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FOUR NEW SPECIES OF ELEPHANTIDAE FROM THE PLIO-PLEISTOCENE OF NORTHWESTERN KENYA

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ABSTRACT. Four new species and one new genus of fossil elephants are described from the Plio-Pleistocene of northwestern Kenya. *Stegotrabelodon orbus* sp. nov. is more progressive and elephantinelike than its north African relative, *S. syrticus*, but it could not have been ancestral to the earliest Elephantinae. *Stegotrabelodon* is placed in the family Elephantidae as a distinct subfamily, the Stegotrabelodontinae. *Primelephas gomphotheroides* gen. et sp. nov. is described as the earliest known genus of the Elephantinae; it is morphologically and stratigraphically suitable as the basal genus from which later elephants could have been derived. *Loxodonta adaurora* sp. nov. is distinguishable from *Mammuthus africanavus*, in skull characters primarily, but also in dentition. It is considered to be the earliest known member of the *Loxodonta* lineage and may have been directly ancestral to the living *L. africana*. *Elephas ekorensis* sp. nov. is clearly related to, but is more primitive than, *E. recki* in both molar and skull morphology and is placed at the base of that lineage.

INTRODUCTION

In 1965, while working in Miocene deposits in Turkana District, northwestern Kenya, an expedition of the Museum of Comparative Zoology, under the direction of Professor Bryan Patterson, discovered fossil-bearing sediments of Plio-Pleistocene age well exposed in the drainage of the Kanapoi, a dry wash tributary to the Kakurio river (Patterson, 1966). The locality is at 36° 04' E and 2° 19' N, 38 miles west and 9 miles south of Teleki's volcano at the southern end of Lake Rudolf (Fig. 1). Clastic sediments predominate with pyroclastics interbedded throughout the sequence. The total measured thickness is over 200 feet but the vertical distribution of fossils indicates no major faunal change, though some new elements appear near the top of the section. Potassium/Argon age determinations of 2.9 ± 0.3 (Patterson, 1966), 2.7 ± 0.2 (Patterson *et al.*, in MS), and 2.5 ± 0.2 million years (Patterson and Howells, 1967) from an overlying basalt are questionable on

faunal evidence. Correlation based on Proboscidea (Maglio, in press) and Suidae (H.B.S. Cooke, pers. comm.) indicate near contemporaneity with Yellow Sands (Mursi Formation) at the base of the Omo sequence, for which the K/Ar date of 4.05 ± 0.2 million years is available (Howell, 1968).

The Kanapoi fauna is rich in vertebrate remains that include: cf. *Australopithecus* (Patterson and Howells, 1967); *Parapapio jonesi* (Patterson, 1968); *Lepus* sp.; *Hystrix* sp.; *Tatera* sp.; *Enhydriodon* sp. nov. (Kurtén, pers. comm.); *Hyaena namaquensis*; *Deinotherium bozasi*; *Anancus* sp.; *Loxodonta adaurora* sp. nov. (this paper); *Elephas ekorensis* sp. nov. (this paper); *Stylohipparion* sp.; *Ceratotherium* sp.; *Nyanzachoerus*, (2) spp. nov.; *Notochoerus* cf. *capensis*; *N.* cf. *N. euilus* (suid identifications by H.B.S. Cooke); Hippopotamidae, sp. nov. (S. Coryndon, pers. comm.); *Okapia* sp.; *Giraffa* sp.; *Tragelaphus* sp.; other Bovidae; *Crocodylus* sp.; *Euthecodon* sp.; *Podocnemis* sp.; *Testudo* sp. cf. *T. ammon*; Trionichyidae indet., (*Chelonia* identifications by R. C. Wood); numerous remains of fish and molluscs.

Overlying the Kanapoi basalt is a small area of poorly exposed sediment at Ekora from which some vertebrate remains have been recovered. The locality is at $36^{\circ} 11' E$ and $2^{\circ} 31' N$, 17 miles NNE of Kanapoi. The Proboscidea are the best preserved and most numerous fossils from these sediments. The tentative faunal list includes: *Anancus* sp.; *Loxodonta adaurora* sp. nov.; *Elephas ekorensis* sp. nov.; *Simopithecus* sp. (Patterson, pers. comm.); and *Ceratotherium* sp.

While exploring for further outcrops of the Kanapoi beds in 1967, a museum expedition worked a richly fossiliferous, thick sequence of sediments at Lothagam Hill (Patterson *et al.*, in MS). The exposures cover about three square miles and are situated at $36^{\circ} 04' E$ and $2^{\circ} 53' N$, some 40 miles north of Kanapoi and three miles southwest of the Kerio delta on the southwestern side of Lake Rudolf. Two fossiliferous levels of coarser, red, fluvial or deltaic sediments are separated by fine-grained lake beds probably representing a significant interval of time. On faunal evidence the upper fluvial beds correlate with those of Kanapoi, but the lower beds, of which up to 1500 feet are exposed, appear to be considerably earlier. Though a K/Ar date of 3.71 ± 0.23 million years has been obtained for a basaltic sill between the lower fluvial and the fine upper lake beds (Patterson, pers. comm.), this may represent no more than an upper limit for the age of the entire sedimentary sequence in the Lothagam area. The actual age of the

lower fluviatile beds would appear to be closer to 5.0–5.5 million years on faunal grounds (Maglio, in press). The fauna has not yet been studied in detail, but it includes: *Australopithecus* sp. cf. *A. africanus* (Patterson and Howells, in preparation); *Macaca* sp.; Anomaluridae, nov.; Hyaenidae indet.; Felinae indet.; Machairodontinae indet.; ?*Civettictis* sp.; Orycteropidae, gen. et sp. nov.

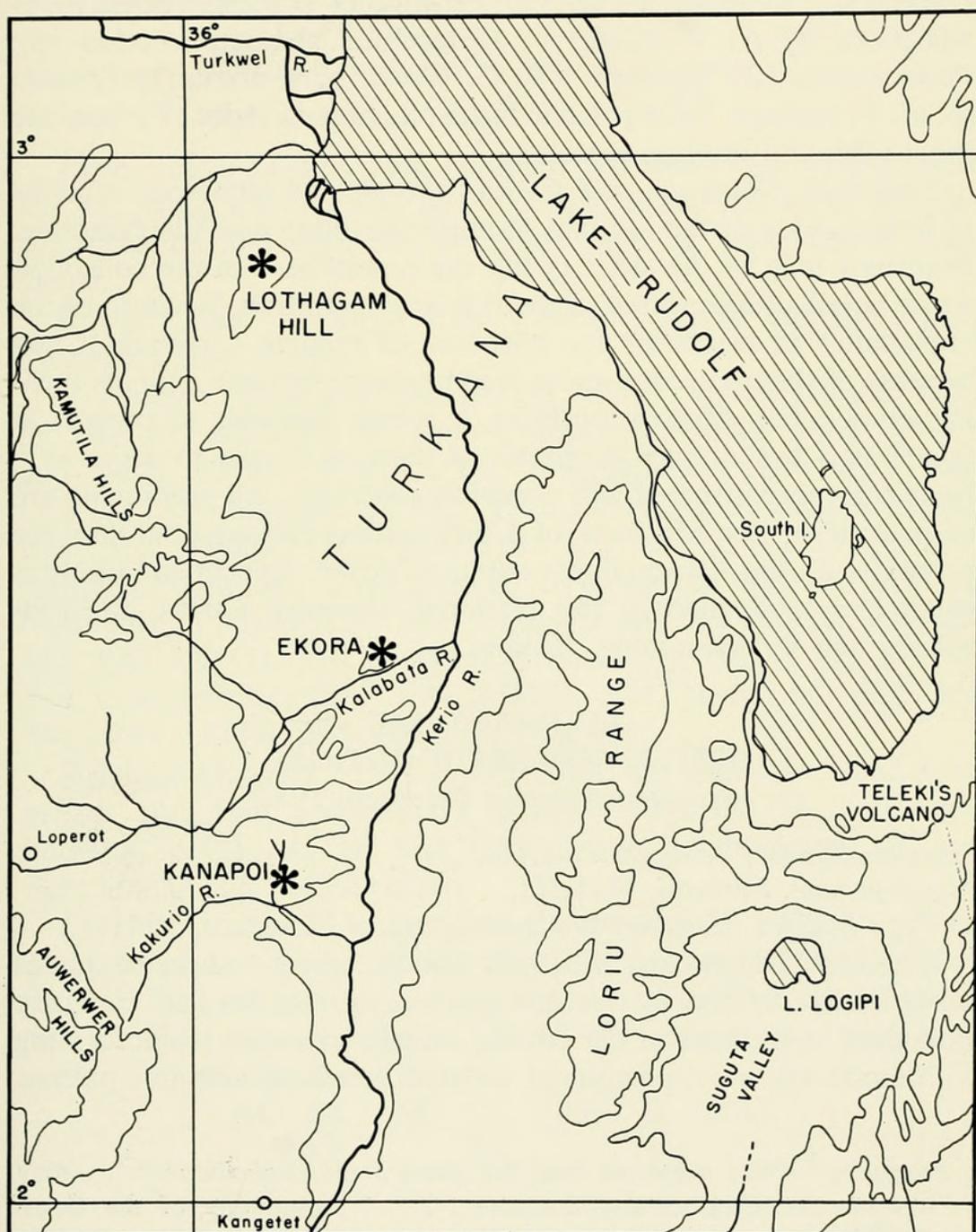


Figure 1. Generalized map of the southern Lake Rudolf area, north-western Kenya, showing locations of the Kanapoi, Ekora and Lothagam deposits.

(Patterson, pers. comm.); *Deinotherium* sp.; Gomphotheriidae indet.; *Stegotetabelodon orbis* sp. nov. (this paper); *Primelephas gomphotheroides* gen. et sp. nov. (this paper); *Stylohipparion* sp.; Rhinocerotidae, Brachypotherinae, nov.; *Nyanzachoerus*, (3) spp. nov. (Cooke, pers. comm.); Hippopotamidae, (2) spp. nov. (Coryndon, pers. comm.); *Giraffa* sp.; *Tragelaphus* cf. *T. nakuae*; *Gazella* sp.; *Redunca* aff. *ancystrocera*; other Bovidae (bovid identifications by A. W. Gentry); *Crocodylus* sp.; *Euthecodon* sp.; *Podocnemis*, (2) spp. nov. (R. C. Wood, pers. comm.); *Testudo* sp. cf. *T. ammon*; Trionychidae indet.; Squamata indet.; Pythoninae indet.; fish and mollusc remains.

Lothagam, Kanapoi, and Ekora have yielded numerous remains of Proboscidea of the families Gomphotheriidae and Elephantidae. Four new taxa of the latter group are represented in the collection and a detailed description of them is in preparation. Because of the importance of elephants for purposes of relative correlation, and because of the numerous, more fragmentary elephant remains turning up at other African localities, it seems desirable to present at this time a preliminary diagnosis of these new taxa to serve as a basis for comparison of less complete material. All specimens are at present in the Museum of Comparative Zoology but are the property of the National Museum, Nairobi. Specimen numbers given are catalogued in the National Museum, Centre for Prehistory and Palaeontology, Nairobi.

ELEPHANTIDAE
STEGOTETRABELODONTINAE *
Stegotetabelodon Petrocchi 1941

Stegotetabelodon, Petrocchi 1941:110.

Stegolophodon, Petrocchi, 1943:123.

Type Species. *Stegotetabelodon syrticus* Petrocchi, 1941.

Emended Diagnosis. M3 with six to seven transverse plates superficially divided by vertical grooves; strong median cleft not extending to the base of the crown; complete enamel loops forming with moderate wear; prominent isolated accessory columns present

* Aguirre (1969) suggested that the genus *Stegotetabelodon* ". . . may be a subfamily, Stegotetabelodontinae . . ." presumably of the Gomphotheriidae, though this is vague. However, no formal action to establish this subfamily was taken at that time. In this paper (and in press) I include this group as a subfamily of the Elephantidae.

behind the plates; crown height less than the width; enamel 4-7 mm in thickness, not folded; transverse valleys between plates open but V-shaped in longitudinal section; plates strongly triangular in longitudinal section; lamellar frequency, 2.5-3. Mandible with long, massive symphysis bearing very long incisors.

Distribution. Late Pliocene, Sahabi beds, Libya; lower fluviatile beds, Lothagam Hill, Kenya.

*Stegotetabelodon orbus** sp. nov.
(Pls. I-II)

Type. PAL.LOTH. 354, complete left lower jaw with unworn left M_3 , worn left M_2 , and left and right lower incisor in situ, incomplete left and right M^3 , complete right M^2 and skeletal fragments.

Horizon and Locality. Late Pliocene, lower fluviatile beds, Lothagam Hill, Kenya.

Hypodigm. Type and PAL.LOTH. 359, complete left and right M_3 , left M^3 and right M^2 from a single individual. PAL.LOTH. 347, worn left M^3 . PAL.LOTH. 349, complete right M_3 . PAL.LOTH. 352, complete left M_3 . PAL.LOTH. 355, partial left and right M_3 . PAL.LOTH. 360, worn left M^3 . PAL.LOTH. 367, complete right M^3 . PAL.LOTH. 374, partial M^3 and skeletal fragments. PAL.LOTH. 342, complete left M_2 and partial right M_2 . PAL.LOTH. 350, complete left and right M_2 . PAL.LOTH. 366, complete left M^2 . PAL.LOTH. 344, partial left dM^4 and dM_4 . PAL.LOTH. 365, complete right dM_3 .

Referred Material. PAL.LOTH. 368, left and right mandibular incisor and right premaxillary incisor. PAL.LOTH. 369, right humerus. PAL.LOTH. 370, right femur, left humerus, left and right fibulae and partial pelvis.

Diagnosis. About 12 per cent smaller than *S. syrticus*. Mandibular incisors short, forming about 38 per cent of the total jaw length. Free columns persisting only behind the first two plates on M_3 ; relative crown height of M_3 13 per cent greater than in *S. syrticus*. Lamellar formula:

$$M_3 \frac{6X}{7X}, \quad M_2 \frac{5X}{6X}, \quad dM_4 \frac{6}{?}, \quad dM_3 \frac{?}{3}$$

* *L. orbus*=childless. In allusion to the terminal position of this species and its apparent non-ancestry to later species of Elephantidae.

Discussion. In a series of papers, Petrocchi (1941, 1943, 1952, 1953) described a genus of Proboscidea, *Stegotrabelodon*, from the late Pliocene beds of Sahabi, Libya. There can be little doubt as to the validity of this genus, but its significance as a morphological intermediate between the Gomphotheriidae and the Elephantidae has only recently been stressed (Aguirre, 1969; Maglio, in press). Petrocchi described two species of *Stegotrabelodon*, *S. syrticus* and *S. "lybicus,"* and one of *Stegolophodon*, *S. "sahabianus,"* from the Sahabi beds. The latter two species were each based on a single molar. The type of *S. "lybicus"* is an unworn lower M3; comparison with the type mandible of *S. syrticus* is difficult owing to excessive wear in the latter. Nevertheless, the only differences between them are those expected to occur with wear. On present evidence the two must be considered conspecific. The type of *Stegolophodon "sahabianus"* is an incomplete M³. Undoubtedly Petrocchi was struck by the progressive aspect of this specimen as compared with the lower molar of *S. "lybicus"* (the upper molars on the type skull of *S. syrticus* are severely worn). However, associated upper and lower molars of the new species from Lothagam described here show that the upper M3 was more progressive in structure than the lower, a common feature in Proboscidea generally. In size, the type molar of *S. "sahabianus"* is larger than the few known specimens of *Stegotrabelodon* from Sahabi, but well within the expected range of size variation as exhibited for molars of the Lothagam species. Without more substantial evidence to the contrary, *Stegolophodon "sahabianus"* should also be considered as a synonym of *Stegotrabelodon syrticus*.

The mandibular tusks of *S. syrticus* are about two-thirds as long as the premaxillary tusks. They are very long and slender, and form 57 per cent of the total jaw length in contrast to only 38 per cent for *S. orbus*. The type mandible of the latter is a young adult, however, and adult size of the mandibular incisors may have been proportionately somewhat greater. These tusks in *S. syrticus* are elliptical in cross-section, being compressed laterally. The lower tusks of *S. orbus* are also elliptical as are the small lower tusks of the dwarfed species, *Elephas celebensis* (Hooijer, 1954). The mandibular tusks of *S. syrticus* are nearly three times longer than in *S. orbus*, though similar in diameter.

The third molars are large and massive in *S. syrticus*; they are proportionately broader than in the Lothagam species (Table 1), but the crown height is about the same, resulting in a lower H/W

index ($100 \times \text{height/width}$). A free column is present behind each molar plate in the Sahabi species, but in *S. orbus* all but the anterior two columns have become incorporated into the plates and are present in the form of small vertical ridges fused into the posterior faces of the plates. These may be absent on the more posterior plates. On molars of *S. syrticus*, a deep cleft divides the plates longitudinally; weaker, but still strong lateral clefts are present so that the apex of each plate is divided into four rather widely separated digitations that fuse with wear. In *S. orbus*, the lateral clefts are very weak and shallow, and all clefts are tightly compressed. Some of the apical digitations tend to be further subdivided into two or more smaller units, each separated by a weak cleft. The crown apex may thus have up to six or seven subdivisions. Upper molars of *S. orbus* are more progressive than the lowers in that the plates are more consolidated, with a weaker median cleft. There are seven plates on the lower and six on the upper M3 in both the Sahabi and the Lothagam species.

The second and first true molars of *S. orbus* are somewhat more progressive in appearance than M3. The plates are more consolidated, and apical digitations are separated only by weak and compressed clefts. The deeper median cleft persists on the anterior two or three plates until intermediate stages of wear, but a complete enamel figure is formed on the remaining plates in early wear.

The enamel is very thick and smooth. Cement is abundant, but it usually does not fill the valleys completely nor does it usually invest the apex and sides of the molar plates.

The mandible is long anteroposteriorly in both species, but in *S. syrticus* the symphysis is 70 per cent longer than in *S. orbus*, though there is no difference in symphyseal width. Proximal tusk separation is nearly twice as great in *S. syrticus* as in the Lothagam species.

The systematic position of *Stegotrabelodon* is clearly transitional between the Gomphotheriidae and the Elephantidae. Yet in spite of certain conspicuous gomphothere characters, such as long mandibular incisors and a prominent median cleft on M3, the molars are in general more elephant-like than gomphothere-like. In this genus, the inner and outer cones of the ancestral gomphothere molar are obliterated by median compression and fusion to form very platelike structures. The gomphothere trefoil pattern is gone and the old median folds that formed them persist as the free columns in the transverse valleys. Median swellings toward the base of the plates are all that remain of the anterior trefoil, whereas

the posterior one first became a prominent isolated column, and in the more advanced Elephantinae was fused into the plate face. These fused columns are responsible for the development of median "sinuses" on the wear figures of many elephant molars. *Stegotetrabelodon* is best placed in the family Elephantidae as a primitive subfamily.

With respect to reduction of mandibular incisors, increased relative crown height, fusion of isolated columns into the molar plates, and reduced division of the crown through compression and shallowing of clefts between the apical digitations, *S. orbus* sp. nov. would appear to represent a more progressive species than *S. syrticus*. Though very close in many particulars to the earliest Elephantinae, *S. orbus* was probably not ancestral to any known species of elephant, and occurs in the same deposits as the earliest species of Elephantinae (see below).

ELEPHANTINAE

Primelephas† gen. nov.

Type Species. *Primelephas gomphotheroides* sp. nov.

Diagnosis. Molars very low crowned, the height being one-half to three-fourths of the width; the median cleft lacking, but strong grooves superficially dividing the plates into prominent columns; plates wear as complete enamel loops; plates triangular in longitudinal section, wider toward the root; transverse valleys open to the base, but strongly V-shaped in cross-section; enamel 3-6 mm in thickness, not folded; lamellar frequency, 3-4. Cement abundant but usually not filling valleys completely. Mandible with very small but prominent incisors in some individuals, possibly males only; symphysis short. Lamellar formula:

$$\begin{array}{ccc} \text{M3 } 7\text{X}, & \text{M2 } 5\text{X}, & \text{M1 } ? \\ \hline & 8\text{X} & 6 \quad 5\text{X} \end{array}$$

Distribution. Late Pliocene, lower fluviatile beds, Lothagam Hill, Kenya; Kolinga and ?Koulà, Tchad; Nyawiega, Kaiso beds, Uganda.

Included Species. *Stegodon korotorensis* Coppens, 1965.

Discussion. This genus is distinguished from the more primitive *Stegotetrabelodon* in having much reduced mandibular incisors and a short symphysis. The molars are elephantine in structure, lacking median clefts and having stronger plate development. In later

†*L. primus* = first, and *L. elephas* = elephant.

TABLE 1

Comparative measurements of *Stegotetabelodon orbus* sp. nov.
and *S. syrticus* for M3 and the mandibular incisors, in mm.

	<i>Stegotetabelodon orbus</i> sp. nov.		<i>Stegotetabelodon syrticus</i>	
	M ₃	M ₃	M ₃	M ₃
Length	234.3-280.3	212.1-255.9	280.0-317.4	232.0-242.0
Enamel thickness	5.0-6.9	4.0-7.4	5.5-6.0	5.3-7.2
Lamellar frequency	2.7-2.9	2.4-3.0	2.6-2.9	2.8-3.2
No. of plates	7X	6X	7X	6X
Maximum width	98.0-109.3	93.4-110.5	115.0-123.4	109.8-122.0
Maximum height	75.1-81.6	69.8-75.1	74.1	73.0-80.1
H/W index	69-87	68-75	60	66-67
Symphyseal length		513.2		869.6
Incisor length (exposed)		602.0		1671.0
Horizontal diameter		53.6		72.0
Vertical diameter		62.5		89.8
Proximal separation		18.2		29.5

genera of Elephantinae, the mandibular incisors disappear externally though they were probably present as tooth buds in symphyseal crypts in the early species of *Loxodonta* and *Elephas* (see below). In one case, mandibular incisors reappeared, possibly through paedomorphosis, in the dwarfed species *Elephas celebensis* Hooijer. The crown height is lower than in the most primitive species of later genera, and the number of plates is lower also. This genus appears structurally and chronologically to have been a member of the basal group from which later Elephantinae were derived.

In later genera the crown height is greater and the plates are not strongly triangular in longitudinal section; the anterior and posterior faces of each plate are nearly parallel. The transverse valleys between plates are broadly open and U-shaped, and the enamel is considerably thinner. In all but the most primitive known species of *Mammuthus*, the number of plates for each molar is greater than in *Primelephas*.

*Primelephas gomphotheroides** sp. nov.
(Pls. III-IV)

Type. PAL.LOTH. 351, associated left and right M³, left M₃ and fragmentary palate.

Horizon and Locality. Late Pliocene, lower fluviatile beds, Lothagam Hill, Kenya.

Hypodigm. Type and PAL.LOTH. 358, left and right M², right M₂, left and right M₁, and mandibular symphysis. PAL.LOTH. 363, partial right M³ and mandibular symphysis. PAL.LOTH. 375, incomplete right M₁.

Referred Material. PAL.LOTH. 364, fragmentary M₃. PAL.LOTH. 371, molar fragments, calcaneum, astragalus, incomplete fibula and an occipital condyle. PAL.LOTH. 376, molar plate.

Diagnosis. Lower crowned than *P. korotorensis* (Coppens), crown height for M³ 60-65 per cent of crown width at base. Other characters as for the genus.

Discussion. Until recently, the most primitive known species of the Elephantinae was *Mammuthus subplanifrons*, a poorly known species from the older gravels of the Vaal River of South Africa, Kanam, and the Chemeron beds in east Africa, and the Chiwondo beds in Malawi (see Maglio, in press). Available data suggest that this species occurred in Africa earlier than the first

* *gomphotheroides* = gomphothere-like.

appearances of elephants in Europe and Asia (*M. meridionalis* and *E. planifrons* respectively), and it has been considered close to the ancestral stock of all later elephants. Recent study (Maglio, in press, and in preparation) has shown that *subplanifrons* is on the *Mammuthus* lineage and therefore did not occupy the more broadly ancestral position once allocated to it.

The stratigraphic position of *Primelephas gomphotheroides* is lower in the Pliocene section of Africa than is *M. subplanifrons*, or in fact any other known member of this subfamily. Morphologically, it is generalized enough to have served as the basis for later specializations that were to characterize the three later genera of elephants (*Elephas*, *Loxodonta*, and *Mammuthus*). The molars of *P. gomphotheroides* have a strong vertical ridge near the center of the plate faces, except on the first or second plates where the vertical ridges are free and columnar at their apices. With wear, these ridges form the median loops or sinuses so typical of early elephants. The number of plates is fewer and their relative height lower than in any other species of Elephantinae (Table 2). The enamel is thick and unfolded as in other early species. Transverse valleys between the molar plates are V-shaped in longitudinal section, but not compressed at the base as in the stegodonts. In all later species, including *M. subplanifrons*, the valleys are broadly open and U-shaped at the base; this serves to maintain the efficiency of the tooth as a grinding surface into late stages of wear by keeping the enamel ridges separated by a cement interval down to the base of the crown.

The symphysis of the jaw is much shorter than in *Stegotrabelodon*, even though small incisors are present. As a result, the root of the incisor passes into the horizontal ramus. These incisors are no longer closely appressed in the midline of the symphysis as in *Stegotrabelodon*, but lie on either side of the "spout" formed by the downturned symphysis. They extend along the ventral wall of the horizontal ramus anterior and somewhat beneath the front portion of the mandibular canal. There is some indication of variation in size for these incisors; in two very fragmentary mandibles there apparently were no external tusks but only a pair of deep cavities lateral to the symphysis and connected to the mandibular canal by a short channel. These two specimens may represent juvenile individuals, but it is also possible that incisor size or even their presence or absence was a sexual character, being larger in the males.

Specimens referable or probably referable to *Primelephas* are known from other African localities. Several molar fragments

from Nyawiega in the Kaiso sequence indicate the presence of a closely related form. Although tentatively referring this material to *M. subplanifrons* (Cooke and Coryndon, in press), H. B. S. Cooke independently recognized the primitive nature and generic distinctness of some of the specimens, but was unable to diagnose this new form without better material. All of the Kaiso material referred by Cooke and Coryndon to *M. subplanifrons* is the same and should be referred to *Primelephas*. Although additional data may show this form to be specifically distinct, on present evidence it is best referred to *Primelphas gomphotheroides*.

A small fragment was described by Coppens (1965) from Tchad as *Stegodon korotorensis* sp. nov. This specimen is very incomplete, consisting of the posterior three plates of a lower M3, but it is clearly not a true *Stegodon*. The plates are divided apically into only a few well-separated digitations, and, though V-shaped in longitudinal section, the transverse valleys are not compressed at the base as they are in stegodonts. The only other known specimen, an equally incomplete upper M3, is similar to the type. This form is very close to the Lothagam and Kaiso specimens and should be included in the genus *Primelephas*. These two specimens of *P. korotorensis* are distinguishable from *P. gomphotheroides* in being proportionately higher crowned, but otherwise they are too fragmentary for diagnosis of the species, and more detailed comparisons with material from other localities is not possible. On present evidence we must recognize two species of *Primelephas*—*P. gomphotheroides* and *P. korotorensis*.

Loxodonta F. Cuvier 1825

Type Species. *Loxodonta africana* (Blumenbach) 1797.

Loxodonta adaurora† sp. nov.

(Pls. V-VI)

Elephas cf. *meridionalis* Nesti, MacInnes, 1942: 92.

Archidiskodon exoptatus Dietrich (in part), Dietrich, 1942: 72.††

†*L. adaurora* = at dawn.

††In a review of the syntype collection of "*Archidiskodon exoptatus*," I (1969) have shown that two distinct taxa are present—one is referred to *Elephas recki* Dietrich 1916, and is represented by the better specimens in the collection; the other taxon is a more primitive species. The specimens of the latter taxon are insufficient for the establishment of a species and a *recki* specimen was chosen as the lectotype of "*A. exoptatus*." The non-*recki* material in the syntype collection from Laetolil is here referred to *L. adaurora* sp. nov.

TABLE 2

Comparative measurements in mm for M3 of *Primelephas gomphotheroides* gen. et sp. nov. from Lothagam Hill with specimens from other African localities. Superscripts "e" indicate an estimated value.

	<i>Primelephas gomphotheroides</i> gen. et sp. nov.			<i>P. korotorensis</i>	
	LOTHAGAM	KAISO	TCHAD	M ₃	M ³
Length	M ₃ 247.5	M ₃ —	M ₃ —	—	—
Enamel thickness	3.5-5.1	4.0-4.9	4.0-4.5	5.0-6.0	—
Lamellar frequency	3.3	3.6	3.8	3.4	—
No. of plates	8X	7X	—	—	—
Width	93.2	109.5	89.2	86.3	85.0 ^e
Height	61.2	52.1	52.8	65.0 ^e	60.0+
H/W index	65	57	59	72 ^e	76 ^e

Elephas cf. *planifrons* Falconer and Cautley, Arambourg, 1947: 114.

"*Elephas* . . . close to *E. exoptatus*", Patterson, 1966: 5.

Type. PAL.KANAP. 385, a nearly complete skeleton, the skull and jaws bearing partially worn last molars in situ.

Horizon and Locality. Plio-Pleistocene, Kanapoi beds, Kenya.

Hypodigm. Type and PAL.LOTH. 353, skull with left M²-M³, right M³ and left premaxillary incisor. PAL.KANAP. 383, left and right M³, worn left M³ and incomplete left and right M₃. PAL.KANAP. 390, complete right M³. PAL.KANAP. 407, complete right M₃. PALEKA. 423, palate with left and right M³. PAL.KANAP. 386, left M². PAL.KANAP. 389, incomplete right M². PAL.KANAP. 403, partial ramus with incomplete left M₂. PAL.KANAP. 406, jaw ramus with r.M₁-M₂. PAL.KANAP. 381, jaw with left and right M₁. PAL.KANAP. 391, right dM⁴. PAL.KANAP. 411, right dM⁴, left and right dM₃. PAL.KANAP. 382, right dM³. PAL.KANAP. 396, right dM³. PAL.KANAP. 392, right dM². PAL.KANAP. 400, left dM₂.

Localities for Hypodigm. All from the Kanapoi beds except 353, which is from the upper fluvial beds at Lothagam Hill, and 423, from Ekora.

Diagnosis. Molars low crowned, the height equal to or less than the width; enamel thickness 3-5 mm and not folded; very large anterior and posterior enamel folds forming prominent loops or sinuses with wear. Plates thick and well separated, the lamellar frequency being about 2.5-4. Lateral sides of plates lacking the strong tapering as in *M. africanavus*. Skull like that of *L. africana* but with very large and somewhat flaring premaxillae, long frontal, and prominent fronto-parietal ridges lateral to external naris. Parietals and occipitals not expanded. Occipital condyles high and projecting. Tusks long and gently curved in a single plane, not twisted as in *Mammuthus*. Mandible with vestigial incisive cavities. Lamellar formula:

M3	8-10,	M2	7,	M1	?	dM4	5,	dM3	5,	dM2	3.
	<u>10-11</u>		<u>?</u>		<u>6</u>		<u>?</u>		<u>5</u>		<u>3</u>

Discussion. Until now there has been little direct evidence concerning the early stages in the evolution of *Loxodonta africana*. Coppens (1965) placed the north African species *Mammuthus africanavus* on the *Loxodonta* lineage, but recent study and new material (Arambourg, pers. comm.) show that *africanavus* was not on that line.

Other early elephants such as *Elephas planifrons* from the Villafranchian of Asia, and *M. meridionalis* from deposits of similar age in Europe, were already differentiated along different lines and were unrelated to the living African elephant. The African Plio-Pleistocene species, *M. subplanifrons*, though poorly known, has *Mammuthus* affinities and also appears to have been unrelated to *Loxodonta*. From all available evidence, *Loxodonta adaurora* sp. nov. is the only known species certainly on the *Loxodonta* lineage, and extends this line back to the earliest Pleistocene or latest Pliocene in Africa.

The earliest known representatives of the three Pleistocene genera of Elephantinae, *Loxodonta*, *Mammuthus*, and *Elephas*, were not yet greatly differentiated with respect to dentition, though distinct on skull characters. This fact has resulted in the confusion of these lines when only teeth were available for study. In *L. adaurora*, *M. africanavus*, and *E. planifrons*, the molars are all rather low crowned, being about as high as they are wide; the enamel is thick and unfolded with a more or less prominent median fold or loop caused by the partial fusion of intravalley columns into the face of the plates; and the number of plates is similar, about 9-12 for M3 (Table 3). Nevertheless, certain differences occur in the molars that distinguish populations of these three species. In *M. africanavus* the sides of the plates taper strongly toward the apex of the crown, and the molar tends to be proportionately narrower than in either *L. adaurora* or *E. planifrons*. The lamellar frequency for *M. africanavus* is somewhat greater than for *L. adaurora*, the latter being more primitive in this respect. Finally, the relative crown height for M3 of *africanavus* is nearly 20 per cent greater than for *L. adaurora*. The lamellar frequency, crown height, and other parameters for the known specimens of *E. planifrons* from the Siwalik Hills show a considerably greater degree of variation than for other well known species. Yet there exists every intermediate stage between the extremes for each measurable parameter. It seems likely that in *E. planifrons* we are dealing with an evolutionary series of populations for which stratigraphic control is lacking.

Far more important for the determination of generic criteria in these early elephants are the skulls (Figs. 2 and 3), which are very different in the three lines and clearly establish relationships with later species. The cranial morphology for *L. adaurora* and *E. planifrons* are each known from several specimens. The skull of *M. subplanifrons* is unknown and that of *M. africanavus* is known

only from a poorly preserved referred skull recently described by Professor Arambourg. Though this description is not yet published, photographs kindly supplied by Professor Arambourg show that this species is on the *Mammuthus* line and that it was close to, but

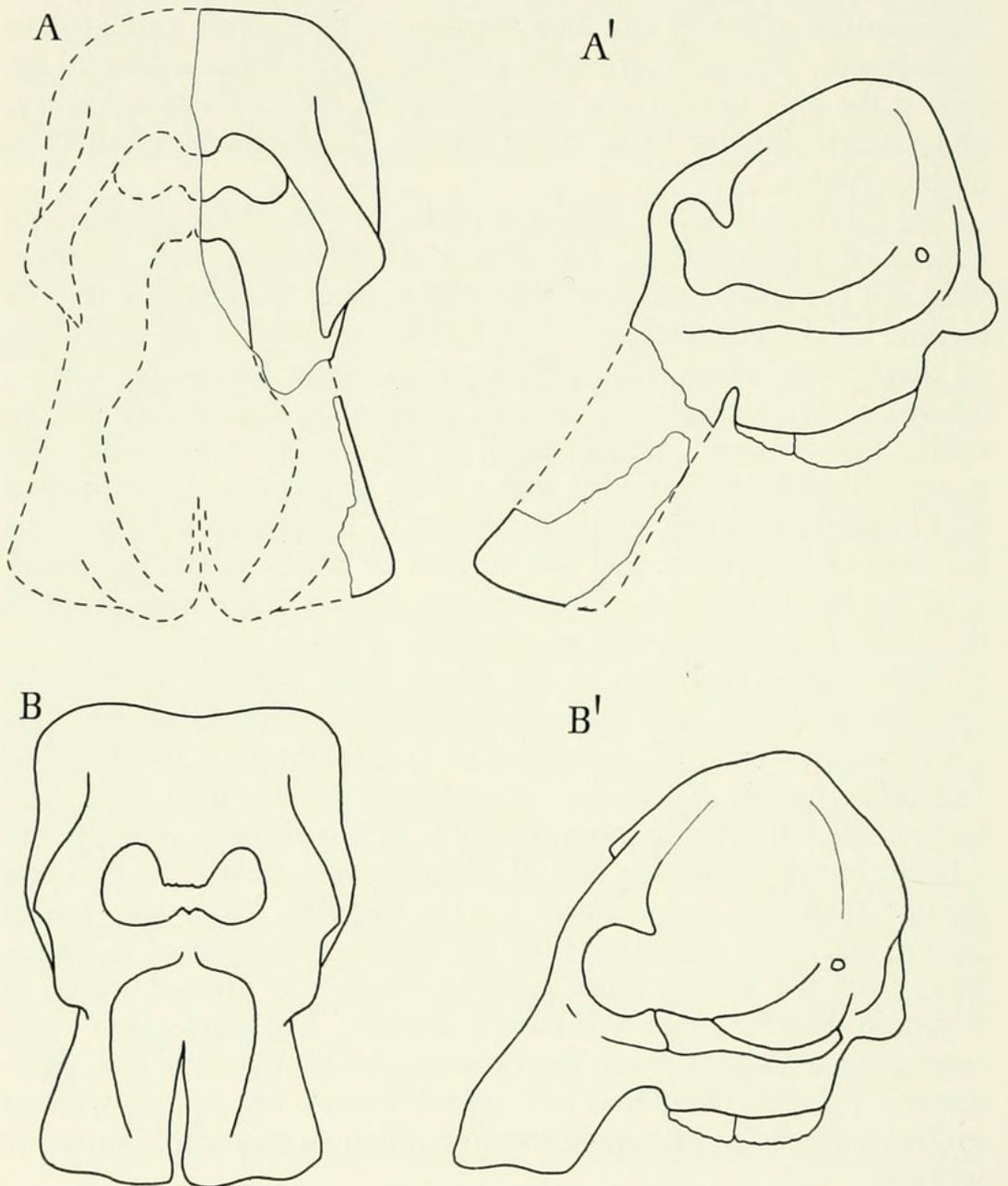


Figure 2. Diagrammatic representation of skull shape for two species of *Loxodonta*. A, *Loxodonta adaurora* sp. nov. B, *Loxodonta africana*. For each: left, anterior view; right, left-lateral view. A is based on PAL. LOTH. 353 (solid line) and PAL.KANAP. 385 (broken line). Not to scale.

more primitive than, *M. meridionalis*. The following cranial comparisons are made with the later species representing the *Mammuthus* type.

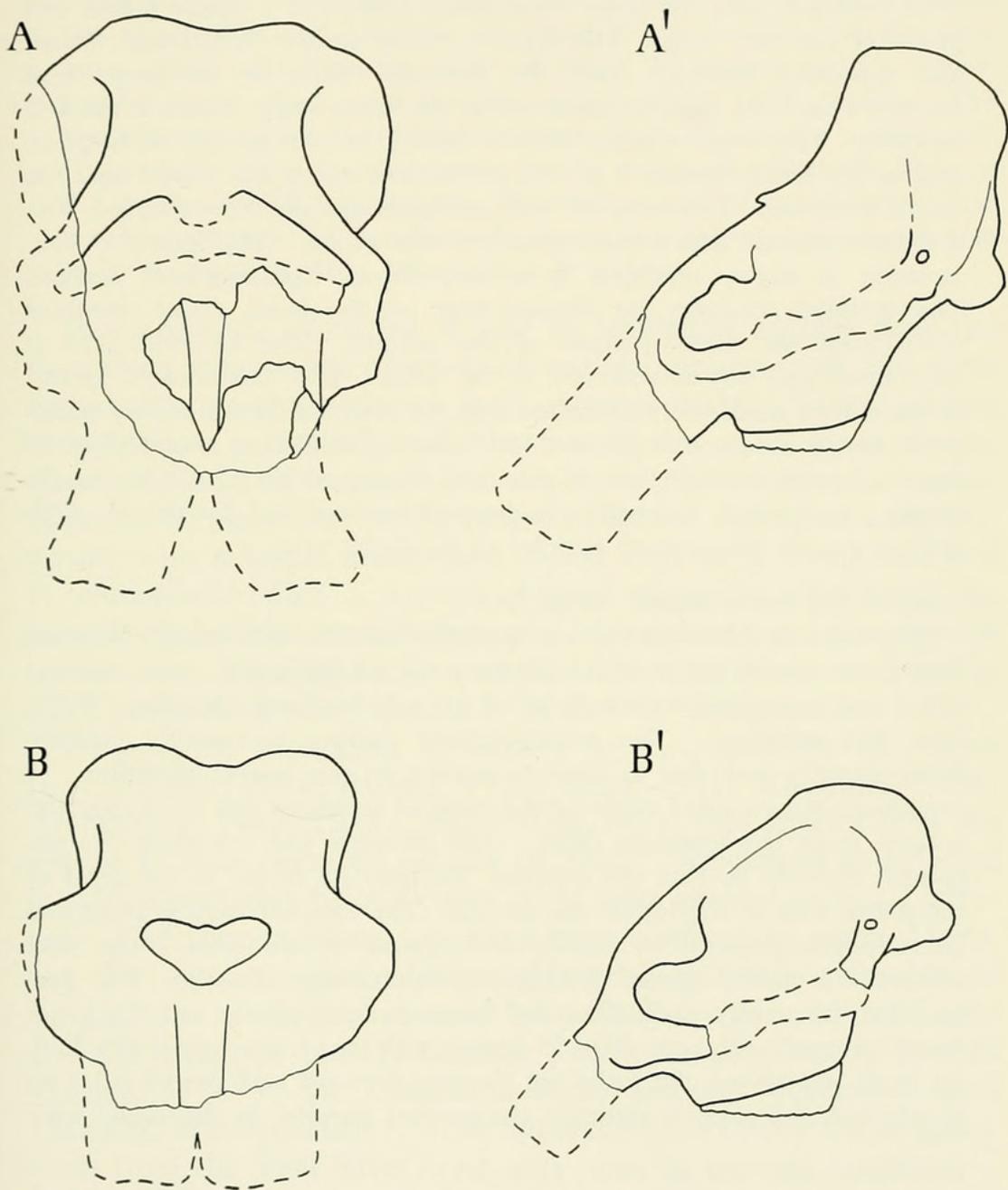


Figure 3. Diagrammatic representation of skull shape for early species of *Mammuthus* and *Elephas*. A, *Mammuthus meridionalis*. B, *Elephas planifrons*. For each: left, anterior view; right, left-lateral view. Reconstructions based on several specimens: A, Geol. Inst., Univ. of Florence Nos. 1049, 1051 and 1054. B, British Museum (N.H.) No. 3060 and Panjab Univ. specimen, no number.

Elephas planifrons, (Fig. 3B).

Although tusks are lacking from the four known skulls of this species, isolated incisors probably referable to it from the Siwalik Hills and an associated tusk with *planifrons* dentition from Bethlehem (Hooijer, 1958) indicate that the tusks were gently curved in a single plane, and probably not very large. The fronto-parietal surface is flat and broad, and separated laterally from the temporal fossa by a sharp ridge formed where the parietal bone makes an acute angle between the two surfaces. This ridge is more sharply defined in later species of *Elephas*, and in the living species it is very prominent along the lateral margins of the forehead. The parietals and occipitals are slightly expanded with a median-sagittal depression typical of this genus. The temporal constriction is slight, resulting in a very broad fronto-parietal surface. The occipital condyles are situated high on the head, about one-third down from the dorsal surface of the occiput. The external naris is very small and not downturned at the sides. The tusk sockets appear to have been moderately separated and the premaxillae are nearly parallel to the fronto-parietal plane. The latter is inclined at about 55 to 60 degrees to the vertical axis of the skull measured perpendicular to the palate. As a result, the tusks are directed forward and downward. The skull is greatly compressed parallel to the facial axis.

Mammuthus meridionalis. (Fig. 3A).

The tusks in *Mammuthus* are typically massive and spirally twisted. The tusks on the skull of *M. africanus* (Arambourg, pers. comm.) and a tusk associated with a molar of *M. subplanifrons* (Meiring, 1955), have this structure. The fronto-parietal surface is strongly concave dorsoventrally and flat to slightly convex in the lateral direction. A prominent but rounded angle of the parietal separates the fronto-parietal surface from the temporal fossa. The parietals and occipitals are expanded dorsally so that the occipital condyles lie closer to the level of the palate than to the top of the occiput. The external naris is large and laterally elongated; it is slightly downturned at the sides. The tusk sockets are closely spaced proximally, but diverge distally. The premaxillae are nearly parallel to the fronto-parietal plane, and the latter forms an angle of about 50 to 55 degrees with the vertical axis of the skull. As in *E. planifrons*, the tusks are directed forward and downward. As in *Elephas*, the skull is strongly compressed parallel to the facial axis.

Loxodonta adaurora sp. nov. (Fig. 2A)

The tusks are massive, but only gently curved upward, and are in a single plane. As in *L. africana*, the fronto-parietal surface is slightly convex in both the dorsoventral and lateral directions, but the frontal is proportionately longer, resembling *Elephas* more in this respect. As a result, the orbits are lower on the head than in *L. africana*. The forehead curves laterally into the temporal fossae without a sharp, angular border. The parietals are not expanded, nor is the occipital region which, like the living African species, is nearly flat posteriorly. The highest point of

the parietals is in the mid-sagittal line; there is no median depression. The temporal constriction is very slight, as in the recent species. The occipital condyles are low on the skull. The external naris is large and weakly downturned at the sides. Tusk sockets are widely separated and flaring distally; these are far more massive than in the living species. The premaxillae and maxillae are fused in the median line for their entire length and form an angle of about 20 degrees to the fronto-parietal plane. In *L. africana* this angle is about 15-20 degrees. The fronto-parietal plane is inclined at about 45 degrees to the vertical axis of the skull, and is therefore more nearly vertical in orientation than in *E. planifrons* or *M. meridionalis*. The skull is only slightly foreshortened in the anteroposterior direction and the skull is more nearly rounded in shape than it is in either *Mammuthus* or *Elephas*.

In *Loxodonta adaurora*, a pair of elongated cavities near the symphysis suggests the presence of vestigial incisive buds, but these apparently never developed into external tusks. These cavities communicate posteriorly with the mandibular canal by a narrow channel. Such structures have also been observed in two mandibles of *E. planifrons* in the Indian Museum. In those early elephants with external mandibular tusks, such as *E. celebensis* and *P. gomphotheroides*, a narrow channel passes forward from the anterior end of the mandibular canal into the enlarged alveolus for the incisor. Vestigial incisive cavities have not been observed in more progressive fossil species or in the two living species.

Despite the numerous references to *E. planifrons* in Africa (e.g. Joleaud, 1928; Romer, 1928; Kent, 1941; MacInnes, 1942; Arambourg, 1947, 1948a, and 1948b, etc.), that species does not appear to have occurred outside of Asia.* Specimens so referred in Africa probably belong either to *M. africanavus* or to *L. adaurora*. The former appears to have been confined to north Africa, but the data are inconclusive. Material probably referable to *L. adaurora* has been recovered from the Kaiso formation (Cooke and Coryndon, in press), Kanam, Yellow Sands (Omo), Laetolil (Maglio, 1969), the Chemeron beds, and the Chiwondo beds (Mawby, in preparation). (See appendix for a discussion of specimens from the Vaal River).

Morphologically, *L. adaurora* is distinct from *M. africanavus*, with which it is often confused on molar evidence alone. It appears to have been the dominant elephant during the late Pliocene and

* Specimens called *E. planifrons* from Europe belong to early stages of *M. meridionalis*.

early Pleistocene of east Africa but was quickly replaced by *Elephas recki*, which became the dominant species until middle Pleistocene times.

All evidence indicates a close relationship between *L. adaurora* and *Primelephas gomphotheroides*. Thus, *Loxodonta* appears to have differentiated very early in the history of the subfamily.

Elephas Linnaeus 1758

Type Species. *Elephas maximus* Linnaeus 1758.

*Elephas ekorensis** sp. nov.

(Pl. VII)

Type. PAL.EKA. 424, left and right M³.

Horizon and Locality. Plio-Pleistocene, Ekora beds, Ekora, Kenya.

Hypodigm. Type and PAL.KANAP. 387, partial right M³ and right M². PAL.KANAP. 395, partial left M³. PAL.EKA. 420, mandible with incomplete left M₂. PAL.KANAP. 412, incomplete right M².

Referred Material. PAL.EKA. 422, skull with eroded palate, lacking teeth.

Localities for Hypodigm. 420 and 422 from the type locality; 395, 387 and 412 from the top of the Kanapoi beds.

Diagnosis. Molars with crown height 10-25 per cent greater than width; M3 broader anteriorly, becoming very narrow posteriorly; anterior and posterior sinuses very prominent; enamel 3-4 mm thick and very weakly folded near the bases of the plates. Plates well separated with a lamellar frequency of about 3.5-4. Eleven plates plus a strong heel on M³. Skull compressed parallel to the fronto-parietal plane; parietals slightly expanded with a mid-sagittal depression; fronto-parietal surface strongly inclined to the vertical axis of the skull; external naris very large; strong fronto-parietal flanges forming a sharp angle between the forehead and temporal fossae; tusk sockets parallel, widely separated and parallel to the facial axis.

Discussion. The molars of *Elephas ekorensis* sp. nov. are clearly distinguishable from those of *Loxodonta adaurora*, with which they occur both in the upper part of Kanapoi and at Ekora. The plates in the former are thinner and more closely spaced, and the enamel is weakly folded on moderately worn plates. The

* *ekorensis* = the elephant from Ekora.

TABLE 3
Comparative measurements for M3 of *Loxodonta adaurora* sp. nov.,
Mammuthus africanavus and *Elephas planifrons*, in mm.

	<i>Loxodonta adaurora</i> sp. nov.		<i>Mammuthus africanavus</i>		<i>Elephas planifrons</i>	
	M ₃	M ₃	M ₃	M ₃	M ₃	M ₃
Length	228.1-302.2	277.1-305.1	?250-300	281.1-295.0	201.0-292.4	181.0-321.3
Enamel thickness	3.1-4.8	3.0-4.8	3.4-5.0	3.0-4.6	2.8-5.2	2.0-5.0
Lamellar frequency	2.5-3.9	2.9-3.9	3.0-4.9	3.6-4.9	2.6-5.5	3.3-5.8
No. of plates	8-10	10-11	9	10-11	9-12	9-13
Width	103.6-124.9	96.5-115.1	88.2-108.0	81.2-105.0	90.0-110.1	72.0-110.0
Height	90.4-109.2	90.1-103.0	84.1-103.2	97.9-114.3	83.0-129.0	75.0-116.0
H/W index	90-99	89-93	93-97	100-118	84-109	72-115

crown height is greater than the width and M3 narrows posteriorly, unlike that tooth in *L. adaurora*. The skulls of the two species are very different. In *E. ekorensis* (Fig. 4A), the premaxillae do not flare as in the Kanapoi species, the parietals are expanded laterally and dorsally with a median-sagittal depression as in *E. planifrons* (Fig. 4D), so that the brain case is widest in this region and not in the auditory region as in *L. adaurora*. The skull is compressed as in *E. planifrons* and *E. recki*, and contrasts with the more rounded skull of *L. adaurora*. The fronto-parietal axis of *E. ekorensis* is strongly inclined to the vertical axis of the skull, again in contrast to the condition in *Loxodonta*. The skull differs from that of *E. planifrons* in having more prominent, widely separated tusk sockets and a very large external naris.

As discussed elsewhere (Maglio, in press), the earliest recognizable stage of *E. recki* (stage 1 of 4 stages there recognized) occurs at Kikagati, Uganda. This form is close to *E. ekorensis*, but differs significantly in having proportionately thinner enamel, a greater lamellar frequency, and a proportionately higher crown. There also appears to have been a greater number of plates on M3. Abundant elephant remains, including skull material, from the White and Brown Sands localities at Omo probably represent stage 1 *recki*, but this material has not yet been studied in detail. The cranial remains are similar to the skulls of stage 2 *recki* described by Arambourg (1947) from the type Omo area (Coppens, pers. comm.), and in the following discussion comparisons of *E. ekorensis* are made with the latter material.

The skull of *E. ekorensis* differs from that of stage 2 *recki* (and probably stage 1 as well), though the differences are in degree only (Fig. 4A and B). The facial compression, expanded parietals, strong frontal flanges, parallel tusk sockets, and inclination of the facial axis to the vertical axis of the skull are characteristic features of the two species, but in *E. ekorensis* these are only weakly developed in comparison with *E. recki*. The fronto-parietal region in the Ekora species is still relatively flat; the anterior expansion of the parietals is not yet evident. In *recki*, the fronto-parietal area is concave anteroposteriorly because of the forward expansion of the parietal vault. The tusk sockets of *recki* are more closely spaced than in *E. ekorensis* and the external naris is larger and strongly downturned at the sides.

In both cranial and dental characteristics, *E. ekorensis* is considerably less progressive than *E. recki*. The Ekora sediments appear to be earlier than Tuff B at Omo, which is the earliest recorded occurrence of *E. recki*. An ancestral-descendent relationship between these two species is indicated by present evidence.

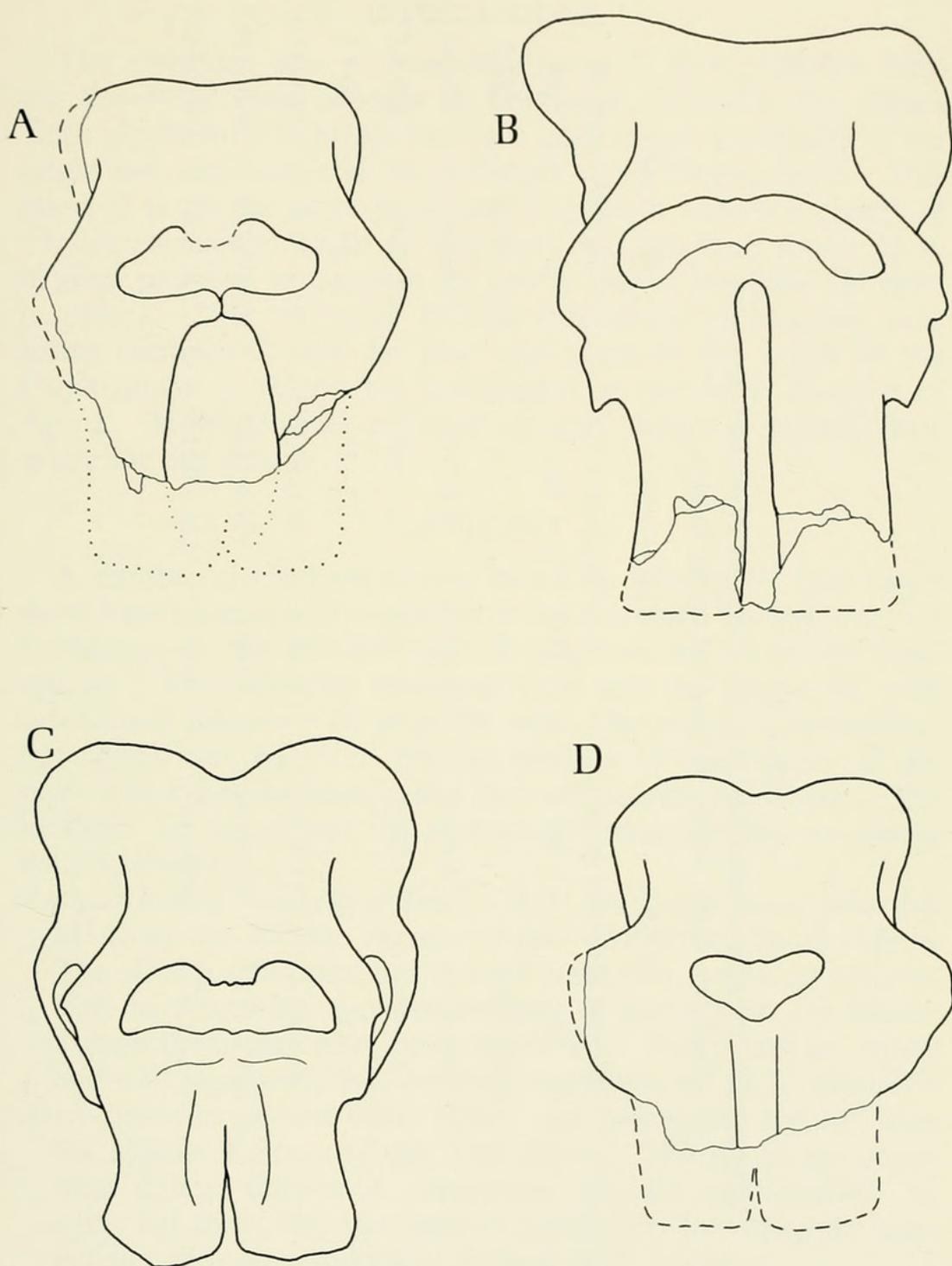


Figure 4. Diagrammatic comparison of skull shape for species of *Elephas*. A, *Elephas ekorensis* sp. nov. B, *Elephas recki*. C, *Elephas maximus*. D, *Elephas planifrons*. Anterior view. Reconstruction in dotted lines for A is conjectural. Not to scale.

TABLE 4
Comparative measurements for M3 for *Elephas ekorensis* sp. nov.
and two early stages of *Elephas recki*, in mm.

	EKORA		KIKAGATI		OMO	
	<i>Elephas ekorensis</i> sp. nov.		<i>E. recki</i> , stage 1		<i>E. recki</i> , stage 2	
	M ₃	M ₃	M ₃	M ₃	M ₃	M ₃
Length	276.9-304.1	—	—	—	205.7-265.0	228.0
Enamel thickness	3.0-4.6	3.4-4.2	2.9-3.1	2.8-3.4	3.0-4.0	2.5-3.5
Lamellar frequency	3.3-3.9	3.8-4.2	4.2	4.7-5.0	5.0-5.8	5.0-5.9
No. of plates	11	—	—	12-13?	12-14	12-13
Width	94.9-96.6	72.7-80.2	86.6	80.1-85.5	81.4-92.9	59.5-83.0
Height	105.6-113.2	87.5-102.3	103.1	104.8-112.2	109.1-127.0	85.0-120.2
H/W index	111.4-117.2	115.8-127.7	119.0	126.6-133.0	123.8-151.1	136.0-153.0

CONCLUSIONS

The abundant new proboscidean material now available from the Plio-Pleistocene deposits at Lothagam, Kanapoi, and Ekora helps significantly to bridge previous gaps in our knowledge of the origin and early stages in the evolution of the Elephantidae. This material is all the more important because it allows a means of relative correlation based on elephants that has been shown to be of great potential value, even for poorly known localities (Maglio, in press). The transition from gomphothere to elephant now seems established, and the time and place of the origin of the Elephantidae is reasonably determined as the later Pliocene of Africa. Morphological evidence strongly favors a monophyletic origin for this group.

APPENDIX

A number of elephant species based on incomplete type specimens have long caused confusion in the literature because they are inadequate to provide the kind of diagnosis necessary for fossil species. The following described taxa may be conspecific with *Loxodonta adaurora* or possibly with *Mammuthus africanavus*, but should not be given priority because of inadequacy of the types which are, in most cases, the only known specimens. The localities are vague and the stratigraphic relationships are essentially unknown.

Archidiskodon vanalpheni Dart, 1929. A single incomplete left M^3 from the Middle Terrace of the Vaal River, South Africa. The stratigraphic relationships are uncertain, and it is not possible to determine the total number of plates with confidence, though there may have been about ten. The plates are broad and well separated; the specimen resembles M^3 of *L. adaurora*.

Archidiskodon milletti Dart, 1929. An incomplete left M^3 from the Middle Terrace of the Vaal River. The plates are somewhat thinner than in *A. vanalpheni*, but not significantly. As with that form, the specimen is insufficient for adequate comparison with other material, without skull evidence.

Archidiskodon loxodontoides Dart, 1929. A single fragmentary left M^3 from the Middle Terrace of the Vaal River. From what remains this specimen appears to be close to the previous two forms, but specific diagnosis is not possible.

Loxodonta griqua Houghton, 1922. Several very fragmentary specimens from the Vaal River gravels, horizon unknown. This material is too incomplete to allow confident specific comparison with any other specimen. It was made the type of a new genus, *Metarchidiskodon*, by Osborn (1934).

From all available evidence, the above material appears to be close to east African material here referred to *Loxodonta adaurora*, and to specimens of *M. africanavus*, but specific identity with either can not be proved because of the incomplete morphological and stratigraphic data. The South African specimens have a greater lateral taper to the plates than do those of *L. adaurora* and in this respect are closer to *M. africanavus*. The types are inadequate for specific diagnosis and in view of the excellent and complete material from other localities, they should not be used as the basis for specific comparison with material for which stratigraphic data and associated faunas are known.

The names *A. vanalpheni*, *A. milletti*, *A. loxodontoides*, and *L. griqua* must be considered *nomina dubia*, and the names applied only to the type specimens.

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PLATES

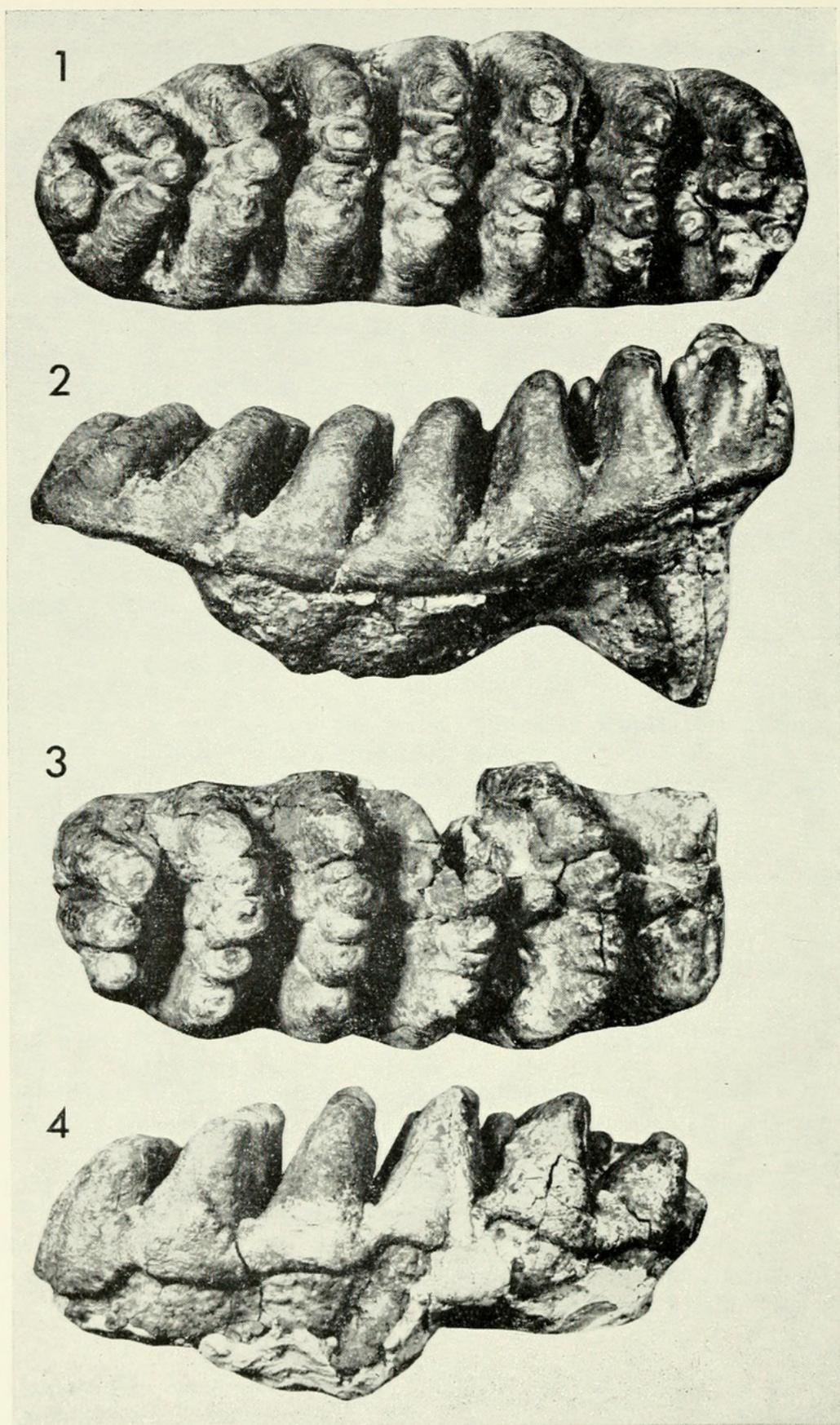


PLATE I

PLATE I

1. *Stegotetabelodon orbus* sp. nov. PAL.LOTH. 359, r.M₃. Occlusal view. $\times \frac{1}{3}$.

2. *Stegotetabelodon orbus* sp. nov. PAL.LOTH. 359, r.M₃. Buccal view. $\times \frac{1}{3}$.

3. *Stegotetabelodon orbus* sp. nov. PAL.LOTH. 359, 1.M³. Occlusal view. $\times \frac{1}{3}$.

4. *Stegotetabelodon orbus* sp. nov. PAL.LOTH. 359, 1.M³. Buccal view. $\times \frac{1}{3}$.

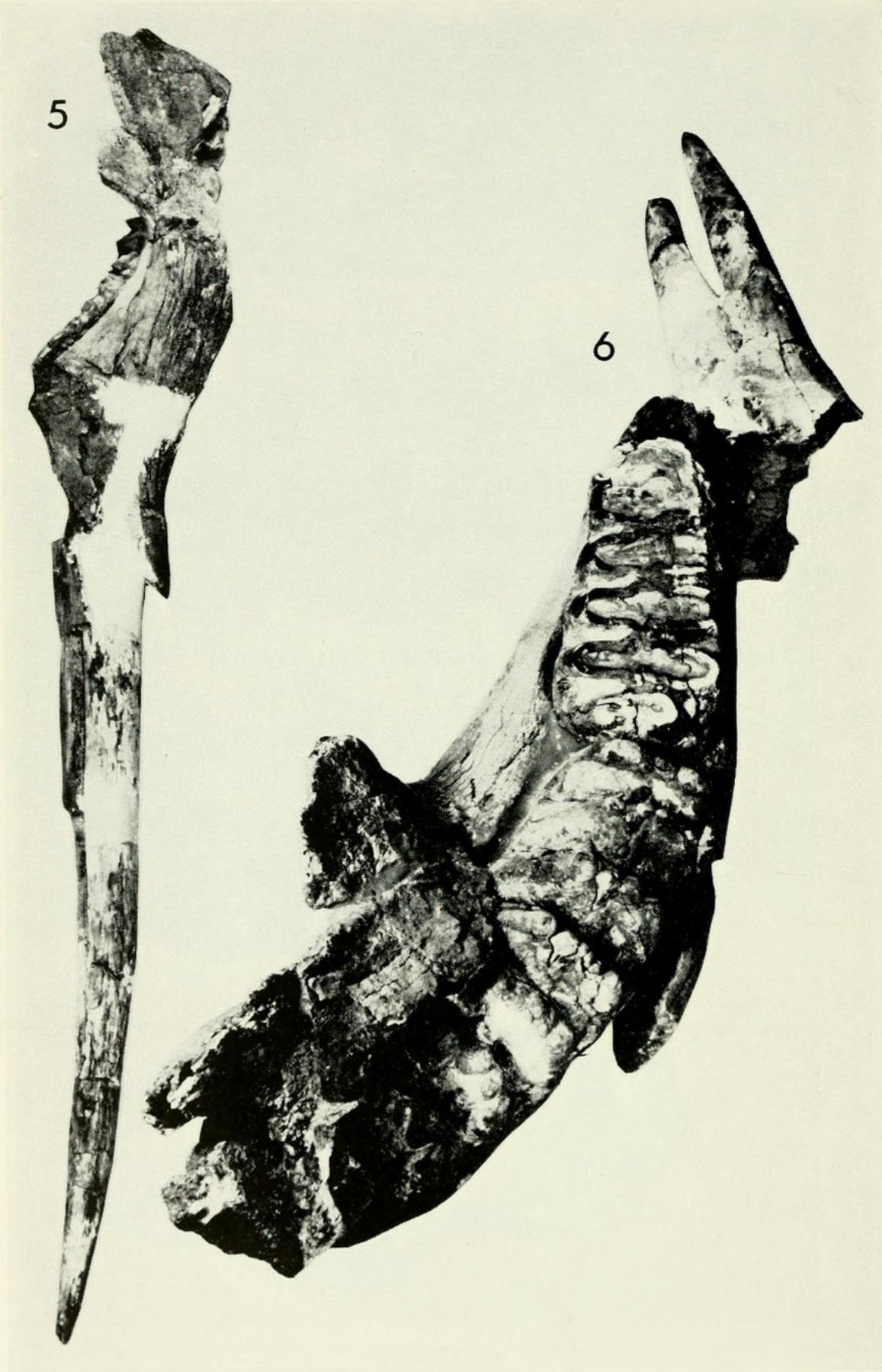


PLATE II

PLATE II

5. *Stegotrabelodon orbus* sp. nov. Type. PAL.LOTH. 354, mandible with M₂-M₃. Left-lateral view. Approx. $\times 1/10$.

6. *Stegotrabelodon orbus* sp. nov. Type. PAL.LOTH. 354, mandible with M₂-M₃. Dorsal view. Approx. $\times 1/4$.

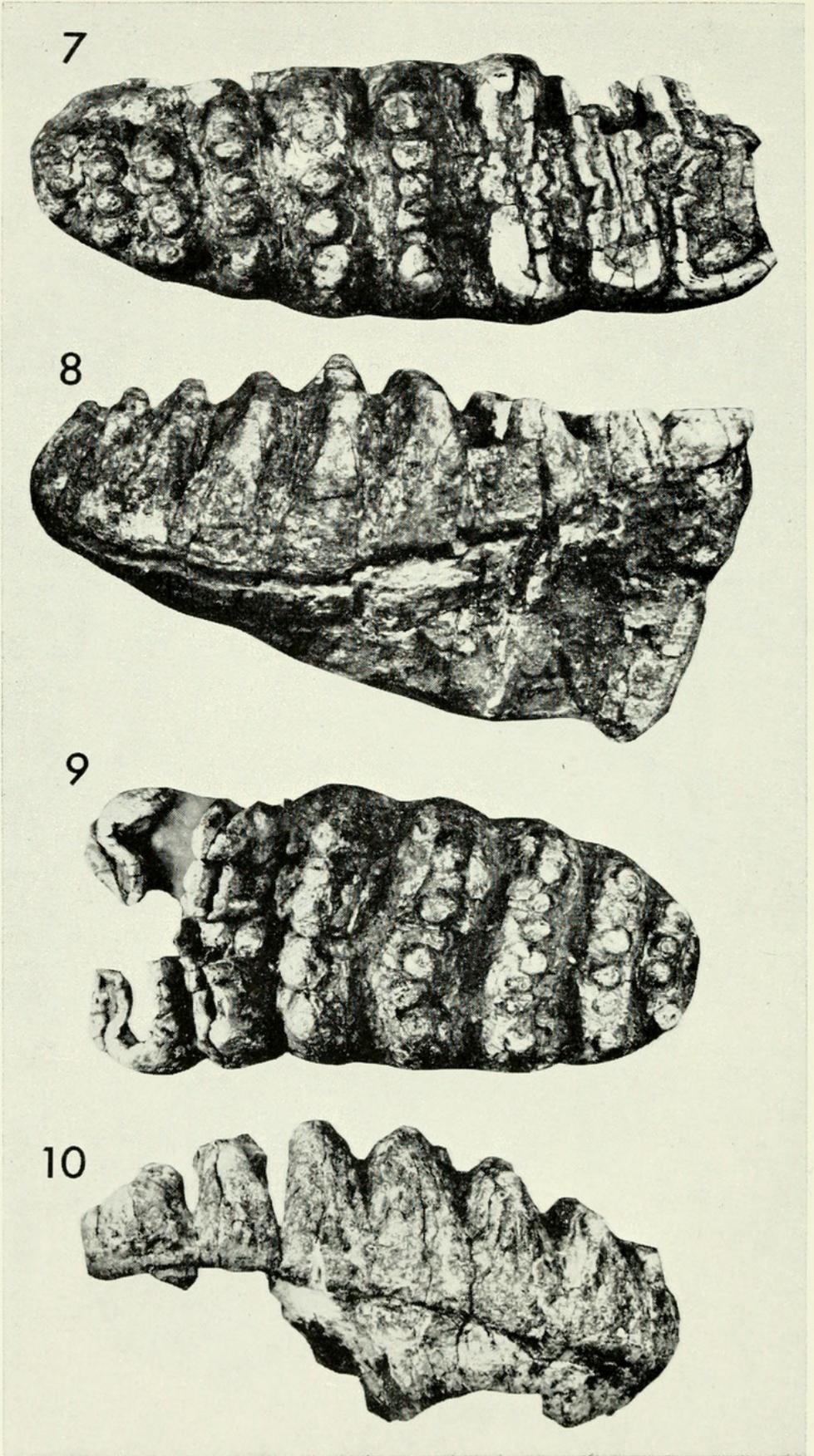


PLATE III

PLATE III

7. *Primelephas gomphotheroides* gen. et sp. nov. Type. PAL.LOTH. 351, 1.M₃. Occlusal view. $\times \frac{1}{3}$.

8. *Primelephas gomphotheroides* gen. et sp. nov. Type. PAL.LOTH. 351, 1.M₃. Lingual view. $\times \frac{1}{3}$.

9. *Primelephas gomphotheroides* gen. et sp. nov. Type. PAL.LOTH. 351, 1.M³. Occlusal view. $\times \frac{1}{3}$.

10. *Primelephas gomphotheroides* gen. et sp. nov. Type. PAL.LOTH. 351, 1.M³. Lingual view. $\times \frac{1}{3}$.

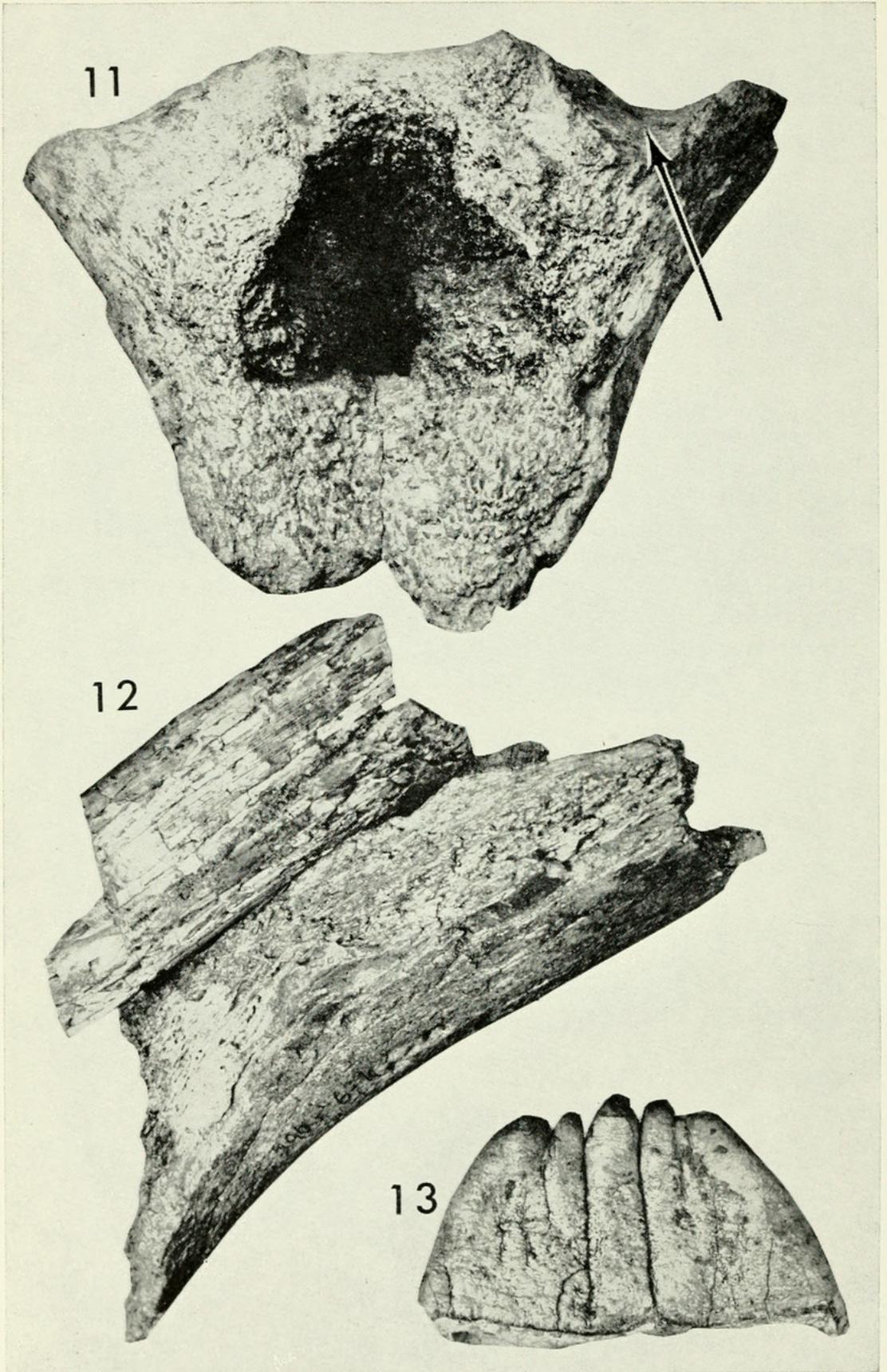


PLATE IV

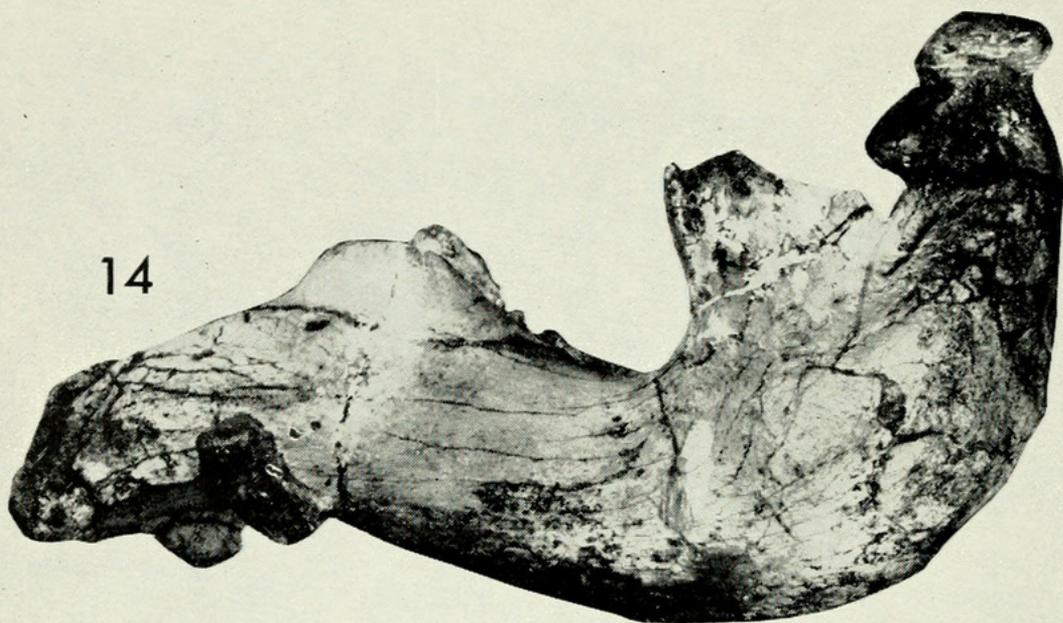
PLATE IV

11. *Primelephas gomphotheroides* gen. et sp. nov. PAL.LOTH. 358, fragmentary symphysis showing ventral border of incisive alveolus (arrow). Anterior view. Approx. $\times \frac{1}{2}$.

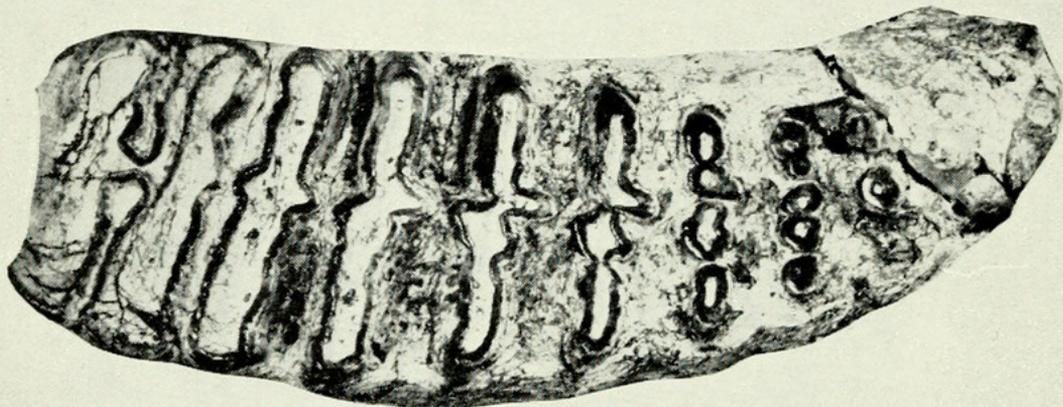
12. *Primelephas gomphotheroides* gen. et sp. nov. PAL.LOTH. 358, symphysis with partial left incisor in place. Left-lateral view. Approx. $\times \frac{1}{2}$.

13. *Primelephas gomphotheroides* gen. et sp. nov. PAL.LOTH. 376, isolated molar plate, ?M³. Anterior view. $\times \frac{1}{2}$.

14



15



16

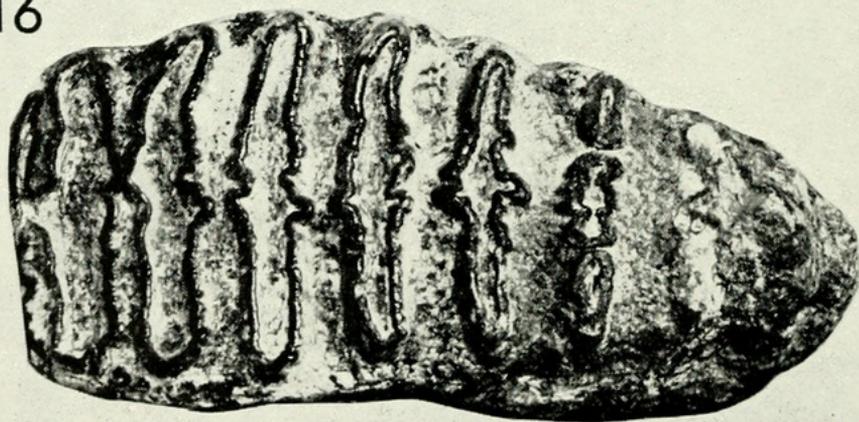


PLATE V

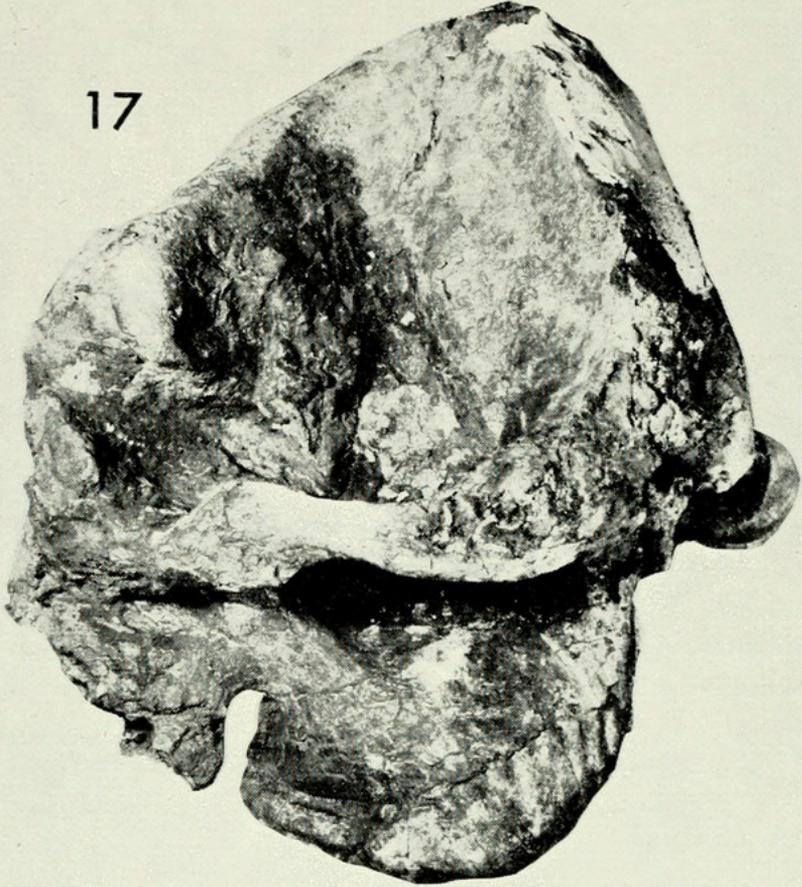
PLATE V

14. *Loxodonta adaurora* sp. nov. Type. PAL.KANAP. 385, mandible. Left-lateral view. Approx. $\times 1/7$.

15. *Loxodonta adaurora* sp. nov. Type. PAL.KANAP. 385, r.M₃. Occlusal view. $\times 1/3$.

16. *Loxodonta adaurora* sp. nov. Type. PAL.KANAP. 385, 1.M³. Occlusal view. $\times 1/3$.

17



18

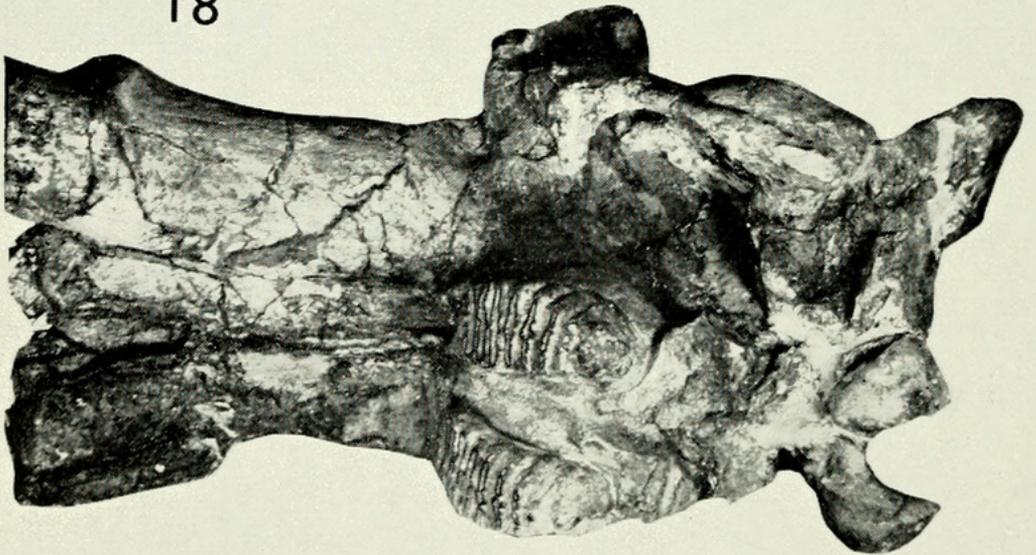


PLATE VI

PLATE VI

17. *Loxodonta adaurora* sp. nov. PAL.LOTH. 353, skull. Left-lateral view. Approx. $\times 1/9$.

18. *Loxodonta adaurora* sp. nov. Type. PAL.KANAP. 385, skull. Ventral view. Approx. $\times 1/11$.

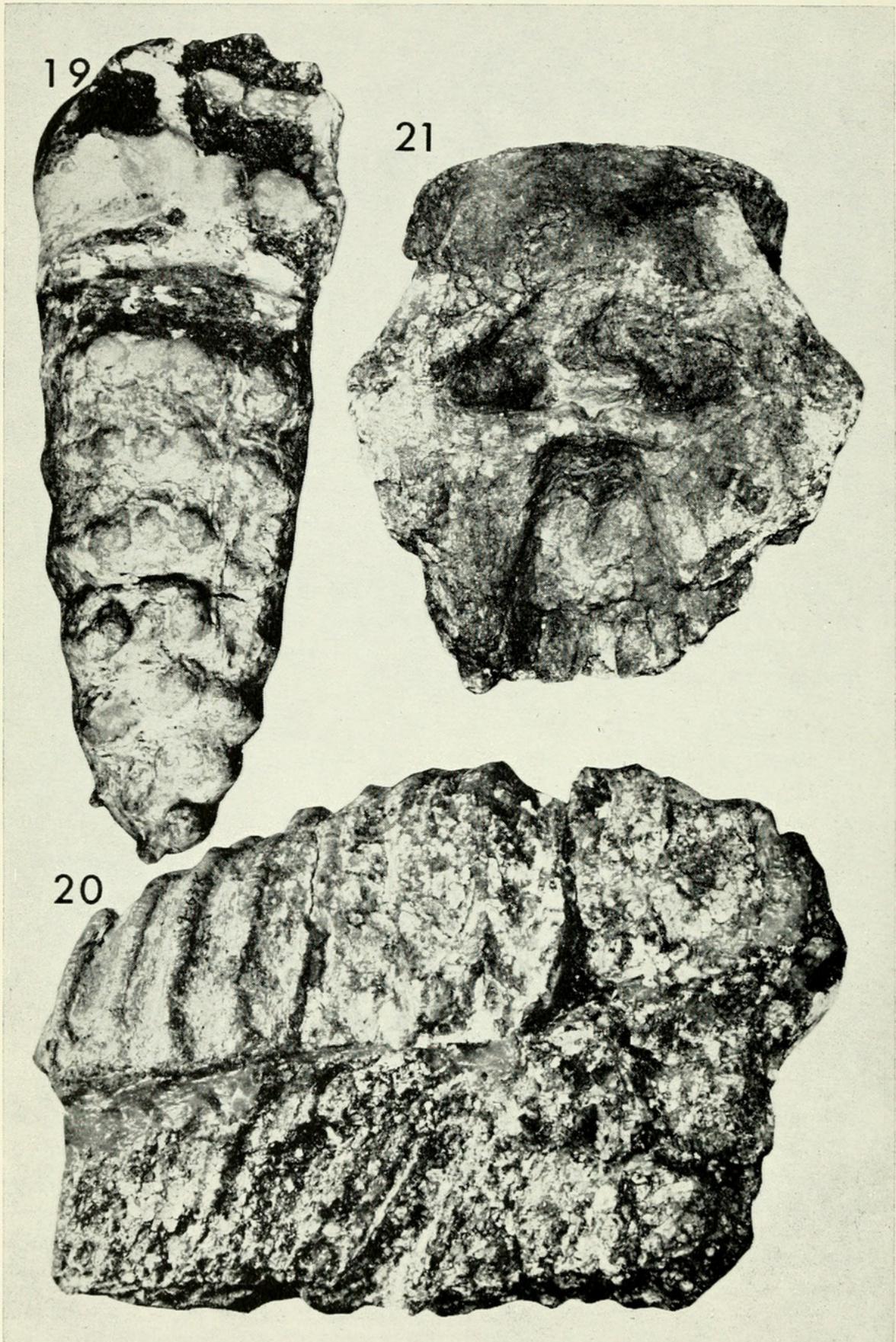


PLATE VII

PLATE VII

19. *Elephas ekorensis* sp. nov. Type. PALEKA. 424, r.M³. Occlusal view. $\times \frac{1}{3}$.

20. *Elephas ekorensis* sp. nov. Type. PALEKA. 424, r.M³. Lingual view. $\times \frac{1}{3}$.

21. *Elephas ekorensis* sp. nov. PALEKA. 422, skull. Anterior view. Approx. $\times \frac{1}{10}$.



Maglio, Vincent J. 1970. "Four new species of elephantidae from the Plio-Pleistocene of northwestern Kenya." *Breviora* 341, 1-43.

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