

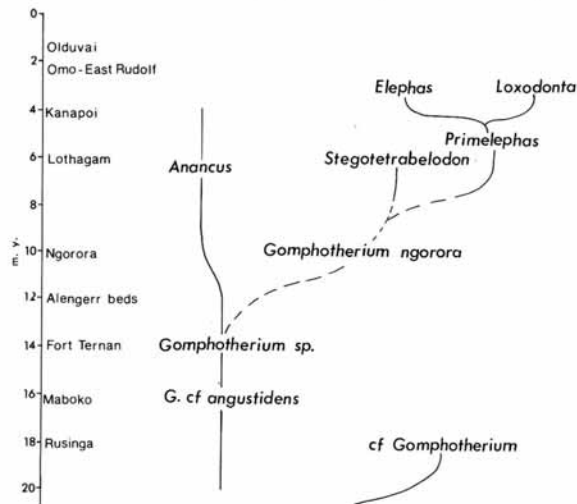
A NEW PROBOSCIDEAN FROM THE LATE MIOCENE OF KENYA

by VINCENT J. MAGLIO

ABSTRACT. A new species of proboscidean, *Gomphotherium ngorora*, is described from the Ngorora Formation which has been K/Ar dated provisionally between 9 and 12 m.y. BP. This new material helps to bridge the morphological gap between the earlier Miocene gomphotheres of Africa and early Pliocene elephants. It confirms earlier views on the origin of the family Elephantidae.

THE late Miocene epoch, between 14 and 6 m.y. ago, was perhaps the most important period in the development of the modern African fauna. Yet, until recently it has remained the poorest known period. Since 1965 a detailed programme of mapping in the Lake Baringo region of the Gregory Rift, central Kenya, has been undertaken by the East African Geological Research Unit based at Bedford College, University of London. The programme has led to the discovery and further investigation of a series of fossiliferous sedimentary units, and potassium-argon ages have been established for associated lavas (Bishop *et al.* 1971; Bishop 1972).

The Lake Baringo sequence consists of twelve sedimentary units ranging in age from 12 to 14 m.y. for the Alengerr beds to less than 0.23 m.y. for the Kapthurin Formation. Large assemblages of mammals occur only in four of these units and a significant gap still remains between 10 and 6 m.y. (text-fig. 1). Nevertheless, the



TEXT-FIG. 1. Suggested phyletic relationships between Miocene gomphotheres of Africa and the earliest elephantids *Stegotetrabelodon* and *Primelephas*. The genus *Anancus* is a late specialization of the Gomphotheriidae.

importance of the Baringo sequence in narrowing this void, and its potential for further closing it, is now being amply demonstrated.

One of the most important of the Baringo units is the Ngorora Formation which was first described by Bishop and Chapman (1970). The formation consists of five members ranging from clays and bedded tuffs at the base (A), through ferruginous channel-conglomerates and grits (B), to tuffaceous silts (C), another series of channel-conglomerates (D), and a capping unit of diatomites and grits (E). Vertebrate fossils are usually concentrated in the channel-conglomerates, but chelonian and fish remains occur abundantly in other units as well. Preliminary potassium-argon determinations for phonolite lavas occurring above and below the Ngorora Formation suggest an age for the deposit of somewhat less than 12 m.y., but greater than 9 m.y. A preliminary faunal list has been recorded by Bishop *et al.* (1971), but much new material has been recovered recently and significant additions to the list will be published shortly. Among the new materials is a proboscidean collected in 1972 by M. Pickford that provides clear confirmation of a gomphotheriid origin for the later elephants. Mr. Pickford has kindly provided the following description of the locality:

The specimen was found on the surface having been derived from a clay horizon the upper part of which graded into a calcrete. The horizon is in a sequence of rhythmic units with alternating coarse pumiceous beds and fine-grained suncracked and frequently calcified lacustrine sediments containing numerous comminuted fish remains. Stratigraphically, it lies in Member E of the Ngorora Formation.

DESCRIPTION

Order PROBOSCIDEA

Family GOMPHOTHERIIDAE

Genus GOMPHOTHERIUM

Gomphotherium ngorora sp. nov.

Plate 100, figs. 1-3

Holotype. KNM-BN 571 and 577, right maxillary fragment with complete M²-M³, posterior part of left M³; KNM-BN 567 and 584B, proximal one-fourth of the left radius and ulna; fragmentary pieces of vertebrae, ribs, carpal bones, and maxillary tusks, all specimens from a single individual. Housed in the National Museum of Kenya.

Type horizon and locality. Upper Miocene of the Ngorora Formation, site 2/49A, Baringo District, central Kenya.

Diagnosis. A species of *Gomphotherium* bearing three cone-pairs on M² and four on M³; pre- and post-trite cones transversely elongated and antero-posteriorly compressed forming very elephant-like plate structures; each cone subdivided into two or three parts by deep anterior and posterior vertical grooves, forming a transverse series of adjacently fused pillars; intravalley columns prominent, isolated apically but fused into cones basally; median clefts persistent between all cone-pairs but very

EXPLANATION OF PLATE 100

Figs. 1-3. *Gomphotherium ngorora* sp. nov., KNM-BN 571 and 577, holotype, right M²-M³. 1, buccal view. 2, occlusal view. 3, lingual view.



MAGLIO, *Gomphotherium*

tightly compressed at apex; enamel thick and smooth except toward base of crown where it becomes coarsely folded; cement present in valley troughs.

Description. *Gomphotherium ngorora* is in many ways a typical gomphothere in which the molar teeth are subdivided into three or four cone-pairs (Pl. 100). Each cone-pair is separated from others by a broad transverse valley. Also typical of the Gomphotheriidae are the isolated enamel columns standing in the transverse valleys and rising to the height of the principal cones. Similar features are seen in East African Miocene gomphotheres (below) and are characteristic of the family.

More advanced elephant-like trends are also seen here which suggest that we are sampling a population that has already diverged from the main gomphotheriid stem. In the upper molars there are three cone-pairs on M^2 and four pairs on M^3 . These are drawn out transversely with the median cleft tightly compressed between buccal and lingual components. This antero-posterior compression results in a plate-like arrangement of enamel folds not seen elsewhere in the family to this degree.

The buccal cone of each pair is swollen basally and subdivided into three parts by vertical grooves on the anterior and posterior surfaces. These subdivisions form free pillars apically, but these fuse into a single transversely elongated hemi-plate as wear proceeds to about one-third of the crown height. The buccal-most division in each case is the largest. In all other known Miocene gomphotheres from Africa, including the Fort Ternan species, the buccal cones are only vaguely grooved and slightly compressed in the fore and aft direction, and the general structure remains that of a cone, not a flattened plate.

The lingual cone of each pair is subdivided into two unequal parts on the first several pairs, but may remain as a single rounded cone on the last pair, as it is on all lingual cones of the Fort Ternan, Rusinga, and Maboko species. Toward the crown base both lingual and buccal cones arise from a common enamel fold so that in heavy wear even the median cleft would be obliterated and a single flattened enamel loop would remain on the occlusal surface. A posterior fold with several small enamel pillars represents the early development of a fifth cone-pair.

These structural features are even more pronounced on the M^3 in which wear has progressed further; the lingual and buccal cones have joined or nearly joined in the mid-line. By the time wear has proceeded to the lower quarter of the crown height a continuous enamel plate remains on the occlusal surface.

The result of these trends is the establishment of a transverse arrangement of enamel and dentine bands with cutting surfaces deployed for a more fore and aft masticatory function. This was the principal feature of the adaptive shift that accompanied the rise of the Elephantidae (Maglio 1972). It is seen in no other proboscidean group except the stegodonts of Asia. However, the Ngorora specimen retains prominent intravalley columns which remain free along their apical half, fusing into the plate-like cone-pairs below. Such structures are always seen on the anterior half of early elephant molars, but never in stegodonts.

Of the post-cranial remains only the radius and ulna fragments are worthy of special mention. The ulna is relatively massive with a very deep interarticular sulcus which separates the capitular and trochlear facets nearly to the base of the short olecranon process. The latter is broad antero-posteriorly and terminates at a large

bulbous rugosity for insertion of the triceps muscle. An oval, flat facet for articulation with the radius is found on the medial side of the capitular facet only; the radius did not fill the interarticular sulcus as it does generally in elephants. These bones resemble more closely the comparable elements of *Gomphotherium* than they do any of the elephants. However, little post-cranial material of any fossil proboscideans has been properly described, and virtually none is available with positively identified dental remains from the African Miocene. The present material thus adds little to our knowledge of the Ngorora species other than to confirm its gomphotheriid affinities.

Although the Ngorora specimen shows a number of elephant-like features, it remains close to other Miocene gomphotheres in basic structure. A number of generic names have been applied to these forms, but until a revision of this group is undertaken it is best to refer the present specimen to the genus *Gomphotherium*.

Dimensions (in mm) of holotype dentition of *Gomphotherium ngorora*, KNM-BN 571 and 577.

| | M ³ (577) | M ² (571) |
|------------------|----------------------|----------------------|
| Cone-pairs | 4X | 3X |
| Overall length | 147.4 | 98.5 |
| Maximum width | 85.4 | 75.8 |
| Maximum height | 61.3 | .. |
| Enamel thickness | .. | 4.0-4.9 |

DISCUSSION

The African Miocene Proboscidea were last reviewed by MacInnes (1942) when he referred material from Rusinga and Maboko to the European species *Gomphotherium angustidens*. He proposed the subspecific name *G. angustidens kisumuensis* for this material from East Africa.

In 1945 Arambourg recognized in MacInnes's 1942 figured hypodigm what he considered to be a distinct morphotype in which the cone-pairs were tending toward alternation of lingual and buccal cones. This condition is seen in exaggerated form in the Pliocene and Pleistocene genus *Anancus*. Arambourg proposed the new name *Protanancus macinnesi* for this material, designating specific figures from MacInnes's monograph as his hypodigm.

An examination of the original collection by the present author does not support Arambourg's contention. Contrary to MacInnes's original analysis, there are two distinct species involved, but their distribution and diagnostic features are not as proposed by Arambourg. This is not the place to go into a review of the Miocene gomphotheres of Africa as the group has not yet been adequately studied, and most of the material is yet to be described. It is clear, however, that the Rusinga species was already specialized in a direction away from the later anancine gomphotheres and elephants, and paralleling the kinds of dental characteristics seen in the Mammutidae. The latter family, long believed to have been excluded from sub-Saharan Africa, is now known to have been present there in early Miocene times, as evidenced by specimens from Napak (W. W. Bishop pers. comm.) and from Moroto 1 and Lothidok (C. Madden pers. comm.). It is possible that the Rusinga material may prove to have been related to early differentiation of this family.

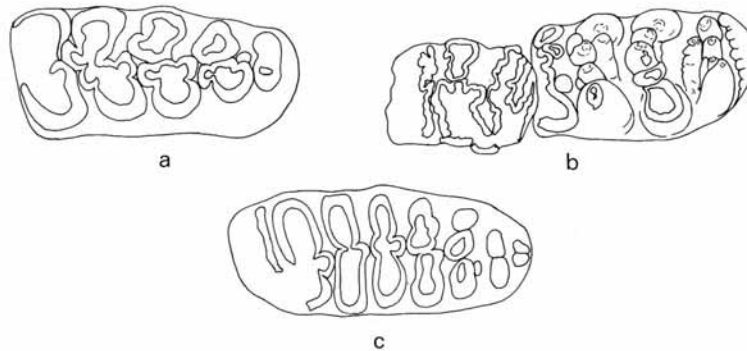
The Maboko proboscidean assemblage, which derives from a somewhat younger

horizon than that from Rusinga (MacInnes 1942; Bishop 1967), retains its distinctive gomphothere dental structures and could easily have been ancestral to the form represented in the younger Fort Ternan deposits.

The Ngorora specimen, younger than the Fort Ternan species, departs from the gomphothere pattern in the development of those features mentioned above, strongly indicative of an approach to the grade seen later in the Elephantidae. The latter family includes the living Asiatic and African elephants, the Pleistocene mammoths, and their extinct relatives. Until recent years the group's ancestry was poorly known and it was believed to have derived from Asiatic stegodonts. On the basis of rather incomplete fossil evidence from Africa, Aguirre (1969) proposed a gomphotheriid ancestry for elephants in Africa via the stegolophodonts. This general picture was later supported with better material from East Africa but it was argued that *Stegolophodon* could not have provided a transitional stage (Maglio 1970). The latter genus is here considered to represent an early stage of the *Stegodon* group.

The origin of elephants, like so many other groups in Africa, has been difficult to interpret because of the 8 m.y. gap in the late Miocene African record. Prior to the gap a series of gomphotheres can be traced through fragmentary evidence from early Miocene deposits at Mfwanganu, Karunga, Maboko and others, to the middle Miocene at Fort Ternan. During this period of some 7 or 8 m.y. a considerable degree of evolution is seen in crown height and molar complexity. After a gap of about 8 m.y. the earliest elephantids of the genera *Primelephas* and *Stegotrabelodon* are recorded at Lothagam (Maglio 1970), Sahabi (Petrocchi 1941), and at several other localities (Bishop 1972). This material is clearly indicative of a gomphotheriid ancestry (Maglio 1973), but no intermediates were known until now.

The Ngorora proboscidean provides this transitional stage (text-figs. 1, 2). From this morphological grade the elephant molar could have been derived merely by an increase in number of cone-pairs, the further obliteration of the median cleft, and



TEXT-FIG. 2. Diagrammatic crown views of proboscidean molar teeth showing major evolutionary trends in thinning of enamel, reduction of intravalley columns, and consolidation of cone-pairs into plates. *a*, *Gomphotherium angustidens*; *b*, *Gomphotherium ngorora* sp. nov.; *c*, *Stegotrabelodon orbus*.

loss of intravalley columns so that only one remains behind each plate. All of these trends are well under way in the Ngorora specimen.

Because of its geological and morphological position it seems reasonable to suggest that *Gomphotherium ngorora* may be close to a true intermediate stage in the evolution of the Elephantidae in Africa. The swollen cone-pair bases and abrupt apical tapering more closely resemble the plate structure in *Primelephas* than in *Stegotetrabelodon*. However, it is too early to be certain whether *G. ngorora* gave rise to the Elephantidae directly or via the *Stegotetrabelodontinae* as a transitional group, if indeed it is itself on the main-line phyletic lineage.

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