species. The tooth appears to have been single rooted.

P^4

A single specimen is tentatively assigned to this species. A strong anterior ridge is formed by a simple fold of enamel. The crown is composed of four individual cone-like pillars arranged in two pairs. The anterior pair is compressed anteroposteriorly and closely appressed in the midline, forming a low, plate-like structure. The lingual cone of this pair is dumbell-shaped with a coarse anterior and posterior constriction at its center; the buccal cone is oval in outline. The posterior cones are smaller and more circular in cross-section so that the tooth in narrower posteriorly. In overall shape, the tooth is triangular with the anterior and lingual sides forming a 90 degree angle with each other.

The hypsodonty index is 45 and the unfolded enamel is 3.8 to 4.2 mm. in thickness.

Mandible

The holotype mandible is of the left side and is essentially complete except for the articular condyle, the tip of the coronoid process, and the distal extremity of the incisive alveoli of the symphysis. The mandible is rather more lightly built than would be expected for a jaw bearing such large incisors. The corpus is long anteroposteriorly, although proportion-

ately no longer than in the living species of *Loxodonta*. That portion of the corpus just below the anterior border of the ramus is about 30 percent wider than high, the midline is nearly isometric, and the anterior portion just at the point where the anterior symphysial ridge begins, is nearly 120 percent higher than wide.

The medial surface of the angle bears a prominent oval depression for attachment of the medial pterygoid muscles on its ventral edge. The medial pterygoid appears to have been more massive than in either of the living species. A linear depression for the mylohyoid muscle runs about 47 mm. below the alveolar border and continues forward as it curves onto the ventral border of the corpus where it passes into the scar for the digastric muscles. The alveolar ridges end anteriorly in sharp crests which slope downward and forward, making an angle of about 45 degrees with the inferior edge of the corpus. Deep, elongated pits on the posteroventral surface of the symphysis mark the insertion of the geniohyoid muscles.

Internally the mandibular canal lies close to the inferior border of the corpus. Anteriorly it communicates with the exterior by a short canal leading to the mental foramen, and a larger canal opening into the posterior part of the enlarged incisive alveolus.

The symphysis is directed downward. In length it is 413 mm. as preserved but must have been about 100 mm. longer when complete. The superior surface is marked by a broad concave groove about 45 mm. across, along its entire length. Lateral to this groove the sides of the symphysis slope outward and downward forming an oblique flat plate along the dorsolateral surfaces. The ventral contour of the symphysis is lacking.

The ascending ramus arises from the corpus about 270 mm. posterior to the anterior edge of the alveolar surface, and slopes backward at about 100 degrees to the ventral border of the mandible. Its anterior edge is large and rounded for attachment of the temporalis tendon. A very broad concave lateral depression for the internal masseter muscle lies immediately behind this edge. The angle contour is lacking. There appears to have been a prominent, rounded protuberance just above the angle, formed by the descending anterior edge of the ramus and superior border of the corpus; it marks the ventral extent of insertion for the buccinator muscle. The medial temporalis fossa is very shallow, the main excavation lying mainly above the occlusal level of the inferior dentition. In *Loxodonta*, the internal temporalis fossa slopes down further to the alveolar border, occupying almost the entire medial surface of the ramus.

Left and right incisor roots penetrate to within 40 mm. of the posterior edge of the symphysis, and are separated from each other by a lamina of bone 5 to 15 mm. thick. The right tusk is 995 mm. in length, with 604 mm. exposed beyond the broken symphysis. They are compressed laterally for most of their length, but become nearly circular in cross-section at about 155 mm. from the distal tip. At 800 mm. from the tip,

the maximum dimensions of the tusk are 61 mm. by 72 mm. The left tusk bears a prominent concave groove, 20 to 25 mm. wide along its dorso-medial side. This groove becomes shallower distally, but the tusk is broken before the groove terminates. The tusks are very gently curved upward, especially for their distal one-third. Medial separation is small, about 15 mm. proximally (at the symphysis), and 24.5 mm. at 30 mm. from the distal tips. The proximal one-third of the tusk surface is marked with numerous longitudinal grooves about 0.5 to 2.0 mm. across. These become weaker distally, and are lacking on the distal third of the incisors.

POST-CRANIAL DESCRIPTIONS

Atlas

Associated with the holotype mandible, this specimen is relatively short, with large articular surfaces. The neural arch is a low knob of bone lacking a central groove. Anterior articular surfaces are relatively higher on the bone than in living elephants, as are those for contact with the axis. Transverse processes are slender and short.

Measurements (in cm.)

Width across transverse processes:	38.5
Maximum height in midline:	21.0
Dorsoventral diameter of the vertebral canal:	10.3

Humerus

One specimen is represented from Lothagam 1 (KNM LT-369). Proximal and distal ends are massively developed compared to the slender shaft. The deltoid ridge is robust and extends for two-thirds the length of the bone, ending just above the medial condyle. The large proximal head lacks a well defined anatomical neck. Lateral to the head is the very large greater tuberosity projecting anteriorly as a massive crest. The biceptal groove is shallow. Distally there is a shallow olecranon fossa, above and posterior to the rounded condyles.

Measurements (in cm.)

Overall length:	96.0
Proximal articular surface, anteroposterior:	18.3
transverse:	13.3
Transverse diameter at midshaft:	17.0
Anteroposterior diameter at midshaft:	13.3
Width across distal condyles:	26.2

Primelephas gomphotheroides Maglio, 1970

Original Reference: Maglio, 1970: 10, pls. III–IV.

Holotype: KNM LT-351, associated left and right M^3, left M_3 and fragmentary palate.

Horizon and locality: Late Middle Pliocene, Lothagam 1, Lothagam Hill, Turkana, Kenya.

Material: Known from several mandibular fragments and isolated teeth only. No post-cranial remains definitely referable.

SUPPLEMENTARY DESCRIPTION:

M^3

Three nearly complete molar fragments represent this tooth. There are seven plates present and an anterior ridge composed of a thin, multicusped fold of enamel extending across the entire width of the molar. Although *P1* is incompletely known, it appears to have had only a very weak median cleft about 20 mm. deep and lateral clefts are present on either side of the midline, dividing the crown into four pillars with further minor subdivisions on some of them. A prominent vertical column, *C1*, is present just lingual to the median cleft on the posterior face and is free only at the apex, being fused to the plate for most of its height. It is variably subdivided at its apex.

P3 retains a very shallow median cleft but the median-buccal pillar is enlarged and divided into three buds, displacing the median cleft lingually. On *P4* to *P6*, the median-lingual pillar tends to be subdivided and enlarged, displacing the median cleft buccally. This overtopping gives the plates a symmetrical appearance. However, in some specimens, both sides of the plate may be equally developed, retaining symmetry around the median cleft.

P7 is simple with only four pillars and the remnants of a median cleft. A weak posterior heel consists of three to four ridges compressed against *P7*.

Cement is abundant but does not usually invest the apices or sides of the plates and does not fill the valleys completely. Transverse valleys are V-shaped as in M3 and the plates are strongly triangular in cross-section. The plates do not taper strongly toward the apex. The maximum taper from base to apex is only about 30 percent.

The molar is broad throughout, attaining its maximum width at *P3*. The maximum height is at *P4* or *P5*, with a hypsodonty index of about 63. The plates are widely spaced with a lamellar frequency of 3.2. The enamel is unfolded with a rough and pitted exterior surface. The thickness is 3.4 to 5.6 mm., becoming thinner toward the base of the crown.

M_3

Only a single specimen of this tooth is known. There are eight plates and a posterior heel. The enamel is lacking from the anterior face of the worn

P1 and it is not possible to determine the nature of the anterior ridge. *P1* is deeply divided by a median cleft to within 15 mm. of the base; the cleft is deeper on the posterior face and persists here into late stages of wear, after the anterior part of the plate is already confluent across the midline. A small, posterior inward fold lingual to the median cleft indicates the remnant of a longitudinal furrow which must have superficially divided the lingual half of the plate into two pillars when unworn. *C1* is very prominent and still free from *P1*, even though this plate is worn to within about 18 mm. of its base in this region.

P2 is about half worn on this specimen, but it is clear that very superficial furrows divided the plate face into pillars. Although a deeper median constriction marks the presence of the former median cleft, the enamel figure is already complete at this stage of wear. A large, but flattened posterior fold represents *C2* which was probably free at the apex. A smaller anterior fold nearly contacts *C1* in the midline.

P3 is slightly worn. Instead of a median cleft, however, there is a strong central anterior and posterior fold demarcated laterally by prominent constrictions, the lingual one being deeper. This fold is in the expected position relative to the posterior fold, and probably represents the fused *C3*. The deeper lingual constriction probably represents a median cleft displaced by "overtopping" of the median-buccal pillar and associated *C3*.

P4 to *P8* are essentially unworn. *P4* has five main apical digitations, but the median pillar is probably due to overtopping from the buccal side. The digitations are closely appressed, but longitudinal furrows persist on the plate faces, except near the base, where only the median constriction is usually visible. *P5* and *P6* have only four main pillars with a deep median constriction and prominent lateral furrows. *P7* and *P8* have a large median pillar flanked by one strong pillar on either side. The posterior heel is a two-cusped tiny replica of a plate, closely appressed to *P8*.

Cement abundantly invests the tooth but does not fill the valleys completely. The molar is broad, attaining its maximum width at *P3*. Although width falls off posteriorly, the width differential between plates, except for *P8*, is not very great. Maximum crown height is at *P5* and the hypsodonty index is about 6.6. Valleys between the plates are V-shaped in cross-section, as in *Stegotetrabelodon*.

The plates are thin throughout, but are triangular in longitudinal-section. They are widely spaced, the lamellar frequency being 3.3 to 3.6. The sides of the plates taper apically and are gently rounded, the apex being two-thirds to one-half as wide as at the base.

Enamel is smooth and rather thick, about 3.5 to 5 mm.. The external surface is generally pitted and strongly rugose.

A strong anterior root underlies the lingual two-thirds of *P1* and the valley between *P1* and *P2*. The intermediate root is lacking due to damage, but a posterior root system supports *P4* to *P8* and the posterior heel.

M^2

This tooth is represented by a pair of complete, unworn molars. There are five plates with a strong anterior ridge and posterior heel. The former consists of a large, double pillar at the anterobuccal corner of the tooth, and a thin coarsely folded ridge along the entire front surface of the molar, extending onto the sides of *P1*.

P1 bears a deep median cleft dividing the plate into two half-plates, each further divided into two prominent pillars. Deep furrows separate the pillars nearly to their base. *C1* is strong, free for about a quarter of its height, and divided into two equal pillars in the anterolingual- posterobuccal direction. It lies behind the median-lingual pillar to which it is fused at the base. The anterior side of that pillar is enlarged into a longitudinal ridge which would form a prominent sinus with wear.

P2 bears six digitations on the left molar and eight on the right one. These are formed primarily by apical budding. Overtopping is so great and the clefts so shallow that the position of the median cleft is obscured, although it can be inferred from the position of *C2*. The extreme lingual and buccal pillars are the largest; the more centrally placed digitations are smaller and more tightly compressed. A small, but prominent vertical fold lies along the anterior surface just to the lingual side of the presumed median cleft, and contacts *C1* for most of its height. *C2* is free at the apex, and may bear up to three small posterior buds. When worn, this would form an irregularly shaped sinus.

P3 retains its basic four-pillared structure, but overtopping is beginning to obscure the ancestral gomphothere symmetry. The extreme lingual and buccal pillars are again simple conical structures, but the two medially-placed pillars are subdivided by apical budding. The process has not yet progressed to the point where the weak median cleft is obscured or displaced in the right tooth. However, in the left tooth, the buccally-placed bud of the median-lingual pillar is enlarged, and by slightly displacing the median cleft buccally has begun to assume a dominant, central position. A strong vertical anterior fold lies on the median-lingual pillar, but no posterior column is visible.

In *P4*, overtopping is complete; a large central column forms the symmetrical center of the plate with two large digitations on either side. The old median cleft passes to the buccal side of the central pillar so that overtopping was achieved by budding from the lingual side. Small anterior and posterior vertical ridges are present on the central pillar in the left molar, but in the right, these are not obvious.

P5 displays variable apical budding in the two molars, but is otherwise similar to *P3* in structure; the extreme lingual and buccal pillars are the largest with smaller, rounded digitations between them.

The posterior heel is very strong, consisting of four to five thick pillars arising from the base of *P5* and separated from it only by several millimeters.

The plates are broader at the base but not nearly as triangular in cross-section as in M3; the plate faces are more nearly parallel. Transverse valleys are V-shaped but are more open than in M3.

The molar is widest at *P4* to *P5* and highest at *P3* and *P4*. The hypsodonty index is 72, and the lamellar frequency is 3.5. It is difficult to measure a range of enamel thickness as the molars are unworn. But from a broken area, the enamel is seen to be 3.9 mm. in thickness. It is unfolded with a finely rugose exterior surface.

The base of the crown is curved downward anteriorly so that *P1* and *P2* are sharply directed forward.

M_2

There are only two specimens of this tooth; the right is nearly complete, the left consisting of only two plates. The last preserved plate on the right specimen is lacking its posterior half, but from the curvature of the crown base, this was probably the last plate. This would give a total of six plates.

The anterior ridge bears a median pillar pressed into the anterior furrow of the *P1* median cleft; the remainder of the ridge consists of a series of small folds and pillars of enamel along the front surface of *P1*. The latter is well divided in the midline by a prominent cleft. A double-pillared half-plate lies on either side of the cleft, the lingual digitation bearing a small medial bud. *C1* is prominent and isolated at its tip, and is compressed anteroposteriorly, being oval in cross-section. As usual with these posterior columns, *C1* rises vertically out of the backward-sloping face of *P1*, becoming incorporated into the latter toward the base.

P2 bears a central pillar, divided apically into anterior and posterior digitations, and with two lingually-placed buds. A strong anterior vertical fold on this central pillar contacts *C1* across the *P1–P2* valley and would form a large anterior sinus with wear. An isolated *C2* lies immediately behind the central pillar. A weak cleft separates this central complex from the single buccal pillar, and an even shallower one from the single lingually-placed pillar.

P3 again bears a central complex, with a single dominant pillar, two lingual buds and a posterobuccal bud. A strong *C3* is present and an anterior fold makes contact with *C2* for most of its height.

P4 is like *P2* and *P3*, but apical digitations are more individualized, although the intervening clefts are still very shallow. *P5* is similar, with a very weak posterior column. *P6* has only four apical digitations lacking vertical furrows on the plate faces. The cleft between the two central pillars is 22 mm. deep versus 18 mm. for the two laterally placed ones, suggesting that it is the median cleft.

The molar is relatively very long and narrow, attaining its greatest width at *P6*. The tooth is strongly curved laterally. Plates are widest at the base and taper toward the apex; the apical width is about two -thirds to one-half that at the base. In longitudinal-section, the plates are triangular,

being thicker at the base, but as with M^2, they are more parallel-faced and plate-like than the corresponding M3. Transverse valleys are V-shaped, but relatively more open and rounded at the base than in M3.

The crown is low; the hypsodonty index is 78. Plates are thick and well separated, and for a small tooth as this, the lamellar frequency is relatively low, being 3.4. The enamel is externally rugose as in M^2, and extremely thick, measuring 5.1 to 5.6 mm..

The roots are lacking for the most part, but the base of an anterior root underlies *P1–P2* for the entire width of the molar.

M_1

This molar bears five plates, an anterior ridge and a small posterior heel. *P1* is only partially preserved and shows a central enlargement bearing a strong posterior sinus. The central pillar is flanked by weak enamel constrictions. On *P2* the central pillar is circular in cross-section; it is separated by strong constrictions from the lingual and buccal pillars, each of which is laterally elongated. A small posterior column lies behind the central pillar. *P3* has a central, rounded swelling on both the anterior and posterior face, with a small constriction on either side. As in *P2*, a small posterior column is present, but this is not free at the apex. On MCZ 290-67K, *P4* bears a central, rounded swelling as in *P3*, with several coarse inward folds posteriorly on either side of the median pillar. A shallow median cleft divides the plate into two, each half bearing two apical digitations. On the buccal side of the median cleft is a small anterior and posterior vertical fold. There are no other longitudinal furrows on the plate face; the plates are solid and unitary structures.

P5 has a narrow vertical fold in the midline of its anterior face, but posterior folds or columns are lacking. Just to the lingual side of this fold is a very shallow cleft only a few millimeters deep. The apex bears four weak digitations.

The posterior heel consists of a broad column arising from the base of *P5*; it is separated from the latter on the lingual side by a deep furrow, but on the buccal side, it merges completely into the side of that plate without demarcation.

The plate faces are nearly parallel, not obviously triangular as in the more posterior molars of this species. Transverse valleys are more broadly open than in M2 and M3. The molars are widest at *P4* and *P5* and the estimated hypsodonty index for *P5* is 68 to 72. Enamel is slightly roughened externally and is 2.3 to 3.9 mm. in thickness. It is unfolded. The lamellar frequency is 4.0 to 4.3.

An anterior root underlies the entire width of *P1*, is B-shaped in cross-section with a median groove along the posterior side of the root. It measures 67 mm. in length, but was certainly at least 40 mm. longer when complete. As is usual for these early forms, the root length is proportionately very great when compared with the crown height. The posterior root

begins under the middle of *P2*. It is triangular in cross-section with one apex of the triangle under the median part of *P2*. It measures about 108 mm. in length. The crown height in this region was about 41 mm..

Mandibular fragments

Several mandibular fragments have been recovered which demonstrate the presence of mandibular incisors in this species. MCZ 290-67K was associated with the $M_{\frac{2}{2}}^{2}$ and M_1's described above and consists of a symphysis, the left-lateral part of the left mandibular corpus, and fragments of one incisor. MCZ 13-68K is the left ventral symphyseal portion of a mandible with an associated partial M^3 and maxillary-malar fragment. MCZ 86-68K is the right-lateral side of the right mandibular corpus including the right side of the symphysis.

In MCZ 290-67K the anterior 100 or so millimeters of the corpus is preserved. On the left side, the ventral portion of the incisive alveolus can be seen. This cavity is rounded laterally indicating an incisor about 30–40 mm. in diameter, and is curved in the longitudinal direction, turning down toward the ventral border of the ramus as it passes posteriorly. As preserved the alveolus is 109.5 mm. in length. The left and right alveoli slightly converge toward the midline anteriorly, but are just beginning to rotate outward where the symphysis is broken. They approach each other to within approximately 70 mm. at about 50 mm. in front of the posterior border of the symphysis. The symphysis itself turns downward immediately; the maximum length is unknown, but was at least 127 mm. long.

Along the ventral border of the corpus, the mandibular canal is visible, extending from a point 100 mm. behind the anterior origin of the ascending ramus and curving forward beneath the molar alveoli.

The fragment is broken just behind the position of the mental foramen as the canal is seen to pass from the ventromedial to the ventrolateral wall of the jaw as it does just behind the foramen in other elephant species. The canal measures 23 mm. wide by 27 mm. high in this region. Just above the anterior-most preserved part of the canal are two small foramina for exit of the mandibular nerve and vessels, but the canal begins to enlarge at this point and clearly continues forward. There are no contacts between this fragment and the associated symphysis, but the canal appears to have been continuous with the incisive alveolus of the latter.

Associated with these two mandibular fragments is an incomplete incisor of the dimensions and curvature to fit into the symphyseal alveolus, although definite contact is not possible. One fragment is broken along a midsaggital plane and represents the open root of a tusk. It measures 96.3 mm. in length and 37.9 mm. in maximum diameter. The center of the fragment bears a conical pulp cavity, the dentine walls of the tusk becoming as thin as 3.5 mm. at the proximal end of the specimen. At the distal end the dentine measures 15.0 mm. in thickness and the pulp cavity must have been only a few millimeters in diameter at this point.

Another fragment is from a more distal segment of the tusk in which the pulp cavity was lacking. This segment is 31.7 mm. in diameter.

Externally, the tusk was sheathed apparently for its entire length with a thin layer of laminated dentine 0.9 to 1.8 mm. in thickness. This layer was very finely striated longitudinally; there were about three to four striations per millimeter. The underlying dentine surface was more broadly straited by very shallow longitudinal ribs and valleys of about a twentieth of a millimeter in depth, and approximately a millimeter apart. In cross-section the dentine shows the spiral-conical structure typical of proboscidean incisors.

In two isolated tips of another pair of lower tusks, the outer laminated dentine is missing. The specimens measure 33.0 mm. in diameter at a point 72 mm. proximal to the tip. The dentine surface bears coarse striations which twist around the circumference of the tusk, spiralling counterclockwise toward the tip through an angle of 40 degrees in a distance of 46 mm. Elephant tusks in general show a more or less prominent outward twist, so that this would appear to be a left incisor. The surface thickens somewhat about 35 mm. behind the tip so that this region is about 1.5 mm. greater in diameter than the portion immediately proximal. From this point, the tusk tapers rapidly toward the tip. The latter is worn on its ventral surface, the wear facet sloping downward and backward and forming an angle of about 35 degrees to the central axis of the tusk.

MCZ 13-68K is the ventral portion of the left incisive alveolus including part of the mental foramen on its proximal end, and extending 154.3 mm. distal to it. The ventral surface of the symphysis appears to have been relatively flat as in MCZ 290-67K. A very large mandibular cavity continues forward from the mental foramen, narrowing anteriorly to an alveolus approximately 50 mm. in mediolateral diameter. The ventral wall of the alveolus is longitudinally convex, curving downward and slightly outward distally as in MCZ 290-67K, so that the tusk must have acquired this directional orientation at emergence from the tusk socket.

POST-CRANIAL DESCRIPTIONS

Humerus

A partial left humerus (KNM LT-370) from Lothagam 1, is the only specimen referred to this species. The proximal half of the bone is lacking and some distortion is evident. Nevertheless, the deltoid ridge appears to have been stronger and longer than in *Loxodonta*, and the lateral supracondylar ridge seems to have extended somewhat higher onto the shaft. This morphology is more like the condition in *Stegotetrabelodon*.

Femur

Associated with the above humerus was a nearly complete femur. In overall morphology it is remarkably similar to that of *Loxodonta adaurora*

from Kanapoi. It differs principally in having a slightly larger proximal head and longer neck, the latter coming off the shaft at a greater angle. Distally, the medial condyle is longer and more extensive on the posterior surface of the shaft. The popliteal fossa was flatter and probably broader.

Measurements (in cm.)

Overall length:	121.1
Transverse diameter at midshaft:	16.4
Anteroposterior diameter at midshaft:	12.0
Anteroposterior diameter of proximal head:	17.9

Loxodonta adaurora Maglio

Original Reference: Maglio, 1970: 12, Pls. V, VI.

Holotype: KNM KP-385, nearly complete skeleton, the skull and jaws bearing partially worn M3's *in situ*.

Horizon and locality: All specimens from the middle Pliocene Kanapoi Formation, Turkana, Kenya.

Material: This is now one of the best known fossil species of elephant from Africa, represented by several complete skeletons, two skulls and many isolated molars.

SUPPLEMENTARY DESCRIPTION:

M^3

Sixteen molars of this group are known to the authors. There are eight to ten plates, an anterior ridge and a posterior heel. The anterior ridge is composed of a series of flattened columns arising from the base of *P1* and closely appressed to it.

The *P1* has a central pillar flanked by deep clefts, the buccal one is deeper and probably represents the old median cleft. The latter persists as a median constriction into late stages of wear. To the sides of the central column are two flattened pillars which are divided apically when unworn. A strong *C1* lies just to the lingual side of the midline. It is free at its apex and nearly fills the *P1–P2* valley. In general the columns fuse with the plate faces at about mid-crown height.

P2 is like *P1* but lacks deep clefts. Soon after wear begins, a complete enamel loop is formed on the occlusal surface. The apex is divided into seven or eight weak digitations with only weak vertical furrows demarcating discrete pillars, but these are not evident in later stages of wear. The plate is well consolidated and unified. There is a strong *C2* as high as its associated plate.

P3 and *P4* are like *P2*, having large size apical digitations with a tendency to develope small accessory buds. *C4* is free only for a few millimeters at its apex.

P5 lacks a free *C5*, but bears a prominent posterior fold that is fused

into the plate face for its entire length. *P6* to *P8* are like the others but lack posterior columns or folds. The last plate may have only two or three pillars with no associated columns or folds.

On the lingual side of the last five transverse valleys there are large single columns about 15 mm. high and free for their entire length.

The plates widen at their bases but the valleys are broadly open and U-shaped except in the midline where the columns and folds of adjoining plates make contact. Enamel is thick, measuring 3.2 to 4.4 mm. and is unfolded except in late stages of wear where it may be very weakly wrinkled. Externally, the enamel is rough and pitted.

The sides of the plates are broad throughout, but taper rapidly near the apex. Distal digitaitions are typically bent forward. Plates are widely separated, the cement interval being wider than the plate thickness. Valleys are completely filled with cement.

The molars are very broad, not tapering posteriorly very much. The anterior two plates are directed forward, but the remainder of the plates are nearly perpendicular to the relatively flat molar base.

A strong anterolingual root supports the lingual side of *P1–P2* and bears a deep vertical constriction on the lingual side. The intermediate root underlies *P2* on the buccal side, and a posterior root system is composed of several large appressed roots joined to each other posteriorly. Although broken, the roots measure at least 120 mm. in length and were therefore considerably longer than the crown.

M_3

In this group there are 10 to 11 plates and a flat anterior ridge. The latter is composed of a compressed enamel pillar closely appressed to *P1*. A posterior swelling lies in the median cleft of *P1*.

A cleft divides *P1* nearly to the base of the crown, becoming obliterated at about two centimeters from the base. On the buccal side of the cleft is a prominent posterior sinus which may have been free at the apex. *P2* lacks a median cleft; the plate is divided apically into five or six digitations which quickly unite with wear. A strong posterior fold wears as a large sinus.

P3 to *P6* are like *P2* in structure. All the plates are well consolidated and with wear present a complete enamel figure with no signs of vertical furrows. Plates 7 to 9 have only four apical divisions and lack accessory columns and folds. The heel is a single pillar arising by an independent base. As in the upper molars, the apices are directed forward.

The enamel is rugose and pitted, marked by horizontal striations. The valleys are nearly completely filled by cement.

The molar is broad, attaining its maximum width at *P4* or *P5*. The plates taper gently toward the apex of the crown. Enamel is thick and unfolded, measuring 2.5 to 4.8 mm.. Plate faces are parelled-sided and are widely separated, the lamellar frequency being 2.9 to 4.4.

M^2

This molar is known only through fragments from the type locality. Referred specimens from Lothagam, Vogelfluss and Sibilot show that there were seven to eight lamellae. The molar is like M^3 in structure.

The apices of the plates bear five to six digitations, with two deep lateral clefts isolating the lingual and buccal pairs from the central group. In the anterior three or four plates, a median cleft is also present between the pillars of the central group. By intermediate stages of wear, the lateral clefts have disappeared and the median one is present only as a weak anterior and posterior constriction. Immediately to the lingual side of the median constriction and lying near the midline of the tooth is a strong posterior fold which wears as a strong sinus. A weaker anterior fold is present, but does not contact adjacent plates until well worn.

There may or may not be a posterior heel; when present, it consists of three or more low, rounded pillars.

The plates widen toward the base as in M^3 so that in very worn specimens the valleys between plates are very small. The valleys are, therefore, open but narrow at the base. More apically, the cement intervals are broader than the plate thickness, giving a low lamellar frequency of 3.3 to 4.9.

The enamel is thick, measuring 3.0 to 4.4 mm., and is unfolded. In late stages of wear, slight wrinkling may be present on the occlusal figure. The molar is broad throughout and the hypsodonty index is approximately 91 to 98.

M_2

There are eleven specimens of this molar. The plate number is 7 to 8. An anterior ridge consists of a strong fold of enamel, stronger on the buccal side. *P1* has a weak median cleft and four poorly defined pillars. The vertical furrows separating the pillars soon disappear with wear leaving only the constriction of the median cleft. There is no *C1*.

P2 consists of five pillars with the old median cleft passing to the lingual side of the median pillar. A small *C2* is present but lower in height than the plate. It is only just barely free at the apex.

P3 to *P5* are like *P2* with five basic pillars with some tendency toward further subdivision by budding. There are no true columns. With wear, continuous loops of enamel are formed without signs of subdivision of the plate. Weak folds may be present on the posterior face, producing weak sinuses with wear.

The enamel is relatively thick, being 3.0 to 4.5 mm.. It is unfolded and has a rugose exterior surface. The sides of the plates taper so that the apical width is about half of the basal width. Plate separation is greater than plate thickness, the lamellar frequency being 3.6 to 5.0. Cement completely fills the valleys.

M_1

There are six plates and a strong posterior heel which may be large enough to be regarded as a seventh true plate. The first three plates are lacking or worn on all specimens. All the plates are very well consolidated, lacking clefts except for a shallow constriction on the buccal side of the median column which persists on the anterior plates to about half of the worn crown height. This is the vestigial median cleft. There are no other furrows. Very small anterior and posterior folds are present and form tiny sinuses even when the plates are well worn. *P5* and *P6* may be composed of as few as three pillars which quickly fuse with wear. The intervening clefts are deeper on these plates than on the more posterior ones. The heel consists of a series of small pillars closely compressed to each other and the total structure may be quite large. Enamel is smooth and in late stages of wear may be very weakly wrinkled. It is moderately thick, measuring 2.8 to 3.8 mm. The plates are widely separated and the transverse valleys are broadly open at the base. Cement completely invests the tooth.

A stout anterior root underlies the buccal side of *P1–P2*.

dM^4

There are five plates and an anterior ridge composed of four small pillars arising out of the base of *P1* and having nearly a full base on the lingual side. The ridge is almost as high as *P1*.

The first plate has a deep median cleft. The apex is divided into six tiny digitations which join in the earliest stages of wear. A tiny *C1* is present just to the lingual side of the cleft. *P2* to *P4* have six or seven digitations, several derived by minor apical budding. There are no furrows demarcating pillars and the plates wear as continuous loops of enamel.

The enamel is rugose and bears longitudinal ridges which, when worn, give it a wavy appearance. It is relatively thick, measuring 2.2 to 3.0 mm. Plates taper only slightly toward the apex where they are about two-thirds of the basal width.

A strong anterior root underlies *P1–P2* across the entire width of the plate. The plates are parallel-faced with open, yet slightly compressed valleys between them. The molar is widest at *P4–P5*. The base of the crown is convex, with *P1–P2* directed more forward and thus diverging apically from *P3*.

dM_4

This molar is known only from one incomplete specimen from the type locality, although several examples are available from other sites. There are five or six plates, each well consolidated with only a vague constriction in early wear indicating the position of the vestigial median cleft. Prominent anterior and posterior folds wear as small, sharp sinuses which contact those of adjacent plates in the midline. They disappear in later stages of wear as they fuse into the plates. Faces of the plates are parallel, not

widening greatly toward the base. The transverse valleys are very broadly open and nearly as wide as the plates themselves. The lamellar frequency is 5.0 to 6.4.

Enamel is thick (2.1 to 2.8 mm.) and in later stages of wear tends to be only very slightly irregular, but not folded. Cement fills the valleys completely.

dM^3

This tooth has five plates. The only specimen known from the type locality is worn. There are no signs of a median cleft or constriction, although one was probably present at the very apex of the anterior lamellae. Plates are thick and more closely spaced than in the more posterior molars; valleys are narrower than the plates themselves, but this may be due to the worn condition of the tooth. The plates are irregular in outline, wearing with an anterior expansion and a posterior concavity in the median portions of the enamel figures. There are no signs of vertical furrows demarcating pillars.

Enamel is weakly folded, even in earlier stages of wear. It is relatively thick for such a small molar, measuring 1.2 to 2.0 mm. Externally, the enamel is rugose, marked by vertical ridges which account in part for folds on the worn surfaces.

The height of several referred specimens from Vogelfluss show that the hypsodonty index was about 100. A strong anterior root underlies *P1–P2* for the entire width of the molar and is slightly directed backward.

dM_3

This molar is known from a pair of worn and poorly preserved specimens from a single individual. There are five or six plates and a small fold of enamel forming the posterior heel. The left tooth is longer than the right by about 20 percent.

An anterior ridge is very large and may be considered as a sixth plate, but although its base on the buccal side is complete, on the lingual side the base is very narrow and merges into *P1*. The ridge consists of two large, centrally-placed pillars, separated by a median cleft that persists to the crown base. The buccal pillar is roughly triangular in outline, with one flat face anteriorly, and another making contact at the cleft with the lingual pillar. The latter is irregularly elongated in the mediolateral direction. A small, rounded pillar is closely compressed to the lingual side of the ridge; it is only about half as high as the latter, remaining unworn until late stages of wear.

P1 is well worn and there is no sign of a median cleft. A small enamel fold on the anterior face may mark the position of a centrally-placed vertical fold. The posterior face is irregular in outline; a posterior column or sinus is lacking on the left tooth. On the right, a small medially-directed

loop is situated just to the buccal side of the midline and may very well have formed a large sinus or isolated column in earlier stages of wear.

P2 is enormously thick on the left tooth, measuring as much as 17 mm. in anteroposterior thickness, with a width of 29 mm. The same plate on the right molar is only 10 to 11 mm. thick. Part of this may be due to distortion, but it seems primarily attributable to unusual individual variation. The plate is too worn to show more than a slight anterior and stronger posterior swelling in the midline.

P3 and *P4* again are well worn and reveal only slight anterior and posterior swellings which contact similar swellings on adjacent plates. These do not, however, form narrow loops as on the more posterior molars. Inoutline, the plates are rather irregular, the lingual half being somewhat more anteriorly placed than the buccal half. This gives the plate the shape of a weak sigmoid curve.

P5 consists of a prominent rounded pillar on the buccal side, separated from the remainder of the plate by a cleft persisting for about a third to half of its height. The plate is irregular as in *P3–P4*, and is thickest at its center. A small, very thin fold of enamel closely appressed to *P5* may be considered as the posterior heel. It is a single thickness of enamel, not enclosing an island of dentine, and it extends across the entire width of the molar.

Enamel is thin, 1.3 to 1.8 mm., and coarsely folded except on the anterior ridge. Transverse valleys are broadly open, remaining well separated to late stages of wear, but at the very base, valleys appear to be more V-shaped than U-shaped. The lamellar frequency is 7 to 9, being lower for the left molar because of abnormal lengthening as noted above.

A strong anterior root, more or less rectangular in cross-section, supports *P1* and the front half of *P2*, and a similar posterior root underlies *P3–P5*. Both are directed backward.

dM^2

There is only a single specimen of this molar in the collection; it is unworn and complete except for the roots. There is no true anterior ridge.

P1 consists of two basic pillars, each subdivided apically into two digitations. Irregular longitudinal furrows divide the plate into a number of pillars, some of which are not free at the apex. Three very small ridges occur on the basal portion of the anterior face, but do not extend to the unworn tip of that plate.

P2 bears four prominent pillars, the median-buccal one with a small apical bud. The buccal half of the plate contacts *P1* for its entire height, but on the lingual half, the two plates are well separated. On *P3*, there are again four pillars; the lingual one is isolated for its entire height and arises out of the base of *P2*. The buccally-placed three pillars are more closely appressed to each other and form a true plate. The posterior heel is

small and consists of three small pillars compressed to *P3* and arising out of them.

Enamel on the lingual side of the tooth extends about 7 mm. lower beyond the plate bases than on the buccal side, giving the molar the appearance of being considerably higher-crowned on this side. All plates are directed forward.

The greatest width (15.5 mm.) is at *P3*, although the tooth is not very much narrower than this even at *P1* (12.7 mm.). The greatest height is 15.3 mm. at *P2*, at which point the hypsodonty index is 98.8.

dM_2

One specimen of this molar in a ramus fragment is available. A single anterior pillar arises from a large base extending across the width of *P1*. This pillar is 13.6 mm. in height and 11.9 mm. in basal width. It tapers to about 3 mm. at the apex.

P1 consists of two closely appressed pillars with a strong anterior and posterior furrow between them. Toward the apex, the lingual pillar is slightly displaced posteriorly so that the apices of the two pillars lie oblique to the long axis of the tooth.

P2 is thinner throughout, and divided into four apical digitations. The plate is strongly concave forward and the buccal pillar bears a rounded posterior vertical ridge which makes contact with *P3* behind.

P3 is the lowest of the three plates and has six apical digitations, the extreme buccal one being half as high as the others. There is a posterior heel of three small vertical pillars arising out of *P3* and closely compressed to it; the lingual-most is the larger.

The molar broadens posteriorly, attaining its greatest width at *P3*. The maximum height is at *P1* giving a hypsodonty index of 94. Valleys are greatly compressed and V-shaped, due to the close spacing of the plates.

Mandible

The corpus is as long as in *Loxodonta africana*, but the symphysis is longer and much more massive, giving the mandible a far more elongated appearance. The symphysis is strongly downturned, with anterior symphyseal crests forming a greater angle with the superior border of the corpus than in the living species. The posterior border of the symphysis falls off vertically between the two corpi, unlike the condition in *L. africana*, where it slopes gently backward.

The corpus is massive, being deeper anteriorly and shallowest where the ramus takes origin. The corpi of both sides are more closely spaced to each other than in the living form, and the symphysis is narrower. One mental foramen exists just below the anterior edge of the alveolar border. Laterally the corpus is flat, forming a straight surface from ramus to the tip of the symphysis; the lateral surfaces of the corpi form an acute angle at the chin. In *L. africana*, the corpus is strongly convex externally, the curve

continuing under the small symphysis. The lingual surface of the corpus is a gentle convex curve in both species.

Two very large, deep and anteroposteriorly elongated pits for origin of the geniohyoid muscles are seen on the ventral surface of the symphysis. A deep depression for the sublingual gland lies just behind the symphysis on the medial surface of the corpus and measures about five by seven centimeters.

The origin of the ramus is near the superior border of the corpus, unlike in *L. africana* where it originates lower down. The ramus in *L. adaurora* lies along the axis of the corpus, whereas in *L. africana*, it is directed forward and outward, forming an angle of 20 to 25 degrees with the corpus. The anterior edge of the ramus for attachment of the temporalis tendon is massive, about 3 cm. thick in contrast to the thin, sharp-edged ramus in *L. africana* where the anterior border is only 1 cm. thick. A sharp crest separates the anterior and lateral surfaces of the ramus and a deep vertical scar for the temporalis muscle lies along an elevated shelf running vertically along the anterior edge. The jaw angle is more sharply rounded in *L. adaurora*, lacking the flattened posteroventral surface of the living form. The masseteric fossa is deep and does not extend as ventral in the fossil as in the recent species. A rounded ridge along the posterior outer border of the ramus for attachment of the superficial masseter extends higher on *L. adaurora*.

The condylar neck in *L. adaurora* is a flat plate of bone, strongly curving medially at its posterior edge and expanded into a flat posterior surface. The condyles are elongated in the transverse direction and directed upward and outward, unlike in *L. africana* where the condyles face upward and inward.

Origin for the digastric muscle is smaller in *L. adaurora*, despite the larger size of the corpus beneath the condyle.

The lateral pterygoid muscle appears to have inserted entirely above the occlusal surface level on the posterior edge of the ramus. In *L. africana*, that muscle inserts slightly lower on the ramus, its lower border lying at a level below the occlusal surface.

A mandibular canal opens just below the condylar neck and well above the occlusal plane. In *L. africana*, it lies much lower.

A small channel continues forward from the mandibular canal opening into a rounded chamber anteriorly. This chamber is about four centimeters in diameter and passes forward, lateral to the symphyseal area, becoming laterally compressed. At the level of the posterior symphyseal surface, the chamber measures 36 mm. by 85 mm. high. The length of the chamber is about five centimeters. As has been suggested previously, these paired chambers may have contained vestigal incisive buds.

Skull

Despite the remarkable similarity between the skull of *L. adaurora* and

L. africana, a number of important morphological differences occur. In general, the forehead is proportionately about 50 percent larger in *L. adaurora* and the vortex of the occiput is higher. Tusk sockets are directed more vertically downward in the fossil species, with the tusk sheathes parallel to the alisphenoid ridge. The occiput in *L. adaurora* attains its greatest width just above the external auditory meatus whereas in *L. africana* the greatest width is about 20 cm. above this point, the skull being distinctly narrower in the region of the meatus.

Occipital condyles are similar in orientation for both species, and located ventral to the glenoid fossa unlike in *Elephas*, but in *L. adaurora* they are less projecting, not extending beyond the occipital plane. The occipital surface is proportionately narrower and rounder in *L. adaurora*, but is relatively flatter, the lateral edges being less expanded posteriorly than in *L. africana*. The fossa ligamentae is 30 percent longer in *L. adaurora*. It is very deep, with sharp edges setting it off from the surrounding occipital surface.

The basioccipital bone is straight, lacking the 45 degree downward flexure of *L. africana*, and is proportionately narrower. A jugular groove separating the condyles from the digastric eminence is deeper in *L. adaurora*. Lateral depressions for origin of the anterior rectus capitus muscles are very deep in *L. adaurora*, giving a narrower appearance to the basioccipital ridge than in the living species.

The auditory bullae are flatter in *L. adaurora* than in *L. africana*, and shorter in their lateral extent where they intervene between the squamosal and occupital bones. The stylomastoid foramina are located in depressions within the posterior surface of the bullae. A vertical groove along the posterior face of each bulla for reception of the styloid process is deeper and narrower than in *L. africana*.

The carotid foramen in *L. adaurora* passes upward and forward on the suture between the auditory bulla and the basioccipital and is therefore bordered by both bones. In *L. africana*, the foramen is surrounded by processes of the bulla. A large medial lacerate foramen is confluent externally with the foramen ovale and passes upward immediately in front of the bulla and medial to the glenoid fossa. In *L. africana*, the opening to the alisphenoid canal lies about 40 mm. anterior to the foramen ovale and is ventral to it. In *L. adaurora*, the two are confluent externally but separated by a lamina of bone about four centimeters into the canal. From this point, the alisphenoid canal passes forward between the maxilla and sphenoid bones, opening into the optic groove along with the optic foramen.

The glenoid fossa is laterally elongated, broadly concave in the lateral direction and convex in the anteroposterior direction. The articular surface lies on a strong eminence of the squamosal bone just lateral to the auditory bulla. Behind the glenoid is a deep post-glenoid depression for attachment of the capsular ligaments and reception of the articular carti-

lage during retraction of the mandible. A post-jugular shelf is prominent and extends ventral to the glenoid surface in sharp contrast to the condition in *Elephas*. Medially, the shelf bears the roughened eminence for attachment of the digastric muscle.

The alisphenoid bone is a thin lamina covering the posterior surface of the maxillary crypt and contacting the squamosal and maxilla at a tight suture just in front, and on the same level as, the glenoid surface. The anterior border of the bone slopes backward and downward as in the living *L. africana* and the edge is raised for origin of the lateral pterygoid muscle.

Internal nares are very narrow due to the close spacing of the pterygoids; the opening is nearly three times as long as wide. In *L. africana*, the nares are only twice as long as wide. A sharp ridge for insertion of the tensor palatine muscle extends dorsally along the pterygoid bone from the small pterygoid process, and defines the posterior edges of the nareal opening.

A peculiar feature of this species is a deep maxillary fossa, 20 cm. long, extending from the alisphenoid-squamosal-maxillary suture to the maxillary base of the zygomatic arch. The fossa is deeper anteriorly where it is 60 mm. below the general maxillary surface, and its edges are nearly perpendicular to the maxilla. The ventral extent of the fossa is 13 cm. above the alveolar border of the maxilla. Distally, it gradually passes into the temporal fossa. This feature is present on the Kanapoi, Lothagam and Sibilot skulls and seems to be a consistent character of the fossil species.

The zygomatic arch is externally flat in *L. adaurora*, not rounded as in the living species. The zygomatic process of the squamosal bone is massive as is typical of *Loxodonta*, even more so than in *L. africana*. The zygomatic bone is more slender in the fossil form.

A maxillary strut which supports the anterior base of the zygomatic arch arises from the maxillary-premaxillary notch and lies in the vertical plane. It is directed upward and forward from the alveolar portion of the maxilla. The zygomatic arch projects sharply outward from this strut, forming nearly a right angle with it, so that the ventral border of the orbit lies entirely lateral to the strut, rather than over it. Thus the strut cannot act as a direct load-bearing buttress as in *L. africana*, where it is broader, directed outward and upward beneath the zygomatic arch, and lies directly along the lines of stress created by pull of the superficial masseter muscle.

The maxilla is about 50 percent deeper below the level of the zygomatic arch in the fossil than in the recent species. The dorsal extension of the maxilla on the face between the frontal and premaxilla is less than in the living form.

The maxillary-zygomatic suture in *L. adaurora* is not straight as in the living form. Maxillary bones curve ventrally beneath the zygomatic for some distance.

The orbit is more anterior in *L. adaurora* and faces more forward than in the living species; the postorbital process is anterior to the maxillary-

zygomatic suture, whereas in *L. africana* it overlies the suture. The orbit is entirely anterior to the maxillary-premaxillary notch in the fossil, but overlies it in *L. africana*. The ventral postorbital eminence in the fossil is on the maxillary portion of the arch. In the living species, it is on the zygomatic bone. The orbit itself is about 25 percent smaller in *L. adaurora*.

The face is not concave as it is in *Elephas*. The orbits do not project forward, but the facial process of the frontal and premaxillary bones lie in the same plane as the ventral border of the nasal aperture.

The external naris is wide and downturned at the sides. The frontal bones form a massive, rounded ridge, nine centimeters wide, extending from just above and lateral to the naris downward and outward to the orbit. Its lateral edge forms a frontal crest which marks the dorsal limit of the temporalis fossa. Medial to this ridge is a very deep depression which continues downward from the sides of the nareal opening and merges distally into the premaxillary fossa. Lying within this depression is the frontal-premaxillary suture. It is lacking entirely in *L. africana*. The frontal crests, which terminate at the postorbital processes, are 60 percent longer in the fossil than in the living species, again reflecting the longer forehead and lower orbits in *L. adaurora*. The nareal opening lies completely above the level of the orbit; its ventral border is 180 mm. above the orbit In *L. africana* the orbit and naris are on the same level.

A deep premaxillary fossa extends up to the ventral border of the naris. Proportionately, the fossa is higher on the face because of the low position of its orbits; in *L. africana* it terminates at the level of the lacrimal bone, whereas in *L. adaurora* it extends about 250 mm. higher. The fossa is flanked on either side by the rounded tusk sockets which extend to the level of the nares.

Premaxilla width at the proximal end of the tusk sockets is about the same in the two species, but the distal width is about 25 percent greater, and the length from the infraorbital canal is 30 percent greater in the fossil species.

The temporal fossa is about 30 percent longer in *L. adaurora* than in *L. africana*, due to the more elevated vortex of the skull. The posterior edge of the fossa lies posterior to the glenoid cavity. The lateral edge of the occiput forms only a thin, sharp border separating the temporalis fossa from the occipital plane. As a result, the lateral nuccal and temporal lines appear nearly to coincide. In *L. africana*, the temporal fossa is displaced forward, anterior to the glenoid cavity; nuccal and temporal lines are separated by a ventral strip of the squamosal bone some eight centimeters wide.

The posterior face of the temporalis fossa in *L. adaurora* slopes sharply backward and outward. In *L. africana*, this surface is nearly in the transverse plane so that the main mass of the temporalis muscle lies farther forward and is about a third narrower.

POST-CRANIAL DESCRIPTIONS

Vertebral Column

A nearly complete column is associated with the holotype skeleton, KNM KP-385. The overall length of the vertebral column is difficult to estimate because several thoracic and lumbar vertebrate are missing. Remaining portions measure 210 cm. from atlas to lumbar series, which must be taken as a minimum length.

Atlas

This bone is anteroposteriorly flattened and relatively massive as compared with the living species. Transverse processes are large and rugose, and contain small transverse foramina. The dorsal surface of the neural arch bears a pair of rounded tuberosities. The vertebral canal forms a prominent figure-eight, being constricted in the center by medially projecting portions of the posterior facets. The lower part of the canal, for reception of the odontoid process, is the smaller of the two portions of the opening.

Articular facets for the occipital condyles are shallow, kidney-shaped, and lateral in position, being slightly more widely separated dorsally. Posterior facets for articulation with the axis are smaller, more ventral in position, and form complex saddle-shaped surfaces.

Measurements (in cm.)

Width across transverse processes:	47.5
Maximum height in midline:	25.0
Dorsoventral diameter of the vertebral canal	11.8

Axis

The axis is a robust bone with a large wing-like neural spine. The latter is weakly grooved anteroposteriorly along its dorsal surface, but this is variable in other species. The odontoid process is damaged, but appears to have been very massive. Posterior zygopophyses of this and other vertebrae are directed more strongly downward than in the living species. The transverse processes are thick and enclose a large vertebral canal.

Cervical

C3–C7 are short bones with small, heavily built transverse spines and broadly overlapping articular processes. C6 and C7 bear modest neural spines directed somewhat posteriorly.

Thoracolumbar

There are at least eighteen thoracic vertebrae and probably three or four lumbars. Centra are longer in the more posterior members of the

series. T2–T5 bear very long neural spines some 57 cm. in length, and probably were directed backward about 20 to 30 degrees in life. These spines enlarge distally, terminating in massive tuberosities. Transverse processes become shorter and more bulbous posteriorly as neural spines become shorter and more slender.

Sacral

Four sacral vertebrae are solidly fused, each with a short blade-like neural spine.

Caudal

Only three remain. These are relatively long with broad transverse processes and short neural spines, some with bulbous distal ends.

Scapula

A single specimen is preserved on the holotype skeleton (KNM KP-385). It is roughly triangular in outline, nearly twice as high as wide. The spine is prominent and terminates in a large acromion process which overhangs the lower portion of the supraspinous fossa. The infraspinous fossa is broader just above the glenoid than in the living species, and is overhung by a large, curved metacromion that reaches nearly to the axillary border. Morphologically this is typically *Loxodonta* in structure.

The glenoid fossa is rectangular in outline, forming a shallow concave articular surface.

Measurements (in cm.)

Overall height, glenoid to cranial border:	105.0
Maximum anteroposterior length, anterior to vertebral border:	51.5
Length of spine:	86.5
Length of metacromion:	21.5
Anteroposterior length of scapular neck:	27.5

Humerus

A left humerus from the holotype is the only specimen available. The shaft is relatively slender in comparison to the very massive articular ends. The proximal head is large and hemispherical and lacks a distinct anatomical neck.

The greater tuberosity is very large and projects above the articular surface. A deep bicipital groove extends along the proximal one-third of the bone, separating the greater from the very small lesser tuberosity. A prominent deltoid ridge extends from just below the greater tuberosity to midshaft on the lateral side.

The laterally flaring distal trochlear region is the broadest part of the bone. A very strong lateral supracondylar ridge projects upward from the condyle to join the midshaft area at about a 60 degree angle. Posteriorly there is a shallow but very broad olecranon fossa.

Measurements (in cm.)

Overall length	116.2
Proximal articular surface	
anteroposterior:	25.2
transverse:	17.0
Transverse diameter at midshaft:	12.8
Anteroposterior diameter at midshaft:	16.8
Width of distal condyles:	28.0
Maximum width across supracondylar crests:	31.2

Ulna

A complete left ulna is present on the holotype skeleton. The bone is a very thick, heavily built structure with a high posteriorly projecting olecranon process. Just anterior to the latter and rising above the proximal articular surface is a short anconial process. There is a deep notch in the shallow articular surface anteriorly for reception of the radial head. A prominent ridge lies along the anteromedial aspect of the shaft and probably served for origin of the pronator muscle. Distally the ulna is as wide as the shaft and bears a flattened laterally concave facet for articulation on the cuneiform bone.

Radius

The radius (KNM KP-385) is relatively slender proximally. It curves along the lateral and anterior surfaces of the ulna, to which it is in firm contact along its entire length. Distally the radius is almost as massive as the ulna; it expands into a convex articular surface for the lunar and scaphoid bones. The styloid process is larger than in the living species, and slightly overhangs the distal facet.

Measurements (in cm.)

Ulna

Overall length:	90.0
Maximum transverse diameter across proximal facet:	14.6
Transverse diameter at midshaft:	7.9
Anteroposterior diameter at midshaft:	5.9

Radius

Overall length:	98.5
Transverse diameter of distal end:	20.6
Anteroposterior diameter of distal end:	17.7

Pelvis

Only one specimen is known (KNM KP-403) consisting of a right ilium, ischium and publis. The ilium is a relatively massive, broad fan-like structure with a strongly convex dorsal crest. The greater sciatic notch is deep and widely open. Posteriorly the ischium projects as a massive process, at least twice as thick as the slender pubis. Between them there is only a small obturator foramen.

The acetabulum is oval, with its long axis oriented dorsoventrally. It is a shallow concave surface, directed downward, backward and outward, and with a weak marginal lip.

Measurements (in cm.)

Anteroposterior length of iliac crest:	82.0+
Maximum height of iliac crest from sciatic notch to dorsal border:	38.0
Transverse width of ischium:	5.5
Transverse diameter of acetabulum:	19.0

Femur

This is represented by a single nearly complete specimen (KNM KP-397) from the right side. The bone is long and slender throughout with a very gentle curve, concave medially. A relatively small proximal articular head is directed upward and slightly medially on a short, poorly defined neck. The greater trochanter is not strongly developed, and the lesser trochanter is a prominent slender ridge extending along the medial one-thrid of the shaft, beginning just below the femoral neck.

The shaft is flattened posteriorly from the intertrochanteric surface down to the popliteal region. In contrast the anterior surface is strongly rounded. The distal condyles are not much wider than the shaft, the lateral articular surface being more massive and slightly longer than the medial, forming a visible carrying angle.

Measurements (in cm.)

Overall length:	136.5
Transverse diameter at midshaft:	18.5
Anteroposterior diameter at midshaft:	11.0
Anteroposterior diameter of proximal head:	18.9

Mediolateral diameter of proximal head:	19.8
Transverse diameter of distal condyles:	25.5

Tibia and Fibula (KNM KP-397)

This is a stout bone of unremarkable morphology. The shaft has a gentle curvature, posteriorly concave. The medial proximal facet is higher than the lateral, and a strong crest runs from the latter down the shaft as it curves onto the anterior surface. The fibula differs little from that of the living species.

Measurements (in cm.)

Tibia

Overal length:	77.2
Anteroposterior diameter, proximal:	18.5
Anteroposterior diameter, midshaft:	11.3
Transverse diameter, midshaft:	25.5

Fibula

Overall length:	80.3
Transverse diameter, proximal:	6.5
Transverse diameter, midshaft:	3.5
Transverse diameter, distal:	8.9
Anteroposterior diameter, distal:	12.2

Manus

The left manus is preserved on the holotype skeleton (KNM KP-385) and is complete except for the lunar bone and terminal phalanges. The specimen is proportionately more massive and broader than in the living species. Metacarpal I is as reduced as in *L. africana*, but MC. V is not reduced, and in this respect is more primitive. MC. II contacts the trapezoid but also has a strong facet for articulation with the magnum. Likewise MC. III has large contact facets with both the magnum and unciform bones. This broad overlapping contact between metacarpals and distal carpals is stronger than in the living species. In most anatomical features the manus is closer to *Loxodonta* than to *Elephas*.

Pes

The holotype skeleton (KNM KP-385) includes a left pes lacking only the phalanges. Except for its larger size and more robust proportions, the fossil is extremely close in all morphological details to *L. africana*, and can be distinguished from *Elephas* on most individual bones.

Elephas ekorensis Maglio

Original Reference: Maglio, 1970: 20, PI. VII.
Holotype: KNM EK-424, left and right M^3.
Horizon and locality: Middle Pliocene deposits at Ekora, probably Kanapoi Formation, Turkana, Kenya.
Material: This species is known from a skull and incomplete dentition from the type locality. Although several additional specimens from other areas are now known, they are very similar and the following descriptions are based on the original hypodigm only.

SUPPLEMENTARY DESCRIPTION:

M^3

This molar is known from the holotype pair and from several additional fragments. There are ten plates plus a very strong posterior heel which may be considered an additional plate. A thin anterior ridge closely compressed against *P1* is present and when worn forms a very thin (one to two centimeters) loop across the anterior face of the first plate and is confluent with the dentine of *P1*. In its median portion *P1* is strongly concave behind and bears a vertical anterior fold. A posterior constriction marks the position of the vestigial median cleft. On the lingual side of this constriction, there is a rounded enamel fold forming a posterior sinus, and it may have been a free column in the unworn state.

P2 had about five or six digitations when complete. There is one central pillar, two on the buccal side and two or three on the lingual; each group is separated by a moderately deep cleft. The clefts betweeen the central pillar and the two lingually-placed groups are 12 mm. deep from the apex, but the crown is worn at least 10 mm. Shallower longitudinal furrows extend down the plate faces forming weak pillars. The pillar just lingual to the median cleft is enlarged anteriorly and posteriorly and when worn, would form small sinuses. There is no *C2* visible, but one may be below the heavy cement cover.

In *P3* there are four apical digitations, each separated by a more or less prominent furrow. The median lingual pillar bears a vertical posterior fold which would wear as a small sinus. A very strong anterobuccally-directed fold or ridge is present on the lingual pillar; it extends about 15 mm. into the *P2–P3* valley.

Six digitations divide the crown of *P4*; each is separated for 15 to 20 mm. from the apex. Shallow furrows on the plate faces demarcate vertical pillars. As in the case with the other plates, an intermediated column (here *C4*) is present, but lies buried beneath the cement in unworn molars. The columns are free for the upper 1.5 to 2.0 cm. of their height and extend nine to ten millimeters into the adjoining valley. They are generally two to three centimeters below the level of the associated plates and therefore not seen in early stages of wear.

On *P6* to *P8* there are four to five digitations. The buccally-displaced vestigial median cleft is 34 mm. deep and is deeper than the other clefts. *P9* and *P10* may have three or four digitations but structurally are like anterior plates.

A posterior heel may be a small single pillar or large enough to be considered as a true plate.

The molar is not very broad anteriorly, attaining its greatest width at *P3*. Width rapidly decreases posteriorly giving the molar a narrow, almost wedge-like shape. Maximum crown height is at *P6* with a hypsodonty index of 111 to 117. Anterior and posterior faces of the plates are very strongly parallel-sided for most of their height. Transverse valleys are broadly open and are skewed U-shaped at the base; the anterior faces are flat, and the posterior faces curve downward and backward at the bottom so that the lowest part of the valley is just at the base of the anterior face of any given plate. The lateral sides of plates taper toward the apex where the crown width is about two-thirds to half that at the base. The plates are widest at the base, unlike the condition in *E. recki*, where they are widest about one-third up from the base.

The plates are thin and widely spaced; the cement interval is as great as or greater than the plate thickness. There are about 3.8 plates in 10 cm. (lamellar frequency).

Enamel is moderately thin, three to four millimeters thick, and is essentially unfolded. Its external surface is roughened by fine horizontal ridges. Toward the crown base the enamal may be coarsely, but very weakly folded, but is never tightly folded as in the later species *E. recki*.

M_3

No examples of this molar are known from the type locality. The following description is based on referred specimens from the Kaiso Formation and from Kwenichum (Baringo).

There are 12 plates plus a large heel and anterior ridge. The latter consists of several large, rounded pillars arising via a separate base on its buccal side, but fuses into *P1* on the lingual side. *P1* consists of six to seven digitations without an obvious median cleft. A free *C1* is present to the buccal side of the midline and closely appressed to *P1*.

The *P2* has six apical digitations which fuse in early stages of wear. There is no sign of a *C2*, but it may lie below the cement cover. From what can be seen of the remaining plates, there are 5 or 6 digitations, the apex being rounded and higher in the midline. In early wear, a series of round enamel loops is formed but these quckly unite to form a continuous enamel figure. There are no signs of posterior columns.

Molar width is greatest at the base of *P2–P4*, and tapers gently posteriorly. The plates are thin and not widely spaced; lamellar frequency is 4.0 to 4.8. Transverse valleys are U-shaped, open to the base and filled with cement. The sides of the plates taper gently toward the apex. In

lateral view, plates are very weakly S-shaped with the apices directed slightly forward.

Enamel is thin, measuring 2.3 to 3.5 mm., and is unfolded. Externally, it is slightly roughened.

M^2

A single, incomplete specimen of this molar is known. There are six plates, plus an anterior ridge preserved, but the total number was greater.

P1 has a strong vertical anterior fold that forms a large sinus when worn. A laterally compressed posterior sinus contacts *P2* behind. Just buccal to the sinuses is a strong vertical constriction of the plate which corresponds to the old median cleft of earlier species. The plate is weakly concave posteriorly. *P2* has only weak clefts. The plate shows a confluent enamel loop early in wear. A median constriction is present just buccal to the median sinuses marking the vestigial median cleft. Several small folds flank the median constriction on the anterior face; these contact the posterior sinus of *P1*. A very strong laterally-compressed posterior sinus is present. Here, in an early stage of wear, a constriction is seen intervening between the sides of the sinus and the posterior face of *P2*, thus isolating the latter to some degree. This suggests that it probably was a free column at the apex when unworn. Although a very weak vertical constriction persists lateral to the sinus, there are no other furrows demarcating pillars.

P3 is damaged, but there appears to have been two central digitations separated by the remains of a median cleft. On the buccal side of these, and separated from them by a shallow cleft, is a flattened pillar which certainly had at least two apical digitations in the unworn state. A prominent anterior sinus meets the posterior one of *P2* and seems to have extended nearly to the apex of the unworn plate. There is no posterior sinus. *P4* is essentially of the same structure except that true sinuses, both anterior and posterior, are lacking. However, small, broad enamel folds are present. *P5* retains a complete apex and has six digitations, and is strongly convex. The median two digitations are about 10 mm. higher than the lateral ones. A median constriction persists to 35 mm. below the apex, but lateral furrows are still present at 37 mm. below the apex. These do not completely divide the enamel figure, however, so that the dentine is confluent across the entire plate. Depth of the lateral furrow on the buccal side is at least 24 mm. from the apex.

It is not possible to determine the total number of plates, but a small impression on the posterior surface of the cement covering of *P6* indicates at least one more plate and the total number may have been as high as eight.

The plates are thin and widely separated; the lamellar frequency is 3.7. Until advanced stages of wear, cement intervals are equal to or wider than the plates themselves. Transverse valleys are open and U-shaped. The sides of the plates taper apically where they appear to have been about half as

wide as at the base. The widest preserved plate is *P4*. The hypsodonty index at *P4* is 116.

The enamel is 2.6 to 3.4 mm. thick and is weakly folded. With wear, the enamel is thrown into loose, open folds, and near the base folding may become quite strong, but still weak as compared to that seen in *E. recki*. In the latter species, especially later stages, each enamel fold appears like a crescent moon in cross-section, closely appressed to its neighbors at the points of the crescent. In *E. ekorensis* the folding is simple, with the enamel essentially retaining a uniform thickness around the fold.

A strong anterior root underlies the buccal two-thirds of *P1*, but the main body of the root forms a circular pillar under the buccal third of that plate, with a lingually-directed lamina extending under its central portion. In cross-section the root is key-hole-shaped. An intermediate root supports the lingual sides of *P1* and *P2*, diverging from the anterior root so that together the roots were wider than the crown. A posterior root system appears to have begun at the *P2–P3* valley.

Skull

On the Ekora skull the palate is eroded off and the tusk sockets are lacking. The specimen is flattened in the facial plane and is very broad, especially in the postorbital region. The forehead is planar for most of its width, and broader than long. The parietals are expanded dorsally and laterally as in *Elephas* generally. The occiput is posteriorly inflated as is typical of the genus. The nuccal line is not a sharp crest as in *Loxodonta*, but a gently rounded surface as in *E. maximus*. Thus skull apex is depressed in the midline.

Behind the orbits the temporal constriction is broad as in *E. recki*. The dorsal margins of the temporal fossa are formed from the raised frontal ridges which lie slightly above the level of the forehead as in *E. maximus* and *E. recki*. These frontal ridges are flat and flare out laterally, where they terminate above the orbits. This flaring is more so than in *E. maximus*, but similar to *E. recki*.

The nasal aperture is broad, but not downturned at the sides as in *E. recki*. The orbit is oriented with its dorsal border more projecting so that the orbital rim faces outward and downward. The circum-orbital torus is massive and appears to have had a ventral process lateral to the infra-orbital canal, as in *E. recki*.

The premaxillary fossa is very deep, but considerably wider than in *E. recki*. The tusks appear to have been slightly diverging.

DISCUSSION

The phyletic history of early elephantids has been discussed elsewhere in broad outline (Maglio, 1973), but the data presented above give additional details worthy of note. Perhaps the most significant conclusion to be drawn here is that the evidence supports the original suggestion that elephants evolved directly out of an African Miocene gomphothere stock. Such a conclusion is strongly borne out by comparative dental morphologies. Unfortuneately, details of gomphothere post-cranial anatomy are largely lacking, especially in Africa, so that such evidence is less useful in this regard.

There seems to be little doubt now that the gomphothere molar pattern underwent a number of structural modifications during late Miocene times, such that a rotary grinding/shearing dentition was rapidly transformed into a fore-and-aft-moving shearing device. This was associated with a remarkable reorganization of cranial-mandibular structure providing a mechanically more efficient masticatory apparatus. We as yet know nothing about the selective forces responsible for this transition, but they must have been strong judging from the rapidity and degree of evolution seen here.

Major features of this dental evolution involved fusion of lingual and buccal cones into a single transverse plate, with obliteration of the intervening median cleft. Superficial symmetry of these plates was achieved by a process of overgrowth either from the buccal or lingual side, such that the vestigial median cleft was displaced. In most later elephant teeth this cleft can be recognized as a weak groove along the plate face to one side or other of the midline. The functional implication of this development is that longitudinally oriented enamel ridges are eliminated in favor of the tandem sequence of transverse ridges so typical of elephant dentitions. Related to this functional shift was the fusion of intravalley columns into plate faces. This was a slower process, however, and vestiges of such columns can be seen as posterior loops on partially worn plates even in Pleistocene elephants. The present collection from Kenya demonstrates without doubt the relationship between these loops and the intravalley columns of gomphothere molars – a point that has not been adequately stressed in the past.

Another interesting evolutionary trend is in the mandible. *Stegotetrabelodon orbus* still retains enormous mandibular incisors of the gomphothere type, and similar structures can be seen in *S. syrticus* from the late Miocene of Libya (see Petrocchi, 1953). It is noteworthy, however, that apparently some members of this group had already reduced or lost these incisors while retaining an elongated symphysis (see Coppens, 1972).

In *Primelephas*, though the evidence is meagre, the jaw and incisor length were clearly greatly reduced. By middle Pliocene times no trace of external lower tusks is seen in *Loxodonta* or *Elephas*, but the presence of incisive germ chambers in both *L. adaurora* and the Asiatic *E. planifrons* is evidence of their former presence, and establishes a further link between these genera and the Miocene elephantids of East Africa.

The skeletal material described above reveals that even in the earliest known members of *Loxodonta* and *Elephas*, cranial and post-cranial elements are clearly identifiable on the generic level. Every foot bone in the holotype skeleton of *L. adaurora* is closer in structure to those of the living African elephant than to any other species. This suggests possible early functional differentiation in locomotion among the various elephant lineages. Unfortunately, too little identified skeletal material is currently available to allow more detailed comparisons. This provides a promising area for future investigations.

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LIST OF CAPTIONS

PLATE I

1. *Stegotetrabelodon orbus*, KNM LT-359, Lothagam 1, Kenya. Left M^3; occlusal and lingual views.
2. *S. orbus*, KNM LT-359, Lothagam 1, Kenya. Right M_3; buccal and occlusal views.
3. *Primelephas gomphotheroides*, KNM LT-358, Lothagam 1, Kenya, Left M_1; occlusal and buccal views.
4. *S. orbus*, KNM LT-354, holotype, Lothagam 1, Kenya. Atlas; anterior and posterior views.
5. *S. orbus*, KNM LT-374, Lothagam 1, Kenya. Single plate of M^3; anterior view.
6. *S. orbus*, KNM LT-354, Lothagam 1, Kenya. Right M^2; occlusal view.
7. *S. orbus*, KNM LT-342, Lothagam 1, Kenya. Right M_2; (reversed).
8. *S. orbus*, KNM LT-365, Lothagam 1, Kenya. Right dM_3 in mandibular fragment.
9. *S. orbus*, KNM LT-369, Lothagam 1, Kenya. Right humerus; posterior view.

(All scales are divided into 5 cm. units).

PLATE II

1. *Primelephas gomphotheroides*, holotype KNM LT-351, Lothagam 1, Kenya. Left M^3; lingual and occlusal views.
2. *P. gomphotheroides*, holotype KNM LT-351, Lothagam 1, Kenya. Lft M_3; occlusal and lingual views.
3. *P. gomphotheroides*, KNM LT-358, Lothagam 1, Kenya. Right M_2; occlusal and buccal views.
4. *Elephas ekorensis*, KNM EK-422, Ekora Formation, Kenya. Skull.
5. *P. gomphotheroides*, KNM LT-370, Lothagam 1, Kenya. Partial left humerus; anterior view.
6. *P. gomphotheroides*, KNM LT-358, Lothagam 1, Kenya. Right M^2; buccal and occlusal views.
7. *P. gomphotheroides*, KNM LT-370, Lothagam 1, Kenya. Right femur; anterior view.
8. *P. gomphotheroides*, KNM LT-358, Lothagam 1, Kenya. Symphysial fragment with partial left incisor. (reversed).

(All scales are divided into 5 cm. units).

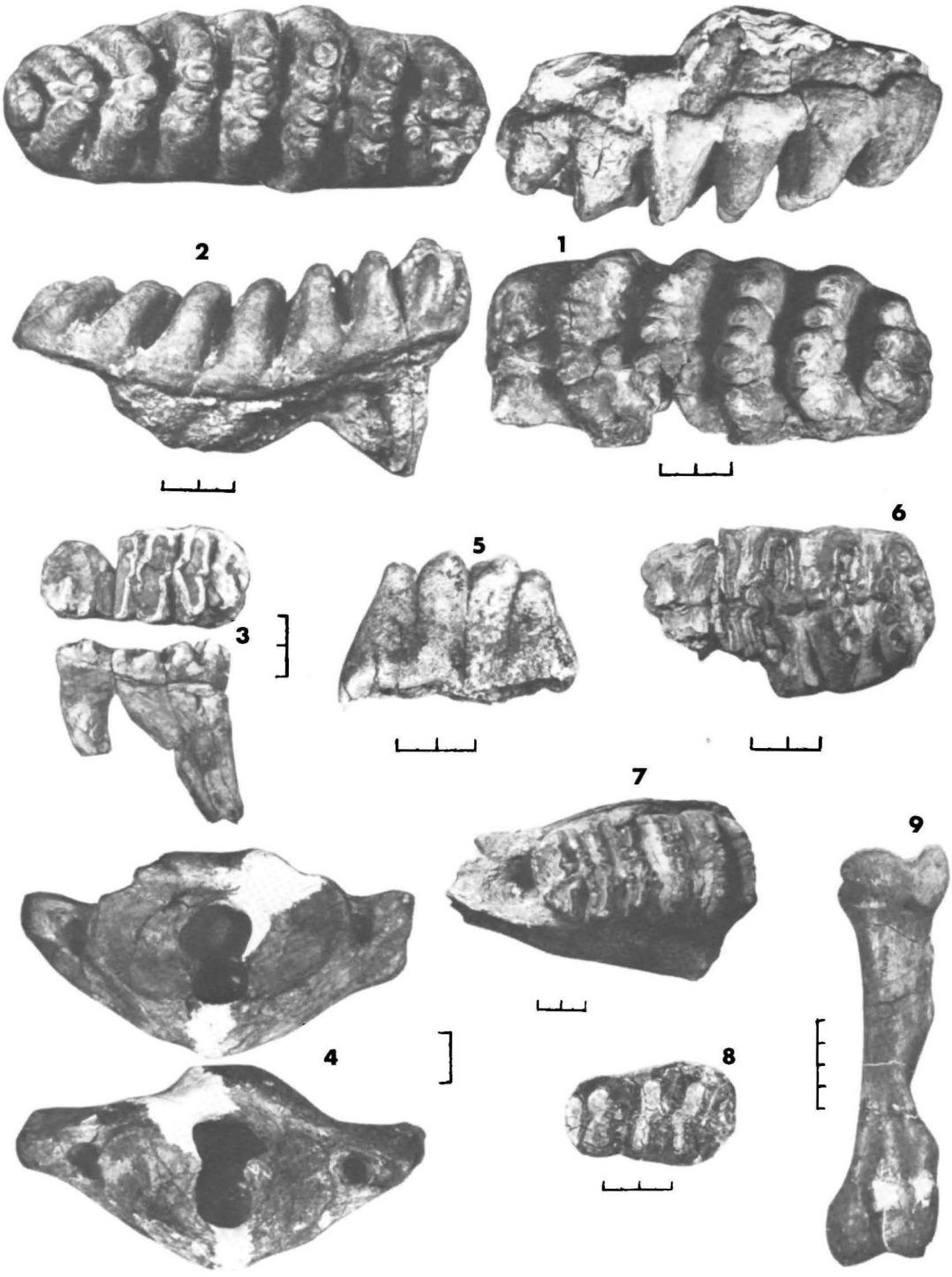
PLATE III

Loxodonta adaurora

1. KNM LT-353, Lothagam 3, Kenya. Skull with left and right M^2–M^3; left-lateral view.
2. Holotype, KNM KP-385, Kanapoi Formation, Kenya. Left mandible with M_3; left-lateral and occlusal views.
3. KNM KP-383, Kanapoi Formation, Kenya. Left M^3; occlusal view.
4. KNM KP-407, Kanapoi Formation, Kenya. Right M_3; occlusal view.
5. Holotype, KNM KP-385, Kanapoi Formation, Kenya. Atlas; anterior and posterior views.
6. Holotype, KNM KP-385, Kanapoi Formation, Kenya. Left pes; anterior view.
7. Holotype, KNM MP-385, Kanapoi Formation, Kenya. Left manus; anterior view.

(All scales are divided into 5 cm. units).

PLATE 1



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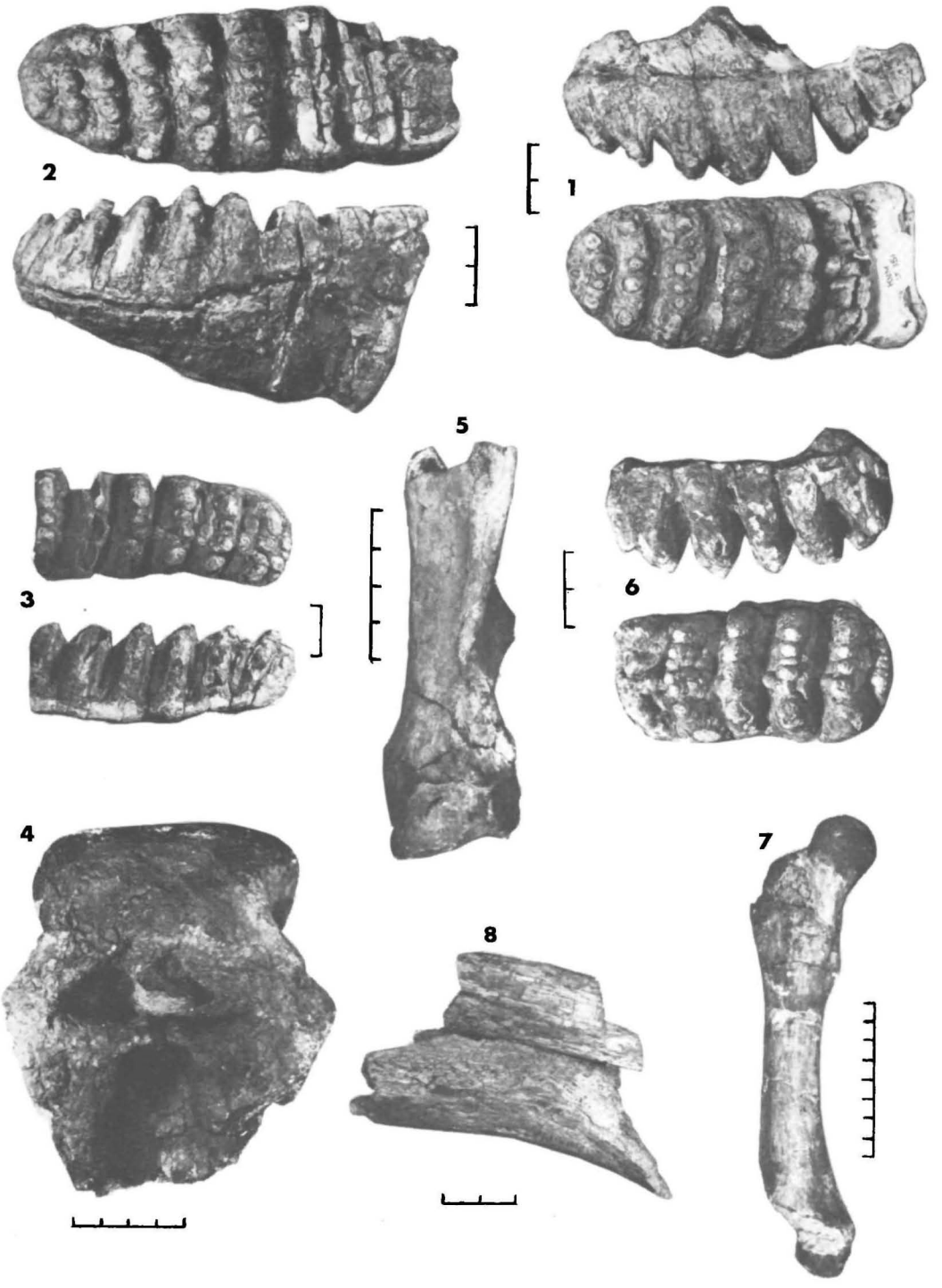

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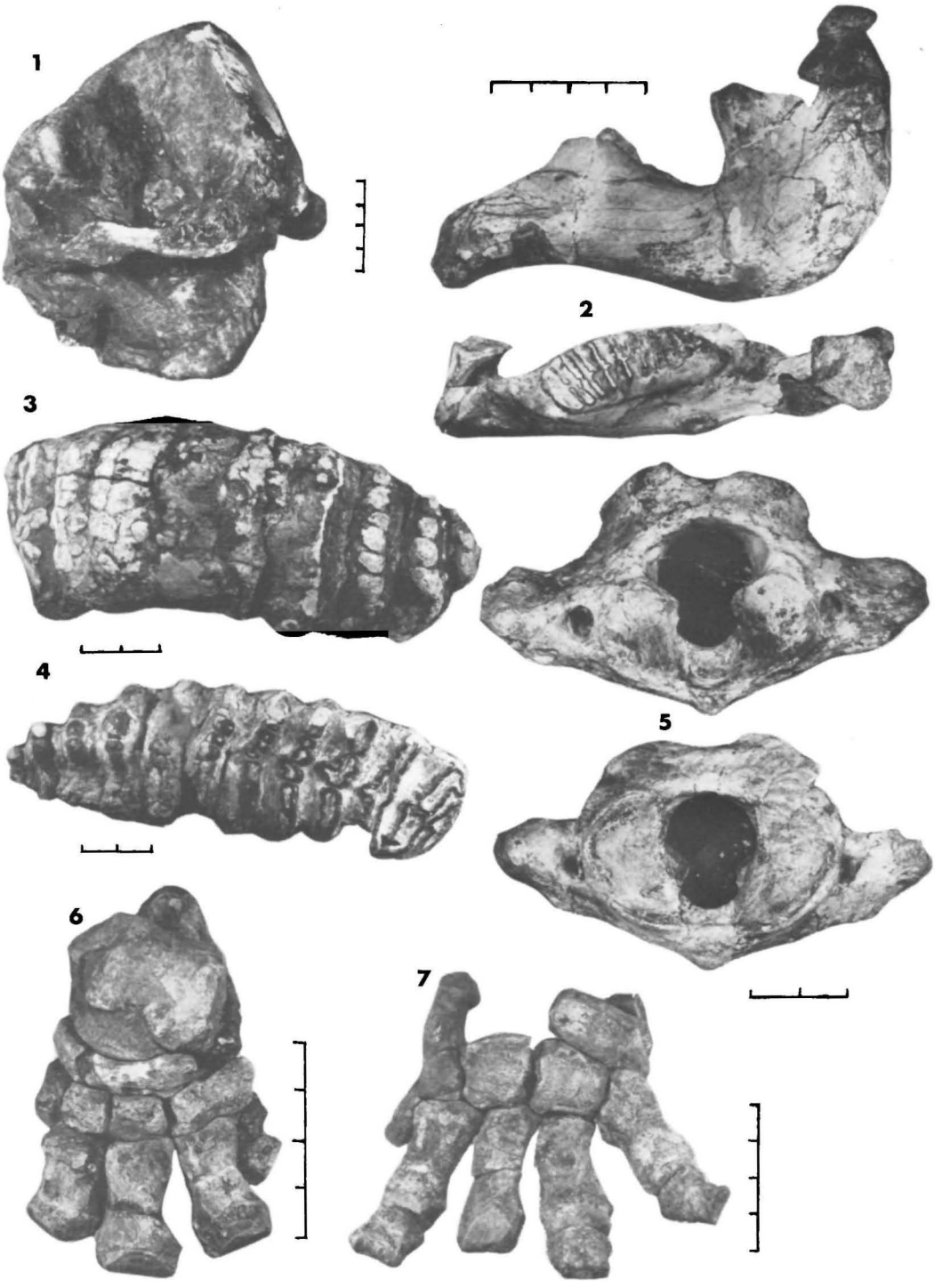

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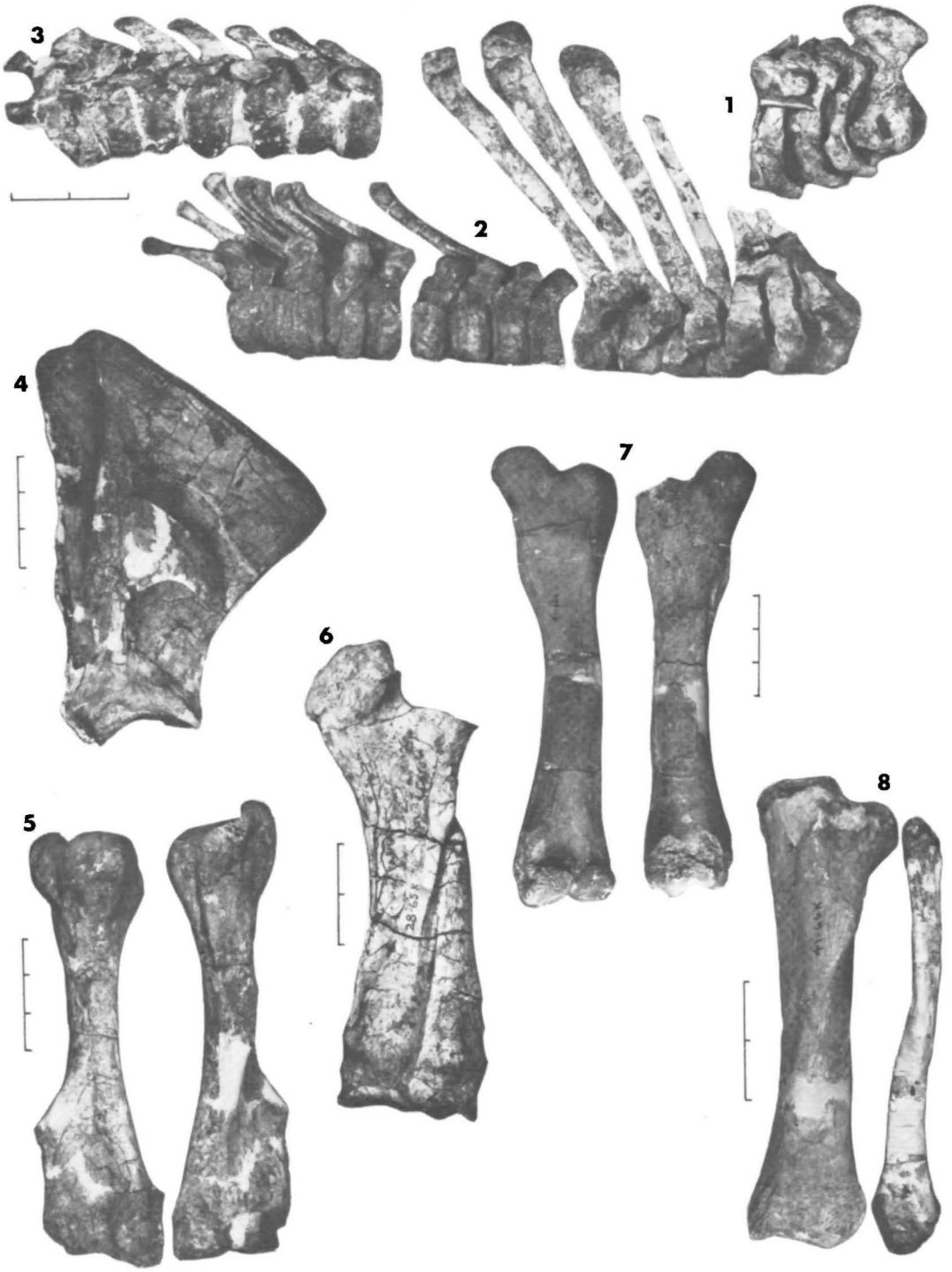

PLATE IV

Loxodonta adaurora

1. Holotype, KNM KP-385, Kanapoi Formation, Kenya. Cervical vertebrae C2-C5; right-lateral view.
2. Holotype, KNM KP-385, Kanapoi Formation, Kenya. C6-C7, thoracic vertebrae T1–T12; right-lateral view.
3. Holotype, KNM KP-385, Kanapoi Formation, Kenya. Thoracolumbar vertebrae T13–T19; right-lateral view.
4. Holotype, KNM KP-385, Kanapoi Formation, Kenya. Left scapula; lateral view.
5. Holotype, KNM KP-385, Kanapoi Formation, Kenya. Left humerus, left figure: anterior view; right figure: posterior view.
6. Holotype, KNM KP-385, Kanapoi Formation, Kenya. Left radius and ulna; posterior view.
7. KNM KP-397, Kanapoi Formation, Kenya. Right femur, right figure: anterior view; left figure: posterior view.
8. KNM KP-397, Kanapoi Formation, Kenya, Left tibia; anterior view, left fibula; lateral view.

(All scales are divided into 10 cm. units).