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*Fossil Mammals of Africa*

No. 15

MIOCENE RUMINANTS  
OF EAST AFRICA

T. WHITWORTH

LONDON

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OF EAST AFRICA

BY

T. WHITWORTH

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## FOSSIL MAMMALS OF AFRICA

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## I. INTRODUCTION AND ACKNOWLEDGMENTS

The fossil ruminants described in this paper were collected from Miocene deposits in East Africa between 1933 and 1952. The principal fossiliferous areas are indicated in Text-fig. 1. Their geology has been described by Oswald (1914), Kent (1944),

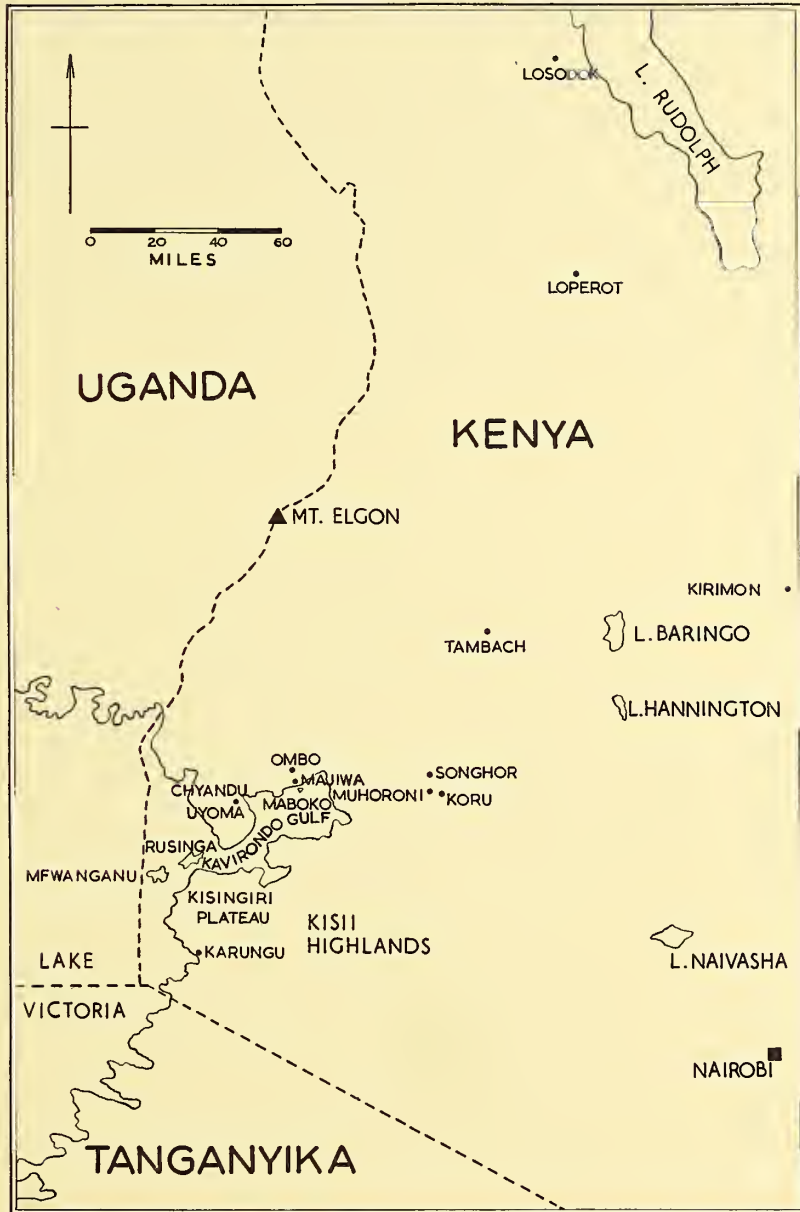


FIG. 1. Map of part of East Africa showing the fossiliferous areas.

Shackleton (1951) and Whitworth (1953). A list of the associated Miocene fauna, together with an account of the stratigraphical relationships of the numerous fossiliferous sites on Rusinga Island, has been supplied by Le Gros Clark & Leakey (1951: 5, 9-10).

## INTRODUCTION AND ACKNOWLEDGMENTS

The greater part of the ruminant material belongs to the Coryndon Museum, Nairobi. Specimens which are the property of the Palaeontological Department, British Museum (Natural History) are distinguished by a registration number which is preceded by the letters B.M. Other prefixes refer to the area in which a specimen was collected: K=Karungu, Mw or Mfw=Mfwanganu, R=Rusinga, Mb or Kb=Maboko, Om=Ombo, Ko=Koru, S or Sgr=Songhor, Kir=Kirimon and Mt=Muruorot which is situated a short distance south of Losodok.

For descriptive purposes, the Cope-Osborn system of dental nomenclature is employed, with additional premolar terminology borrowed from Loomis (1925). The classification is based on that of Simpson (1945). All dimensions given in the text are recorded in millimetres, and are always maxima.

I wish to express my thanks to Dr. A. Tindell Hopwood, Dr. L. S. B. Leakey and Dr. W. D. L. Ride for the valuable advice they have given me during the preparation of this paper. I am indebted to Miss Christine Court and to Miss Margery Beck for many of the figures which illustrate the text.

## II. SYSTEMATIC DESCRIPTION

### Family TRAGULIDAE Milne-Edwards, 1864

#### *DORCATHERIUM* Kaup, 1833, emend.

DIAGNOSIS.—Tragulids of varied size. Median metacarpals distinct; median metatarsals coalesced, but retaining separate medullae. Navicular, cuboid and external cuneiform of tarsus usually fused, but external cuneiform occasionally separate; internal cuneiform always distinct. Dental formula normally  $\frac{0 \ 1 \ 3 \ 3}{3 \ 1 \ 4 \ 3}$ ,  $P_1$  sometimes absent. Molar teeth as in Recent tragulids, but more bunoid in larger species of *Dorcatherium*. Median, external, accessory styloid may be present in lower molars, more often absent. Premolars usually longer, relative to breadth, than in Recent tragulids. Upper canine of male large, recurved, trenchant.

TYPE SPECIES.—*Dorcatherium nauii* Kaup, 1833.

DISCUSSION.—The definition of *Dorcatherium* has been emended in order to embrace the new traguline material from western Kenya. Thomas (1916) concluded that only one character distinguished *Dorcatherium* from the Recent African genus *Hyemoschus* Gray, 1845, namely, the presence of a first lower premolar in the former genus; but it has been shown by Roman & Viret (1934) that the tooth is often absent in individuals of *Dorcatherium crassum* (see also Milne-Edwards, 1864: 144, pl. 11, fig. 2b). It is probable that the Miocene tragulids from East Africa provide additional examples of this partial suppression of the first lower premolar. The diagnosis of *Dorcatherium*, when thus emended, agrees almost exactly with that of *Hyemoschus*, and it could be argued that all Recent African species of chevrotains must revert to the prior name *Dorcatherium*. Here, it is considered that the Recent and Miocene tragulids are sufficiently isolated in time to warrant the retention of the generic name, *Hyemoschus*. The partial persistence of  $P_1$  in *Dorcatherium*, the greater variety in size exhibited by the fossil species, and the occasional preservation of primitive characters in the teeth and ankle joint of *Dorcatherium*, all influence this decision, but cannot be employed in formal diagnosis.

Traguline jaw fragments from the Miocene beds of Rusinga Island are very numerous. On the basis of size, they fall into three distinct and homogeneous groups. The effects of sexual dimorphism cannot be determined, and each of these groups is treated here as a separate species. One is referred provisionally to *Dorcatherium chappuisi* Arambourg, the others are given the new names, *D. pigotti* and *D. parvum*. The existence of these three distinct groups is confirmed by a corresponding trimodal distribution of size in the numerous isolated traguline limb bones collected at Rusinga (see p. 38).

A fourth group of traguline material has been collected from the Miocene of Songhor, 80 miles east of Rusinga Island. The Songhor teeth are intermediate in size between those of *Dorcatherium parvum* and *D. pigotti*, and their dimensions also exhibit a normal distribution. The material from Songhor is segregated under the new specific name *Dorcatherium songhorensis*; firstly, because it can be distinguished quantitatively, and secondly, because it is possible that there may be some slight age or facies difference between the fossiliferous deposits at Songhor and Rusinga (see



p. 46). Further collecting may show that *D. songhorensis* is synonymous with *D. parvum* or with *D. pigotti*, but for the present it seems preferable to treat the Songhor material separately.

***Dorcatherium chappuisi*** Arambourg, 1933.

(Text-figs. 2, 3)

DIAGNOSIS.—A large species of *Dorcatherium*, individuals approximately equal in size to an adult roe deer. Length of lower molar series ( $M_{1-3}$ ) about 43 mm.

DISCUSSION.—The numerous specimens from western Kenya described below are similar to the contemporaneous European species, *Dorcatherium crassum* (Lartet), but differ slightly in size and in the crown pattern of the cheek teeth. Furthermore, the evidence of associated limb bones (p. 41) suggests that this African form retained an independent ectocuneiform bone in the tarsal joint. In *D. crassum*, the ectocuneiform is fused with the cubo-navicular bone.

The most detailed resemblance to the Rusinga specimens is found in the Miocene *Dorcatherium chappuisi* Arambourg from northern Kenya. The holotypic mandible of *D. chappuisi*, however, retains a first lower premolar. The anterior portion of the mandible is very rarely preserved among the remains of large fossil tragulids found at Rusinga Island. In most specimens, it is impossible to determine whether the first lower premolar was present or absent, but it seems likely that the tooth was lacking in at least some individuals. On the other hand, a single specimen possessing a first lower premolar (Text-fig. 3a, b) has been recovered at Maboko Island, and is placed, on morphological grounds, with the material from Rusinga. A partial suppression of the first lower premolar has already been described in *Dorcatherium crassum* by Roman & Viret (1934). It is possible that a similar condition may have existed in *D. chappuisi*, and the Rusinga material is referred, provisionally, to that species. It is unfortunate that Arambourg's material of *D. chappuisi* does not include limb bones for comparison with the large tragulid limb bones found at Rusinga Island.

DISTRIBUTION.—The holotype of *Dorcatherium chappuisi* (right mandibular ramus with  $P_1$  to  $M_3$ , in the Muséum national d'Histoire Naturelle, Paris) was recovered from the Lower Miocene of Losodok, northern Kenya. There are 82 specimens from Rusinga Island which are assigned provisionally to this species, and form the basis of the succeeding description. In 13 examples, the exact geological horizon is unknown. The remainder were distributed stratigraphically as follows: Kathwanga Series (youngest Miocene sediments on Rusinga) 35; Hiwegi Beds 30; Kiahera Series (oldest Miocene sediments on Rusinga) 4. A similar distribution is common to most of the ruminant species found at Rusinga. The Kathwanga sediments are of a type in which fossils are likely to be well preserved (water-laid flags and clays), and probably reflect less arid conditions than the two older formations.

A single specimen from neighbouring Mfwanganu Island and 3 specimens from Maboko Island are also placed, tentatively, with the Rusinga material, and their features are incorporated in the following account.

The new material from western Kenya includes fragments of mandibles and maxillae, and a number of isolated cheek teeth. The anterior dentition of *Dorcatherium chappuisi* is unknown.

LOWER DENTITION AND MANDIBLE.—The mandible is shallow, and the lower cheek teeth form a closed series from  $P_1$  or  $P_2$  to  $M_3$ . The molars increase in size towards the rear, and  $M_3$  is the longest tooth in the lower jaw.  $P_2$  is usually the longest of the premolars. The enamel of all cheek teeth is very finely wrinkled.

The inferior molars are low crowned, but individual cusps, when unworn, are pyramidal and somewhat high in relation to total crown height. In the second molar, the metaconid and entoconid are of equal height and rather bunoid, with smoothly convex lingual faces. Their wear traces are pear-shaped, with the blunter end behind, and lie roughly parallel to the long axis of the tooth. The trace of the metaconid is continuous with that of the entoconid. The metaconid bears a strong,

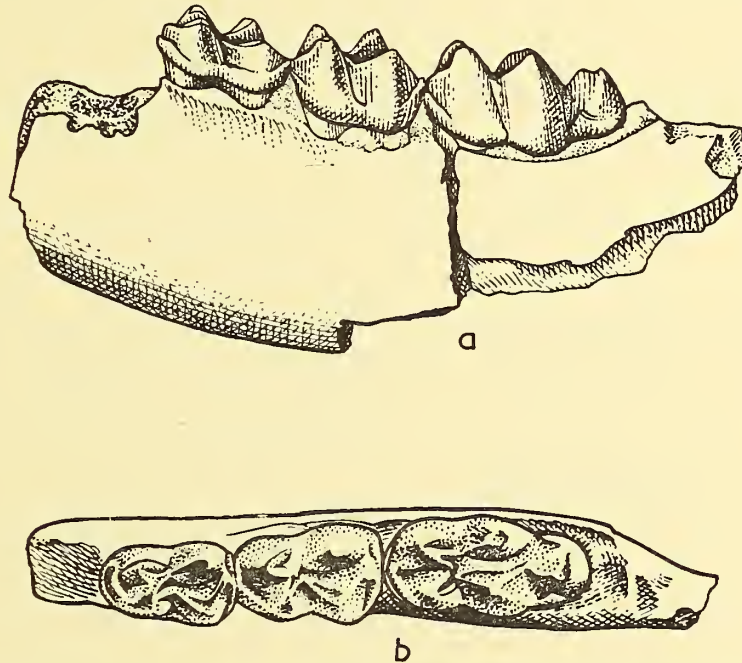


FIG. 2. *Dorcatherium chappuisi*. (a) Lateral aspect, (b) occlusal aspect of left mandibular ramus (785.52) with  $M_{1-3}$ .  $\times 1\frac{1}{2}$ .

postero-internal, accessory fold, which is separated from the rear edge of the metaconid by a deep, vertical sulcus. The unworn protoconid and hypoconid almost equal the inner cusps in height. Externally, they have a plump, rounded appearance. At its posterior extremity, the crescentic wear trace of the protoconid meets the junction of the metaconid and entoconid. A strong *Palaeomeryx*-fold arises from the posterior wall of the protoconid, and is confluent with the anterior extremity of the crescentic hypoconid trace, thus isolating the latter from the other principal cusps. There are strong anterior and posterior cingula, and sometimes an external cingulum is developed. Usually, there is no median, accessory stylid in the external valley, or, if present, it is feeble. Very occasionally, there may be a weak internal cingulum, or a median, internal accessory stylid, as in the specimens from Maboko. The second molar possesses four roots, fused into an anterior and a posterior group.



The first lower molar is similar, but smaller. The third molar, however, possesses an additional posterior lobe. This consists chiefly of a stout, bunoid, outer cusp or hypoconulid, wearing into a crescentic trace. There is also some suggestion of a small, laterally compressed, internal cusp at the posterior extremity of the hypoconulid trace; and there is often a small, accessory stylid closely applied to the outer, anterior wall of the hypoconulid. The third molar probably possesses five roots, fused into a posterior group of three roots and an anterior group of two.

The fourth premolar (Text-fig. 3*d, e*) is a narrow, trenchant tooth, with prominent central cusp joined by a longitudinal, median crest to a low anterior cusp and a tiny posterior cusp or talonid. Both terminal cusps are placed a little inside the mid-line of the tooth. The anterior and the principal cusps are separated, on the inner surface of the crown, by a vertical sulcus. The talonid is separated from the principal cusp by a broad, shallow, external groove. On the lingual side of the fourth premolar, a long fold extends back from the principal cusp, parallel to the median crest, almost as far as the posterior cusp. It is separated from the median crest by a deep, narrow cleft. There is a strong anterior and posterior cingulum, and the tooth possesses two roots, placed at front and rear.

The second and third premolars resemble the corresponding milk teeth in *Hyemoschus*. There is only one example of the third lower premolar (528.50, Text-fig. 3*c*) from western Kenya, and this is badly pitted by weather. The tooth is long, narrow and compressed. The centrally placed, principal cusp is joined by a median, longitudinal crest to a small cusp at the anterior extremity of the crown, and to a similar, small cusp placed halfway between the principal cusp and the posterior margin of the crown. Both subsidiary cusps are separated from the principal one by a shallow, internal groove, and the posterior cusp is also defined by an external groove. There are two roots, and the cingulum forms a pronounced postero-internal stylid. The second premolar is very similar to the third, but is usually a little longer and narrower, with the two roots strongly compressed in a transverse direction. In the collection from western Kenya, the first premolar is represented by one example (788.52), recovered at Maboko Island and only doubtfully referred to *Dorcatherium chappuisi*. Arambourg (1933) has described the first premolar of the holotype as a much reduced tooth, with compressed and trenchant principal cusp and a small talonid. His figure (pl. 1, fig. 9) suggests that the tooth was borne on two transversely compressed roots. In specimen 788.52, the first premolar has been tilted back in the mandible (Text-fig. 3*a, b*), but is clearly very similar to the holotypic first premolar.

The fourth lower milk molar (700.49) is a long, narrow tooth. The posterior portion is exactly similar to a permanent molar, but the crown is prolonged into an anterior third lobe, carried on a single root. The other deciduous molars are not represented.

UPPER DENTITION.—The brachyodont upper cheek teeth closely resemble those of *Hyemoschus*, but the cusps are more bunoid. The teeth form a closed series from P<sup>2</sup> to M<sup>3</sup>, the second or third molar being the largest tooth in the upper jaw. The second upper molar is very low crowned, with strong, conical paracone and metacone. The median, external rib of the paracone takes the form of a forward-projecting fold. In front, the rib is separated from the paracone by a deep, vertical sulcus, but it is

confluent behind with the rear portion of the paracone. The metacone possesses a less prominent, but bunoid, rib. The anterior extremity of the metacone lies outside the paracone, and is attached to a low, conical mesostyle. There is also a strong, stout parastyle. The metastyle is either very feeble or absent. The protocone and metaconule are low and somewhat bunoid. They do not give off subsidiary spurs into the fossettes, but the labial face of the protocone often bears a median, vertical rib. The broad, crescentic trace of the protocone is terminated abruptly against the anterior wall of the metaconule, which is itself prolonged to meet the rear end of the paracone. Frequently, there is an anterior and posterior cingulum, but the cingulum is most powerfully developed on the inner side of the tooth, particularly across the protocone. Sometimes a cingulum is completely lacking. Usually there is no

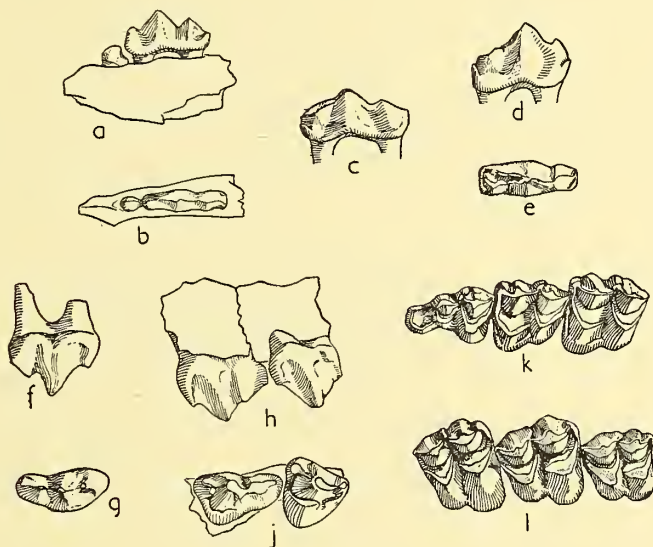


FIG. 3. *Dorcatherium chappuisi*. (a) Medial aspect, (b) occlusal aspect of mandibular fragment (788.52) with right  $P_{1-2}$ , (c) lateral aspect of left  $P_3$  (528.50), (d) lateral, (e) occlusal aspect of right  $P_4$  (790.52), (f) lateral, (g) occlusal aspect of right  $P_2$  (324.47), (h) lateral, (j) occlusal aspect of maxillary fragment (324.47) with left  $P^{3-4}$ , (k) occlusal aspect of left  $dM^3$  to  $M^1$  (201.50), (l) occlusal aspect of right  $M^{1-3}$  (789.52). All natural size.

median, internal, accessory style, or, if present, it is very poorly developed. There are four roots, but the inner pair are fused. The other molar teeth are very similar, although the metaconule of the third molar is a little reduced, and the labial rib of the protocone is never as prominent as it is in the second molar.

The upper premolars (Text-fig. 3f, g, h, j) also resemble those of *Hyemoschus*, but they are narrower relative to their length. In addition, the principal cusps and styles are more bunoid than in the Recent genus. The fourth premolar possesses a large, median, external cusp, flanked by a stout antero-external style and a similar, but slightly taller, postero-external style. All three exhibit a bunoid tendency. Each style is separated from the principal cusp by a broad, shallow groove. At the lingual margin of the crown there is a low, median cusp, wearing into a crescentic trace, and somewhat compressed against the inner wall of the principal external cusp. The

horns of the crescent link with the anterior and posterior styles. There are three roots, two external and one below the inner median cusp. The third premolar is similar to the fourth, but it is a little longer, owing to an increase in the length of the talon bearing the posterior external style, and it is also narrower. The internal cusp is ill-defined and pressed tightly against the lingual wall of the principal external cusp. The three roots are arranged in the same way as those of the fourth premolar. The second premolar is long, narrow and trenchant, with the high central cusp and smaller posterior and anterior cusps or styles disposed serially along the mid-line of the crown. The styles are separated from the central cusp by internal and external grooves, and there is a weak, internal cingulum. There are two large roots, one at the front, one at the rear of the crown, and a tiny vestige of a third root lies below the centre of the lingual margin.

TABLE I  
LOWER DENTITION OF *DORCATHERIUM CHAPPUISI*

| Catalogue No. | Locality            | dM <sub>4</sub> |     | P <sub>1</sub> |     | P <sub>2</sub> |     | P <sub>3</sub> |     | P <sub>4</sub> |     | M <sub>1</sub> |     | M <sub>2</sub> |     | M <sub>3</sub> |     |
|---------------|---------------------|-----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|
|               |                     | a.p.            | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. |
| 352.47        | R.1                 |                 |     |                |     |                |     |                |     |                |     | 11.6           | 7.6 | 12.9           | 9.0 | 18.8           | 8.7 |
| 700.49        | R.75                | 14.5            | 5.0 |                |     |                |     |                |     |                |     |                |     |                |     |                |     |
| 528.50        | R.3                 |                 |     |                |     |                |     | 13.5           | 5.1 | 12.3           | 6.0 |                |     |                |     |                |     |
| 785.52        | R.III               |                 |     |                |     |                |     |                |     |                |     | 11.7           | 7.2 | 12.5           | 8.5 | 18.0           | 8.7 |
| 786.52        | Rs.                 |                 |     |                |     | 13.5           | 4.6 |                |     |                |     |                |     |                |     |                |     |
| 787.52        | R.32                |                 |     |                |     | 13.9           | 4.2 |                |     |                |     |                |     |                |     |                |     |
| 788.52        | Maboko              |                 |     | 3.0            | 2.2 | 11.8           | 3.6 |                |     |                |     |                |     |                |     |                |     |
| Holotype      | Losodok,<br>Turkana |                 |     | 6.0            | 2.5 | 13.5           | 5.0 | 13.0           | 5.5 | 12.5           | 6.0 | 12.0           | 8.0 | 13.0           | 9.5 | 19.0           | 9.5 |

(R.75=site 75 on Rusinga Island; Rs.=surface find, Rusinga)

TABLE II  
UPPER DENTITION OF *DORCATHERIUM CHAPPUISI*

| Catalogue No. | Locality  | dM <sup>3</sup> |     | dM <sup>4</sup> |      | P <sup>2</sup> |     | P <sup>3</sup> |     | P <sup>4</sup> |     | M <sup>1</sup> |      | M <sup>2</sup> |      | M <sup>3</sup> |      |
|---------------|-----------|-----------------|-----|-----------------|------|----------------|-----|----------------|-----|----------------|-----|----------------|------|----------------|------|----------------|------|
|               |           | a.p.            | tr. | a.p.            | tr.  | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr.  | a.p.           | tr.  | a.p.           | tr.  |
| 324.47        | R.1       |                 |     |                 |      | 13.0           | 6.2 | 12.0           | 7.5 |                |     | 11.1           | 12.2 | 12.4           | 14.5 | 12.2           | 14.6 |
| 201.50        | Kathwanga | 12.6            | 8.0 | 10.8            | 10.0 |                |     | 12.5           | 7.0 | 9.6            | 9.2 |                |      |                |      |                |      |
| 789.52        | Rs.       |                 |     |                 |      |                |     |                |     |                |     | 11.3           | 11.5 |                |      |                |      |
|               |           |                 |     |                 |      |                |     |                |     |                |     | 11.0           | 11.0 | 12.3           | 12.9 | 12.0           | 13.7 |

The fourth upper milk-molar is very similar to the permanent molars, but smaller. The third milk-molar (Text-fig. 3*k*) is a long, narrow, trilobed tooth. It resembles a permanent molar, with the protocone much reduced and preceded by a low, elon-



gate, anterior lobe. There is a close similarity to the corresponding tooth in *Hymoschus*. Two roots are placed transversely beneath the posterior lobe, and one beneath each of the other two lobes. The second upper milk molar is not preserved.

*Dorcatherium pigotti* sp. nov.

(Text-figs. 4-6)

DIAGNOSIS.—A species of *Dorcatherium* of medium size. Length of lower molar series ( $M_{1-3}$ ) about 30 mm.

DISTRIBUTION.—Type area and formation, Lower Miocene of Rusinga Island, western Kenya. There are 85 specimens from Rusinga. In six cases the stratigraphical horizon is not known. The remainder were distributed as follows: Kathwanga Series 54; Hiwegi Beds 21; Kiahera Series 4. In addition, 5 specimens from Mfwanganu Island, 2 from Karungu and 2 from Ombo are included here. 21 specimens from Maboko Island are also referred provisionally to this species, although they are a little smaller than the typical Rusinga material, and the exact dating of specimens from Maboko is controversial (see p. 48).

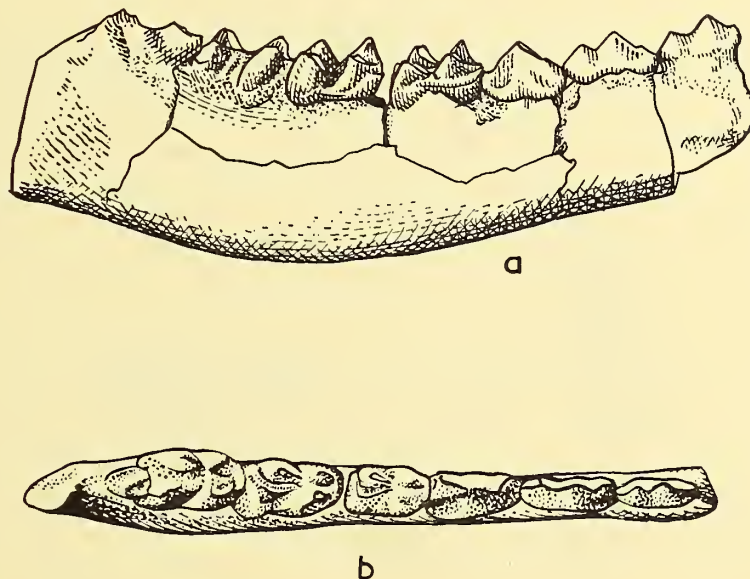


FIG. 4. *Dorcatherium pigotti*. (a) Lateral view of right mandibular ramus of holotype (737.52), with  $P_2$  to  $M_3$ , (b) occlusal aspect of same.  $\times 1\frac{1}{2}$ .

HOLOTYPE.—Portion of a mandible (737.52, Text-fig. 4) with right  $P_2$  to  $M_3$  and left  $P_3$  to  $M_2$ . Right and left upper canine, right articular process of a mandible and two upper molars intimately associated. Rusinga, ?R.106.

The remainder of the material consists of mandibular and maxillary fragments, isolated teeth and an associated tarsus.

DENTITION.—The cheek teeth of *Dorcatherium pigotti* are appreciably smaller than those of *D. chappuisi*. Any other differences are trivial. For example, the

cheek teeth of *D. pigotti* are slightly less bunoid than those of *D. chappuisi*, and the metastyle of the upper molars is sometimes a little more pronounced and angular. In addition,  $P_2$  is shorter than  $P_3$ , whereas in *D. chappuisi* it is usually a little longer. Finally, the median internal cusp is better developed in the third and fourth upper premolars, which, in this respect, approximate more closely to the corresponding teeth in *Hyemoschus*. The lower premolar formula is unknown.

The upper canine of the male is large, recurved and tusk-like (Text-fig. 5a). The labial surface is concave, the lingual convex: the anterior edge is rounded, the posterior sharp and cutting. Portions of four male canines are preserved. Their dimensions follow:

|          | Length preserved | Maximum breadth of blade |
|----------|------------------|--------------------------|
| 737.52   | — mm.            | 5.6 mm.                  |
| Mb.18.49 | 27.0             | 5.0                      |
| Mb.25    | —                | 5.6                      |
| Mb.220   | 22.1             | 5.5                      |

The deciduous dentition is represented by three specimens of the fourth lower milk molar (F.3198.42, 795.50 and 1498.50). The tooth is very similar to that found

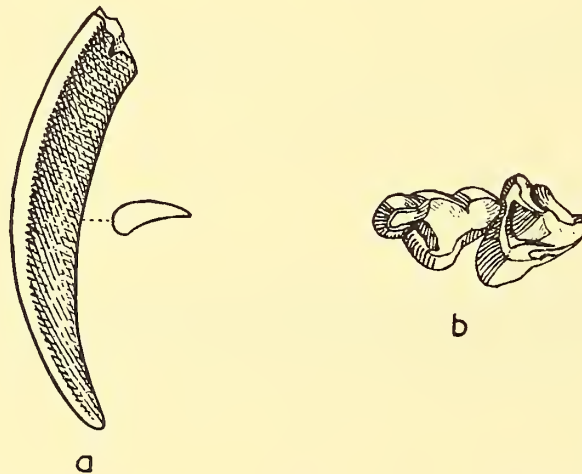


FIG. 5. *Dorcatherium pigotti*. (a) Lateral aspect of left upper canine (Mb. 18.49), (b) occlusal aspect of left  $P^{3-4}$  (1897.50).  $\times 2$ .

in *Dorcatherium chappuisi*. There are two transversely placed roots under the rear portion of the crown and a median-external root, all fused into a single posterior group. There is no median-internal root. The anterior lobe is supported by a single root.

TABLE III  
LOWER DENTITION OF *DORCATHERIUM PIGOTTI*

| Catalogue No.      | Locality          | dM <sub>4</sub> |     | P <sub>2</sub> |     | P <sub>3</sub> |     | P <sub>4</sub> |     | M <sub>1</sub> |     | M <sub>2</sub> |     | M <sub>3</sub> |     |
|--------------------|-------------------|-----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|
|                    |                   | a.p.            | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. |
| F.3198.42          | R.7               | 12.0            | 5.2 |                |     |                |     |                |     |                |     |                |     |                |     |
| 837.47             | R.75              |                 |     | 7.1            | 2.5 | 8.5            | 3.1 | 7.9            | 3.8 | 8.2            | 4.8 | 10.0           | 6.0 | 14.0           | 6.0 |
| 737.52 (HOLO-TYPE) | Rs.               |                 |     |                |     | 8.4            | 3.1 | 7.8            | 3.7 | —              | —   | 8.9            | 5.3 | —              | 5.5 |
| 790.52             | R.38              |                 |     |                |     |                |     |                |     |                |     | 8.7            | 5.4 | 13.8           | 6.0 |
| 791.52             | Kachuku, Karungu. |                 |     |                |     |                |     |                |     |                |     | 8.2            | 5.6 | 14.0           | 5.9 |
|                    |                   |                 |     |                |     |                |     |                |     |                |     | 9.5            | 5.7 |                |     |

TABLE IV  
UPPER DENTITION OF *DORCATHERIUM PIGOTTI*

| Catalogue No. | Locality | P <sup>3</sup> |     | P <sup>4</sup> |     | M <sup>1</sup> |     | M <sup>2</sup> |      | M <sup>3</sup> |      |
|---------------|----------|----------------|-----|----------------|-----|----------------|-----|----------------|------|----------------|------|
|               |          | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr.  | a.p.           | tr.  |
| 331.47        | R.1A     |                |     |                |     | 8.1            | 9.6 | 9.0            | 10.8 | 9.6            | 11.5 |
| 791.50        | R.104    |                |     | 7.0            | 7.5 | 8.0            | 9.0 | 9.0            | 11.0 |                |      |
| 1895.50       | R.3A     |                |     |                |     | 7.5            | 8.7 | 8.8            | 10.0 | 9.0            | 10.2 |
| 1897.50       | R.3A     | 8.0            | 5.1 | 6.7            | 7.8 |                |     |                |      |                |      |
| 302.51        | R.3      |                |     | 7.0            | 8.0 | 7.8            | 9.0 | 9.0            | 10.0 | 10.0           | 10.8 |
| 747.52        | R.12     |                |     | 6.5            | 7.5 | 7.9            | 8.6 | 9.0            | 10.2 | 9.1            | 11.0 |
| Mb.210        | Maboko   | 7.3            | 5.5 | 6.2            | 6.8 | 6.1            | 8.0 | 7.6            | 9.4  | 8.0            | 9.0  |

POST-CRANIAL SKELETON.—A right tarsus (738.52, Text-fig. 6) and the proximal portion of the corresponding cannon-bone were closely associated with a mandibular fragment of *Dorcatherium pigotti* from R.38, Rusinga. The navicular, cuboid and external cuneiform bones are fused into a single unit, but the internal cuneiform, which is missing, remained distinct. The compound tarsal bone measures 13.5 mm. across, 12.8 mm. from front to rear and 14.0 mm. in height at the lateral margin. The metatarsals are fully fused, but each retains an individual marrow-cavity. The metatarsals are angular in front and separated by a deep, longitudinal sulcus. Posteriorly they are flat, and their union is marked by a very narrow, impersistent cleft. As in *Hyemoschus*, the proximal articulatory surface of metatarsal III is higher than that of metatarsal IV. The transverse diameter of the cannon-bone shaft measures about 10.5 mm.

*Dorcatherium parvum* sp. nov.

DIAGNOSIS.—A species of *Dorcatherium* of small size. Length of lower molar series (M<sub>1-3</sub>) about 20 mm. Some individuals lacked P<sub>1</sub>.



DISTRIBUTION.—Type area and formation, Lower Miocene of Rusinga Island, western Kenya. 189 specimens from Rusinga are referred to this species. They were distributed stratigraphically as follows: Kathwanga Series 77; Hiwegi Beds 87; Kiahera Series 9; horizon unknown 16. In addition, 12 specimens from Karungu, 1 from Maboko Island, 1 from Muruorot and 1 from Kirimon are included here.

HOLOTYPE.—Fragment of left mandibular ramus (750.52), with  $M_{1-3}$ . Rusinga, R.39.

The rest of the material consists of maxillary and mandibular fragments, isolated cheek teeth and a single upper canine.

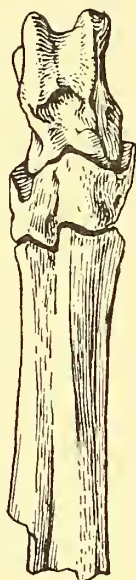


FIG. 6. *Dorcatherium pigotti*. Anterior view of right tarsus (lacking calcaneum) and proximal portion of corresponding metatarsus (738.52). Approximately natural size.

DENTITION AND JAWS.—The mandible of *Dorcatherium parvum* is characteristically shallow, deepening very gradually towards the rear. In the holotype, the depth of the horizontal ramus is 7.0 mm. beneath  $M_1$ , and 8.0 mm. beneath  $M_3$ . The cheek teeth are similar to those found in *Dorcatherium chapuisi* and *D. pigotti*, but they are smaller and less bunoid. The lower molars do not possess the median, external styloid which is occasionally developed in the larger African species of *Dorcatherium*; and the internal accessory fold of the metaconid and the *Palaeomeryx*-fold are sometimes very feeble, particularly in the smaller individuals. The lower cheek teeth may be closed either from first premolar, or from second premolar, to third molar. A first premolar is present with the second premolar, in specimen 1171.47, a portion of a right mandibular ramus from Kathwanga, Rusinga Island. Both teeth are narrow and possess two roots. The first premolar measures 2.1 mm. in length and 1.6 mm. in breadth: the second premolar, which is placed directly above the mental foramen, measures 3.5 mm. in length and 1.9 mm. in breadth. On the other hand, in specimen

846.48, a length of the alveolar margin is preserved in front of the second premolar and lacks any sign of a first premolar. *Dorcatherium parvum* resembles *D. pigotti* and differs from *D. chappuisi* in possessing a second lower premolar which is shorter than the third, but the inferior premolars of *D. parvum* all tend to be a little narrower, relative to their length, than their counterparts in *D. pigotti*.

The upper molars of *Dorcatherium parvum* possess a very strong, shelf-like, internal cingulum across the protocone, but a postero-internal cingulum is seldom developed, and there is no median, internal style. The external rib of the metacone is very weak, and sometimes absent. The metastyle, although low, is frequently strong and angular, particularly in the smaller individuals. The upper premolars are similar to those of *D. pigotti*, but their cusps are less bunoid. Consequently, the teeth are almost indistinguishable from the corresponding premolars in *Hyemoschus*. A left upper canine is included in specimen 1164.50, and is very similar to that found in Recent male chevrotains. The antero-posterior diameter of the crown is about 3.1 mm., the estimated height of the crown about 15.0 mm.

The deciduous dentition is represented by  $dM_{3-4}$  and  $dM^{2-4}$ . All these closely resemble the corresponding teeth in *Hyemoschus*. Indeed, *D. parvum* seems to be a somewhat advanced form which, in many respects, approximates more closely to the Recent tragulid condition than do any of the larger Miocene species. One minor difference, however, is the absence of a median, external root from the third upper milk molar of *D. parvum*.

The numerous teeth and jaws assigned to *Dorcatherium parvum* form a homogeneous group of material, but they exhibit an appreciable range of variation in size. The examples given in Tables V and VI have been selected to demonstrate this variation.

TABLE V  
LOWER DENTITION OF *DORCATHERIUM PARVUM*

| Catalogue No.        | Locality    | $dM_3$ |     | $dM_4$ |     | $P_2$ |     | $P_3$ |     | $P_4$ |     | $M_1$ |     | $M_2$ |     | $M_3$ |     |  |
|----------------------|-------------|--------|-----|--------|-----|-------|-----|-------|-----|-------|-----|-------|-----|-------|-----|-------|-----|--|
|                      |             | a.p.   | tr. | a.p.   | tr. | a.p.  | tr. | a.p.  | tr. | a.p.  | tr. | a.p.  | tr. | a.p.  | tr. | a.p.  | tr. |  |
| 665.47               | R.3         | 5.4    | 1.5 | 6.0    | 2.0 |       |     |       |     |       |     | 5.5   | 2.8 |       |     |       |     |  |
| 751.47               | R.106       |        |     | 7.1    | 2.2 |       |     |       |     |       |     |       |     |       |     |       |     |  |
| 801.47               | R.3         |        |     |        |     |       |     |       |     |       |     |       |     |       |     |       |     |  |
| 846.48               | R.106       |        |     |        |     | 6.0   | —   | 7.0   | 2.5 | 6.8   | 2.7 |       |     |       |     |       |     |  |
| 485.49               | R.3A        |        |     |        |     |       |     |       |     |       |     |       |     | 5.8   | 3.4 | 7.8   | 3.6 |  |
| 1171.50              | Kathwanga   |        |     |        |     |       |     |       |     |       |     | —     | 3.6 | 7.1   | 4.6 | 9.9   | 4.4 |  |
| 1180.50              | West Hiwegi |        |     |        |     |       |     | 5.8   | 1.9 |       |     |       |     |       |     |       |     |  |
| 56.51                | R.3A        |        |     |        |     |       |     |       |     | 5.2   | 2.0 |       |     |       |     |       |     |  |
| 308.51               | R.3         |        |     |        |     |       |     |       |     | 7.2   | 3.6 |       |     |       |     |       |     |  |
| 612.51               | Kathwanga   |        |     |        |     |       |     |       |     | 5.2   | 2.3 | 5.8   | 3.1 |       |     |       |     |  |
| 750.52               | R.39        |        |     |        |     |       |     |       |     |       |     | 5.2   | 3.0 | 5.7   | 3.3 | 8.0   | 3.6 |  |
| (HOLOTYPE)<br>795.52 | R.110       |        |     |        |     |       |     |       |     |       |     | 5.0   | 2.8 | 6.3   | 3.6 | 8.0   | 3.7 |  |

TABLE VI  
UPPER DENTITION OF *DORCATHERIUM PARVUM*

| Catalogue No. | Locality  | dM <sup>2</sup> |     | dM <sup>3</sup> |     | dM <sup>4</sup> |     | P <sup>2</sup> |     | P <sup>3</sup> |     | P <sup>4</sup> |     | M <sup>1</sup> |     | M <sup>2</sup> |     | M <sup>3</sup> |     |     |
|---------------|-----------|-----------------|-----|-----------------|-----|-----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|-----|
|               |           | a.p.            | tr. | a.p.            | tr. | a.p.            | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. |     |
| 505.47        | R.1A      |                 |     |                 |     |                 |     |                |     |                |     |                |     |                |     |                | 6.1 | 7.0            | 6.1 | 6.8 |
| 1225.47       | Kathwanga |                 |     | —               | 3.7 | 5.4             | 5.8 |                |     |                |     |                |     |                |     |                |     |                |     |     |
| 490.49        | R.3A      |                 |     |                 |     |                 |     |                |     |                |     | —              | 3.8 | 5.2            | 5.2 | 5.5            | 6.0 |                |     |     |
| 891.50        | R.1       |                 |     |                 |     |                 |     |                |     |                |     |                |     |                |     | 7.0            | 6.7 | 6.1            | 6.8 |     |
| 996.50        | R.1       |                 |     |                 |     |                 |     |                |     |                |     |                |     |                | 5.6 | 5.6            | 6.7 | 6.2            | 6.1 | 6.5 |
| 1164.50       | R.1       |                 |     |                 |     |                 |     |                |     |                |     |                |     |                | 5.1 | 5.2            | 7.0 | 6.1            | 7.1 | 6.1 |
|               |           |                 |     |                 |     |                 |     |                |     |                |     |                |     |                |     |                |     |                |     |     |
|               |           |                 |     |                 |     |                 |     |                |     |                |     |                |     |                |     |                |     |                |     |     |
| 1215.50       | R.1A      |                 |     |                 |     |                 |     |                |     |                |     |                |     |                |     |                |     |                |     |     |
| 1217.50       | R.1A      |                 |     | 5.8             | 2.8 | 4.9             | 4.1 | 5.5            | 2.3 |                |     |                |     |                |     |                |     |                |     |     |
| 1658.50       | Kathwanga |                 |     |                 |     |                 |     |                |     |                |     |                |     |                | 5.7 | 6.0            | 6.0 | 7.1            | 6.1 | 7.3 |
| 694.51        | Kathwanga |                 |     |                 |     |                 |     |                |     |                |     | 5.6            | 5.4 |                |     |                |     |                |     |     |
| 1239.51       | Kathwanga | 7.8             | 3.1 |                 |     |                 |     |                |     |                |     |                |     |                |     |                |     |                |     |     |
| 751.52        | Rusinga   |                 |     |                 |     |                 |     |                |     |                |     |                |     |                | 6.0 | 6.8            | 7.4 | 8.0            | 7.3 | 8.0 |

*Dorcatherium songhorensis* sp. nov.  
(Text-figs. 7, 8)

DIAGNOSIS.—A medium-sized *Dorcatherium*. Length of lower molar series ( $M_{1-3}$ ) about 24 mm.

DISTRIBUTION.—Type area and formation, Lower Miocene of Songhor, western Kenya. 45 specimens from Songhor are referred to this species, and 2 from the neighbouring locality of Koru.

HOLOTYPE.—Portion of a right mandibular ramus (F3205.41) with  $M_{1-3}$ , from Songhor.

The remainder of the material consists of maxillary and mandibular fragments, and isolated cheek teeth. The anterior dentition is unknown.

DENTITION AND JAWS.—The mandible is shallow and slender. The holotype ramus is 10.0 mm. deep and 5.0 mm. thick beneath  $M_1$ , and 12.5 mm. in depth beneath  $M_3$ .

The permanent cheek teeth are very similar to those of *Dorcatherium parvum*, but they are a little larger. They differ from the cheek teeth assigned to *Dorcatherium chappuisi* and *D. pigotti* in the following characters. The principal cusps of all molar teeth are less bunoid. The median, external styloid, found occasionally in lower molars of the larger species, is very rare, and when present, is extremely feeble. The lower premolars are a little narrower, relative to their length, than in *D. pigotti*. The metastyle of the upper molars is not so well developed as in *D. pigotti*, but the anterior, internal cingulum is very pronounced.

The fourth lower milk molar (756.52) is exactly similar to its counterpart in *Dorcatherium pigotti*. It only differs from the corresponding tooth in *Hyemoschus* by having a slightly stronger accessory fold upon the lingual side of the median, internal cusp. The third lower milk molar (516.49) is very long and narrow, with three com-



pressed cusps, of which the central cusp is the highest, arranged serially along the mid-line of the crown. There is also a prominent postero-internal stylid or heel at the rear margin of the crown. The fourth upper milk molar (85.47) is a reduced version of the permanent molars, the third is only represented by the posterior

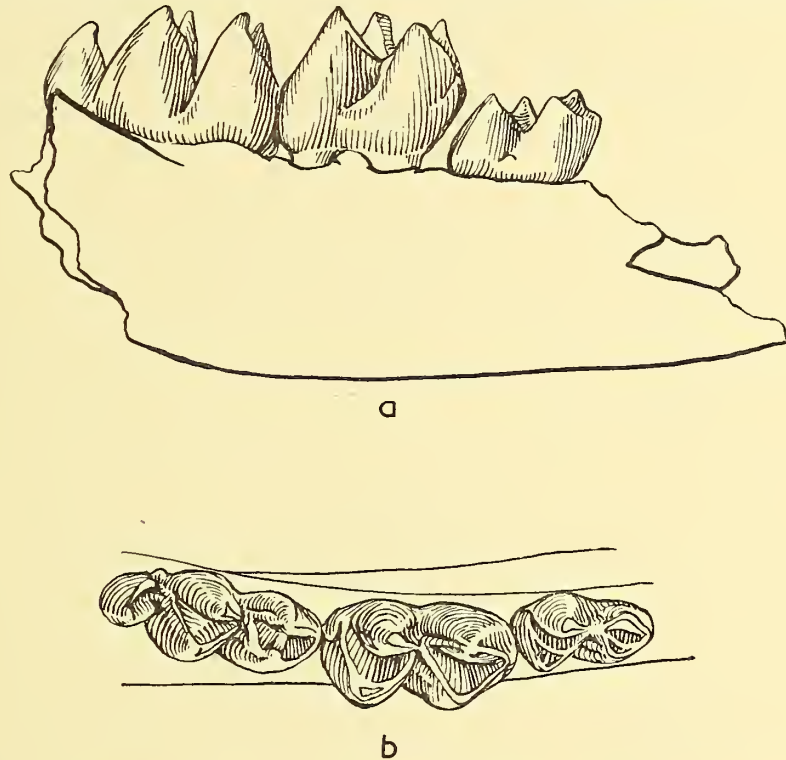


FIG. 7. *Dorcatherium songhorensis*. Holotype (F.3205.41). (a) Lateral, (b) occlusal aspect of mandibular fragment with right  $M_{1-3}$ .  $\times 3$ .

portion of the crown. The second upper milk molar (564.49) resembles the corresponding tooth in *Hyemoschus*. It is long and narrow, with a principal, central cusp and subsidiary anterior and posterior cusps, arranged along the mid-line of the crown. The central cusp possesses an external rib, and, on the outer side of the crown, is separated from the subsidiary cusps by vertical grooves. At its lingual margin, the crown is bevelled by an inward-sloping wear surface. There are two roots, placed at front and rear. No other tooth of the deciduous dentition has been recovered.

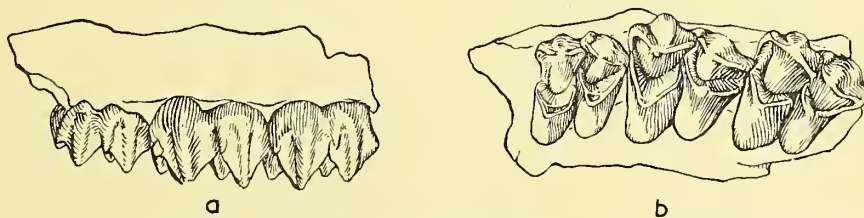


FIG. 8. *Dorcatherium songhorensis*. (a) Lateral, (b) palatal aspect of maxillary fragment (Sgr.107.48), with left  $M^{1-3}$ .  $\times 2$ .

TABLE VII  
LOWER DENTITION OF *DORCATHERIUM SONGHORENSIS*

| Catalogue No.           | Locality | dM <sub>3</sub> |     | dM <sub>4</sub> |     | P <sub>3</sub> |     | P <sub>4</sub> |     | M <sub>1</sub> |     | M <sub>2</sub> |     | M <sub>3</sub> |     |
|-------------------------|----------|-----------------|-----|-----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|
|                         |          | a.p.            | tr. | a.p.            | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. |
| F.3193                  | Songhor  |                 |     |                 |     | 7.2            | 2.2 | 6.8            | 2.7 |                |     |                |     |                |     |
| F.3205.41<br>(HOLOTYPE) | Songhor  |                 |     |                 |     |                |     |                |     | 6.4            | 4.0 | 7.6            | 4.6 | 10.5           | 5.0 |
| F.3207                  | Songhor  |                 |     |                 |     |                |     |                |     | 7.0            | 4.4 |                |     |                |     |
| 448.48                  | Songhor  |                 |     |                 |     | 7.8            | 2.5 | 7.6            | 3.0 |                |     |                |     |                |     |
| 36.49                   | Songhor  |                 |     |                 |     |                |     |                |     |                |     | 8.0            | 4.2 |                |     |
| 367.49                  | Songhor  |                 |     | 8.0             | 2.7 |                |     |                |     |                |     |                |     |                |     |
| 516.49                  | Songhor  | 8.3             | 1.9 | 8.0             | 2.8 |                |     |                |     |                |     |                |     |                |     |
| 518.49                  | Songhor  |                 |     |                 |     |                |     |                |     |                |     |                |     | 12.1           | 5.1 |
| 519.49                  | Songhor  |                 |     |                 |     |                |     |                |     |                |     | 6.8            | 3.7 |                |     |
| 754.52                  | Songhor  |                 |     |                 |     |                |     |                |     | 6.2            | 3.7 | 7.4            | 4.5 | 10.5           | 4.7 |
| 756.52                  | Songhor  |                 |     | 8.0             | 3.1 |                |     |                |     | 6.6            | 4.0 | 7.2            | 4.5 |                |     |
| 758.52                  | Songhor  |                 |     |                 |     |                |     |                |     |                |     |                |     | 10.1           | 4.2 |

TABLE VIII  
UPPER DENTITION OF *DORCATHERIUM SONGHORENSIS*

| Catalogue No. | Locality | dM <sup>2</sup> |     | dM <sup>3</sup> |     | dM <sup>4</sup> |     | P <sup>3</sup> |     | M <sup>1</sup> |     | M <sup>2</sup> |     | M <sup>3</sup> |     |
|---------------|----------|-----------------|-----|-----------------|-----|-----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|
|               |          | a.p.            | tr. | a.p.            | tr. | a.p.            | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. |
| 85.47         | Songhor  |                 |     | —               | 4.7 | 5.5             | 6.0 |                |     |                |     |                |     |                |     |
| 107.48        | Songhor  |                 |     |                 |     |                 |     |                |     | 7.1            | 6.5 | 7.7            | 7.7 | 8.1            | 8.0 |
| 316.49        | Songhor  |                 |     |                 |     |                 |     |                |     |                |     | 7.1            | 7.6 | 7.1            | 7.3 |
| 564.49        | Songhor  | 7.8             | 2.7 |                 |     |                 |     |                |     |                |     |                |     |                |     |
| 761.52        | Songhor  |                 |     |                 |     |                 |     |                |     | 6.0            | 6.2 | 7.3            | 8.1 | 8.3            | 9.0 |
| 762.52        | Songhor  |                 |     |                 |     |                 |     |                |     | 7.5            | 7.6 | 8.1            | 8.1 |                |     |
| 763.52        | Songhor  |                 |     |                 |     |                 |     | 8.7            | 5.0 |                |     |                |     |                |     |

Family CERVIDAE Gray, 1821

Subfamily PALAEOMERYCINAE Matthew, 1904

*PALAEOMERYX* Meyer, 1834

1904 *Lagomeryx* Roger, p. 18

1937 ?*Heterocemas* Young, p. 228

AMENDED DIAGNOSIS.—Cervids of varied size. Non-deciduous "antlers", with whorl of rather short tines borne on long pedicle, present in some species. Mandible very shallow. Brachyodont, selenodont molar teeth quadricuspid and of cervid pattern. Enamel wrinkled. Lower cheek teeth in a closed series from P<sub>2</sub> to M<sub>3</sub>; P<sub>1</sub> usually isolated by very short diastema. Lower molars with prominent metastyloid and



entostylid, strong median external tubercle, pronounced anterior and posterior cingula. *Palaeomeryx*-fold developed to varying degree. Lower premolars long, with internal crescents poorly developed or absent. Anterior lower dentition incompletely known. Upper cheek teeth probably forming a closed series from P<sup>2</sup> to M<sup>3</sup>. Molars with prominent, rather angular parastyle, mesostyle and antero-external rib; postero-external rib very feeble or absent; small, angular metastyle usually present. Mesostyle links equally with para- and metacone. Small accessory crests often developed in fossettes. Accessory tubercle in median, internal valley; strong anterior and posterior cingula. P<sup>4</sup> short; anterior upper premolars less reduced than in Recent cervids.

SYNONYMY OF *PALAEOMERYX* and *LAGOMERYX*.—*Palaeomeryx* was first described by Meyer (1834), who based his original diagnosis on certain teeth of large size which, in his opinion, possessed cervid characteristics. Subsequent authors have added new species to the genus, including some species which contained individuals of small size. During the latter half of the nineteenth century, the idea arose that branching "antlers" of a non-deciduous type were confined to the smaller species of *Palaeomeryx* (cf. Fraas, 1862 & 1870; Rüttimeyer, 1883; Roger, 1898), although Hofmann (1893) tentatively referred isolated "antler" fragments to one of the larger species. In 1902, Schlosser suggested that the teeth of the smaller species differed in a constant manner from those of the larger species, and differed sufficiently to warrant their removal into a new genus. The only differences mentioned were size and an alleged absence of accessory crests from the upper molars of the smaller species. Study of Recent Bovidae and Cervidae shows that similar accessory crests may be absent from some teeth and variably developed on the other teeth of a single dentition, and are thus of limited taxonomic value. Schlosser not only failed to appreciate this, but, in addition, completely overlooked Hofmann's (1893) diagnoses of two small species of *Palaeomeryx* (*P. meyeri* and *P. escheri*), in which the upper molars possessed "Dicrocerus-like" accessory crests. It is evident that Schlosser was aware of Hofmann's two species, since he quoted (1902) one of them (*P. meyeri*) as an example of the forms requiring generic differentiation. Schlosser also assumed that "antlers" were invariably confined to the smaller species. Roger (1904) then adopted Schlosser's suggestion, and segregated the small species of *Palaeomeryx* under the name, *Lagomeryx*. In establishing the new genus, he repeated Schlosser's invalid generalizations concerning the teeth of the smaller species and the distribution of the "antlers", and included a description of the latter in his definition.

In 1939, Teilhard de Chardin described various pecoran dentitions from the Miocene of Shantung. They represented two distinct groups of material which he termed forms A and B. Form A was equal in size to a red deer; form B was equal in size to a roe deer, and approximately half as large again as the small species of *Palaeomeryx* originally transferred to the genus *Lagomeryx*. Teilhard de Chardin said that the dentitions would clearly be referred to *Palaeomeryx*, but for the occurrence in the same deposits of *Lagomeryx*-type "antlers" corresponding in size to form B; and added that "antlers" corresponding in size to the still larger form A might also be expected. It can only be assumed that he regarded the possession of "antlers" as the sole distinguishing feature of *Lagomeryx*. Roger's initial separation of *Lagomeryx* from *Palaeomeryx* relied, however, on a number of distinctions, namely size, a

difference in the dentitions, and the restriction of "antlers" to the smaller forms. The assumption that the dentitions of the smaller species of *Palaeomeryx* differed from those of the larger species in a constant and significant manner is shown to be incorrect by Hofmann's descriptions (1893) of complex upper molars in the small species, *Palaeomeryx meyeri* and *P. escheri*. Teilhard de Chardin's account of a rather large *Palaeomeryx*-type dentition associated with correspondingly large "antlers" of *Lagomeryx*-type, seems to dispose of another of the original distinctions between the two genera. Thus, the only remaining difference between *Palaeomeryx* and *Lagomeryx* employed by Roger is that of size. Size does not seem to constitute a sufficient basis for the generic separation of otherwise morphologically similar mammals. (See, for example, Oldfield Thomas's treatment of *Macropus*, 1888: 11.) *Palaeomeryx* and *Lagomeryx* must clearly be treated as synonymous. *Palaeomeryx* takes priority, and any subsequent reference to *Lagomeryx* in this discussion means, by implication, the prior name, *Palaeomeryx*.

One final consideration must be disposed of. In his definition of *Lagomeryx*, Zittel (1925: 199), seems to imply that the name *Lagomeryx* can be reserved for the *Lagomeryx*-type "antlers" alone. This is again contrary to Roger's original definition of *Lagomeryx* which employed all three features of size, "antlers" and complex upper molars. Furthermore, the recurrent association of the *Lagomeryx*-type "antler" with the *Palaeomeryx*-type dentition in Miocene deposits strongly favours the assumption that they belonged to the same animal.

AFFINITIES OF *PALAEOMERYX*.—Teilhard de Chardin (1939) proposed that "a new and special family should be erected for *Lagomeryx*, *Procervulus* and other so-called Cervids (with non-deciduous antlers) of the Old World Miocene", and concluded that "*Lagomeryx* may just as much be regarded as an aberrant giraffid as an aberrant cervid". He agreed that the usual reference of *Lagomeryx* to the Cervidae was supported by the general appearance of the creature, but stated that this was contradicted by: (i) the unequal development of anterior and posterior external ribs on the upper molars; (ii) the characteristically corrugated enamel of the teeth; (iii) the occurrence of a permanent velvet over the bony part of the "antlers". Subsequently, Pilgrim (1941a) adopted Teilhard de Chardin's suggestion and erected a primitive giraffoid family, Lagomerycidae, with *Lagomeryx* as type genus.

The three features which Teilhard de Chardin (and, presumably, Pilgrim, too) considered evidence of the giraffid nature of *Lagomeryx* require further consideration. According to Matthew (1908), the superior development of an anterior external rib on the upper molars is the precise character that distinguishes the cervid from the giraffid condition. In fact, an unequal development of the anterior and posterior external ribs is found, to a varied degree, in most cervids and giraffids alike; although, generally speaking, the anterior rib is more angular and better defined in deer than in Giraffidae. There is also a tendency for the anterior rib to become more rounded and less distinct in larger Giraffidae; but a similar tendency is found, perhaps to a lesser extent, in the larger Cervidae. The upper molars of *Palaeomeryx* possess an anterior external rib which is angular and well-defined in the more typically cervid manner. The second feature mentioned by Teilhard de Chardin is also unreliable, since the condition of the enamel seems to vary in different species of the same ruminant genus. Examination of various Recent Pecora suggests that the degree of corruga-



tion of the enamel may be, in many cases, a function of size. Certainly, in Recent deer, the enamel possesses a corrugation comparable to that found in Recent giraffes of similar size. Finally, to regard the possession of non-deciduous, velvet-covered "antlers" as diagnostic of early Giraffoidea is contrary to Pilgrim's own repeated opinion (1941 and 1947) that this was as likely to be the primitive cervoid condition as the giraffoid.

None of the characters discussed above seems to provide a clear-cut distinction between giraffes and deer. The condition of the external cusps of the upper molars may, however, be more helpful in determining the systematic position of *Palaeomeryx*. In Giraffidae, the metacone of the upper molars is obliquely placed, so that its wear trace projects forward outside the posterior margin of the paracone trace, where it unites with the mesostyle. The paracone is thus isolated. In Pecora of undoubted cervid status, the paracone and metacone tend to lie parallel to the labial face of the molar crown, and the wear traces of both cusps turn out abruptly at right angles into the mesostyle, with which they unite equally and symmetrically. This latter condition characterizes the upper molars of *Palaeomeryx*. Further evidence is perhaps afforded by the limb bones associated with *Palaeomeryx africanus* at Songhor (see p. 23). One at least is of diagnostic cervid pattern, and possesses characters which are not found in the corresponding limb bones of any authentic Giraffidae.

It is clearly very difficult to assess the exact affinities of *Palaeomeryx* (and, indeed, of many Miocene Pecora), since we are probably dealing with a genus close to the origin of one pecoran group from another. Nevertheless, in *Palaeomeryx*, the dentition does possess certain properties which are characteristic of later deer, while lacking others which specially distinguish later giraffes. On the balance of evidence, it is more logical to retain *Palaeomeryx* (which includes all species formerly assigned to *Lagomeryx*) with the Cervoidea.

The synonymy of *Lagomeryx* with the cervoid genus *Palaeomeryx* affects the systematics of the Giraffoidea, since Pilgrim (1941a) employed *Lagomeryx* as the type genus of a giraffoid family, the Lagomerycidae. The family accommodates two other genera, *Procervulus* and *Climacoceras*. If these two "lagomerycid" genera prove to be authentic giraffes, a new giraffoid family name will have to be chosen in place of the now inapplicable name, Lagomerycidae.

***Palaeomeryx africanus* sp. nov.**

(Text-fig. 9)

DIAGNOSIS.—A species of *Palaeomeryx* about the same size as *Moschus moschiferus* L. Probably lacking "antlers". Length of lower molar series ( $M_{1-3}$ ) about 37 mm.

DISTRIBUTION.—Type area and formation, Lower Miocene of Songhor, western Kenya. 56 specimens from Songhor (including 1 from the Mtete Valley site), 1 from Koru, 2 from Muruorot and 71 from Rusinga Island are referred to this species. The Rusinga material was distributed stratigraphically as follows: Kathwanga Series 42; Hiwegi Beds 19; Kiahera Series 4; horizon unknown 6.

HOLOTYPE.—Right mandibular ramus (Sgr. 73.48, Text-fig. 9a, b), with  $P_3$  to  $M_3$ , from Songhor.

LOWER DENTITION.—The mandible is very shallow and the inferior cheek teeth

form a more or less continuous series from  $P_1$  to  $M_3$ . The lower premolars are much longer, relative to the molars, than in Recent genera of Cervidae, although the cheek teeth increase in size towards the rear. The enamel is marked by fine, vertical corrugations.

The lower molars are brachyodont and of selenodont pattern. The first molar possesses somewhat compressed and obliquely placed meta- and entoconids. On the lingual face of each of these cusps there is a very weak and rounded, median rib. The protoconid and hypoconid are lower than the inner cusps, and their crescentic wear traces are somewhat angular. The rear wall of the protoconid supports a feeble *Palaeomeryx*-fold. In wear, the crescentic trace of the protoconid links with the entoconid, thereby isolating the hypoconid. At the rear of the metaconid there is a robust metastylid, and a similar entostylid lies at the postero-internal extremity of the hypoconid trace. The presence of the metastylid emphasizes the oblique disposition of the metaconid, and the combined metaconid and metastylid wear trace overlaps the entoconid on its lingual side. In this respect, the tooth differs from the corresponding tragulid molar. The cingulum is well developed across the anterior and posterior faces of the first lower molar, particularly the former, but there is no external cingulum. There is, however, a stout accessory stylid of conical shape in the median, external valley between the protoconid and hypoconid. Each of the two antero-posteriorly compressed roots is probably formed by the fusion of two roots.

The second lower molar is of similar pattern, but is a little larger, and the *Palaeomeryx*-fold may be very feeble or absent. The third molar is the longest tooth in the lower jaw. It resembles the anterior molars, but is prolonged into a third posterior lobe with an external crescentic trace like that of the protoconid and hypoconid. There is no corresponding internal cusp. Instead, a rim of enamel extends from the posterior horn of this third crescent around the postero-internal margin of the crown to the entostylid, and encloses a deep basin or fossette. There are five roots. Three are fused beneath the rear half of the crown, and two in front.

The fourth premolar possesses a stout, median-external, primary cusp, from which a transverse, median crest runs inward across the tooth. The lingual portion of the crest bends forward to meet a median-internal cusp, usually equal in height to the primary cusp, but always more delicately constructed, and occasionally much reduced. The anterior and posterior (external) crests are well developed, but they are much lower than the primary cusp. There is a strong, posterior intermediate crest, and a feeble, anterior intermediate crest. The basins between the crests are open internally. The third premolar is smaller than the fourth, and lacks the median-internal cusp and anterior intermediate crest. In addition, the median, transverse crest inclines uniformly towards the rear, and does not bend forward at the inner side of the crown. In one specimen (Sgr.M.10) the posterior crest possesses a forwardly projecting spur which meets the posterior intermediate crest and divides the posterior basin into internal and external halves. The second premolar (Text-fig. 9e, f) is similar to the third, but is smaller and narrower relative to its length. The first lower premolar, which is separated from the second by a very brief diastema, from 1 to 2 mm. in length, is a small, narrow tooth. It possesses a high, median cusp and an appreciably lower, posterior cusp or talonid. The cusps are placed along the mid-line of the crown, and are joined by a median, longitudinal crest which extends to the anterior



margin. All the premolars possess two roots. In the third and fourth premolars, the posterior root is broad and compressed from front to rear, and possibly represents the fusion of two roots.

The lower anterior dentition is represented by an isolated tooth (Sgr.74.48) found in close association with molar teeth of *Palaeomeryx africanus*. It is probably an incisiform canine of the right side. The crown is long, narrow and spatulate, and bears enamel on all its faces. The dimensions of the tooth are:

|  |         |
|--|---------|
| Maximum diameter of crown . . . . .                                | 3.1 mm. |
| Height of crown from lower margin of enamel to extremity . . . . . | c. 7.0  |
| Length of root . . . . .   | 12.0+   |

The fourth lower milk molar (Sgr.445.48, Text-fig. 9*h*) is a long, narrow tooth. It resembles a first permanent molar, but possesses a third anterior lobe. Between this anterior lobe and the protoconid, is an external accessory tubercle. The *Palaeomeryx*-fold is barely discernible, and the metastylid and entostylid are very small. There are four roots, one anterior, one median-external and two fused beneath the rear

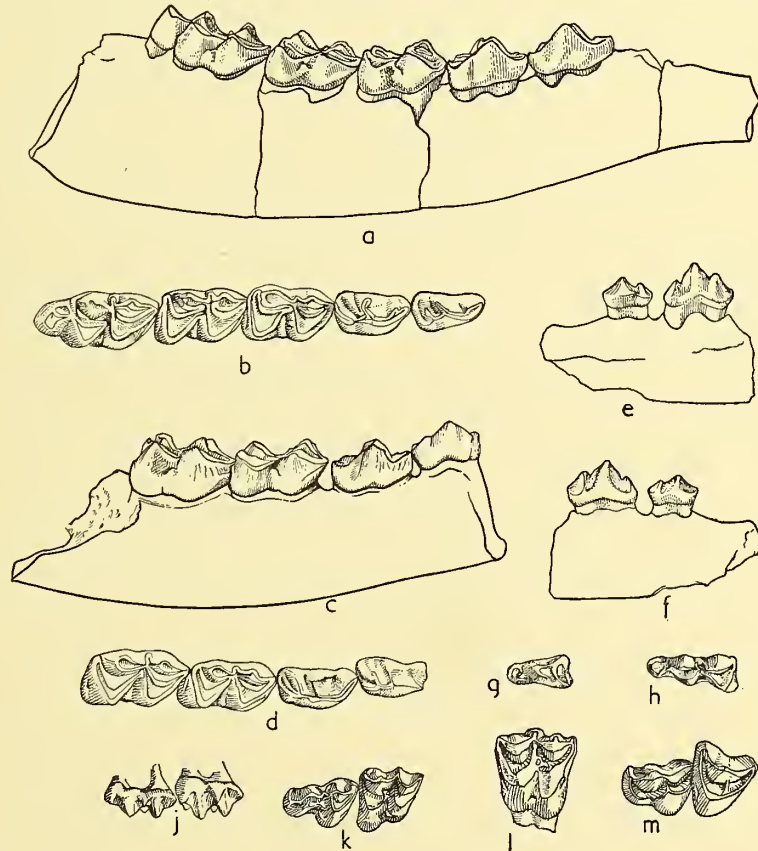


FIG. 9. *Palaeomeryx africanus*. (a) Lateral view of holotype (Sgr.73.48), right mandibular ramus with  $P_3$  to  $M_3$ , (b) occlusal aspect of same, (c) lateral view of right mandibular ramus (Sgr.M.10), with  $P_3$  to  $M_2$ , (d) occlusal aspect of same, (e) lateral view of mandibular fragment (Sgr.366.49) with left  $P_{1-2}$ , (f) medial view of same, (g) occlusal aspect of right  $dM_3$  (1840.50), (h) occlusal aspect of left  $dM_4$  (Sgr.445.48), (j) lateral aspect of left  $dM_{3-4}$  (Sgr.449.48), (k) occlusal aspect of same, (l) occlusal aspect of worn upper molar of the right side (Sgr.74.48), showing the accessory crests developed in the anterior fossette, (m) occlusal aspect of left  $P_{3-4}$  (791.52). All natural size.

portion of the crown. The third lower milk molar is represented by a single example (R.1840.50, Text-fig. 9g). It can be distinguished from the third premolar, because it is narrower relative to its length, and possesses a well-developed anterior, intermediate crest. The other milk teeth are not represented.

UPPER DENTITION.—The upper cheek teeth form a closed series from P<sup>2</sup> to M<sup>3</sup>, the second and third molars being the largest teeth in the upper jaw. Each molar is low crowned, selenodont and quadri-cuspid, consisting of somewhat compressed paracone and metacone, and stouter, lower protocone and metaconule. The crescentic wear trace of the protocone terminates abruptly against the anterior wall of the metaconule. Usually, at an early stage in wear, two small spurs or subsidiary crests arise near the junction between the protocone and metaconule and, projecting forward into the prefossette, unite there to enclose a small enamel island (Text-fig. 9l). Externally, there is a stout parastyle and mesostyle, and frequently a metastyle which is smaller, but angular and well defined. The mesostyle is low and conical (although the external styles of the upper molars in *P. africanus* are normally less bunoid than in the tragulid molar), and unites equally with both paracone and metacone. The paracone possesses an external, median rib: the metacone does not normally possess a rib; if one is present, it is very feeble. There is an accessory tubercle in the median, internal valley, and a strong cingulum is developed on the inner portion of the anterior and posterior walls of the crown. Usually, an internal cingulum is lacking. Each molar possesses four roots, the inner pair being intimately fused. The enamel of the molar teeth is finely corrugated.

A number of isolated upper molars from the East African Miocene closely resemble those of *P. africanus*, but exhibit a varied development of small accessory crests. They are regarded, provisionally, as intra-specific variants of the normal *P. africanus* pattern.

The fourth upper premolar of *Palaeomeryx africanus* (Text-fig. 9m) is a short, brachyodont tooth, resembling a single lobe of one of the molars. There is an internal cusp with crescentic wear trace, and a much higher, median, external cusp with strong, somewhat angular, external rib. From the base of the crown, the rib inclines slightly towards the rear. There is also a prominent, antero-external style, and a weaker, postero-external style. Both are more angular than those found in the corresponding tragulid tooth. Usually, the posterior horn of the inner crescent gives off a single spur into the basin of the tooth. Cingula are developed at the anterior and posterior, internal margins of the crown. There are three roots, two beneath the labial border of the crown and one beneath the internal crescent. The third premolar (Text-fig. 9m) is a little longer and lower than the fourth. Internally, it is divided by a vertical groove into a wider posterior lobe, carried on two roots, and a narrower anterior lobe with one root. Externally, there is a principal cusp, somewhat anteriorly placed and bearing a strong, median outer rib, and there is a robust, antero-external style. During wear, the two inner cusps develop into a small, anterior and a large, posterior crescent. The latter gives rise to a diminutive spur which projects into the basin of the tooth. Only one damaged specimen of the second premolar (R.695.47) is preserved. The tooth seems to have been an elongate version of the third premolar, with the antero-external style and antero-internal crescent expanded to form a more prominent anterior lobe. The disposition of the three roots is the same.





TABLE X  
UPPER DENTITION OF *PALAEOMERYX AFRICANUS*

| Catalogue No. | Locality | dM <sup>3</sup> |     | dM <sup>4</sup> |     | P <sup>3</sup> |     | P <sup>4</sup> |      | M <sup>1</sup> |      | M <sup>2</sup> |      | M <sup>3</sup> |      |
|---------------|----------|-----------------|-----|-----------------|-----|----------------|-----|----------------|------|----------------|------|----------------|------|----------------|------|
|               |          | a.p.            | tr. | a.p.            | tr. | a.p.           | tr. | a.p.           | tr.  | a.p.           | tr.  | a.p.           | tr.  | a.p.           | tr.  |
| Sgr.3209      | Songhor  |                 |     |                 |     |                |     | 8.4            | 9.0  |                |      |                |      |                |      |
| Sgr.449.48    | Songhor  | 10.0            | 6.8 | 9.0             | 9.1 |                |     |                |      |                |      |                |      |                |      |
| Sgr.27.49     | Songhor  |                 |     |                 |     |                |     | 7.2            | 9.0  | 9.3            | 10.2 |                |      |                |      |
| 547.47        | R.106a   |                 |     |                 |     | 8.7            | 7.2 | 6.6            | 8.7  | 9.5            | 10.0 | 10.6           | 12.0 | 9.8            | 11.0 |
| 694.47        | R.106    |                 |     |                 |     | 9.1            | 6.7 | 7.7            | 8.6  | 10.2           | 11.1 | 11.1           | 12.1 | 11.7           | 11.9 |
|               |          |                 |     |                 |     |                |     |                |      | 10.4           | 11.6 | 11.1           | 11.9 | 11.7           | 11.6 |
| 901.51        | R.3/R.3a |                 |     |                 |     | —              | 8.1 | 8.5            | 10.7 | 12.0           | 12.5 | —              | 14.0 | 13.0           | 14.0 |
| Mt.67.51      | Muruorot |                 |     |                 |     |                |     | —              | 11.5 | 12.0           | 13.4 |                |      |                |      |

surface of the cervid metatarsus is more deeply grooved by a median, longitudinal sulcus than is usual in Bovidae. In all respects Sgr.232.49 conforms to the cervid pattern. It was collected at Songhor, where *Palaeomeryx africanus* is well represented, and where no other ruminant dentition of equivalent size has been recorded.

? *Palaeomeryx* sp.

Part of the left ramus of a large pecoran mandible (776.52), bearing the fourth premolar and the roots of the first molar, was found in the Lower Hiwegi Beds at site R.1, Rusinga Island. The fourth premolar is precisely like that of *Palaeomeryx africanus*, but is much larger. The dimensions, length 17.0 mm. and breadth 9.5 mm., are almost identical with those of the corresponding tooth in the European species, *Palaeomeryx bojani* Meyer. The depth and thickness of the mandible beneath the fourth premolar suggest a creature equal in size to an adult red deer.

Four isolated cheek teeth from the Kiahera Series and Hiwegi Beds of Rusinga are of comparable size, and may belong to the same species as 776.52. Included among them is a trilobate, third lower molar (442.51), measuring 27.9 mm. in length and 12.6 mm. in breadth. The tooth is brachyodont and selenodont, although the outer cusps are very stout. The enamel is finely wrinkled, and the roots are fused into an anterior and a posterior group. The entoconid links with the trace of the protoconid, so that the hypoconid is isolated from the metaconid. The crown is damaged, but there seems to have been a prominent metastylid. There is also a robust entostylid, and a small tubercle between the protoconid and the hypoconid, but no *Palaeomeryx*-fold. Two specimens of the third upper premolar (825.50 and 1099.51) are very similar to the corresponding tooth in *Palaeomeryx africanus*. They differ in their greater size, and in the posterior position of the transverse accessory crest. The dimensions are:

|         | Length   | Breadth    |
|---------|----------|------------|
| 825.50  | 17.1 mm. | c 12.5 mm. |
| 1099.51 | 16.7     | 12.1       |

The remaining tooth (644.49) is an isolated and damaged upper molar. This tooth possesses many characters found in molars of *Palaeomeryx africanus*, in particular,



the strong cingulum on the inner portion of the anterior wall of the crown, the angular parastyle, and the prominent external ribbing of the paracone. The breadth of 644.49 is about 21.0 mm.

## Family BOVIDAE Gray, 1821

(Text-fig. 10)

Isolated teeth, which seem to represent two or three groups of indeterminate Bovidae, have been found in the Miocene beds of Maboko Island, western Kenya.

The material includes a right mandibular fragment (Mb.242.49, Text-fig. 10*a, b* and *c*) bearing the second molar, and a left maxillary fragment (Mb.228.49) with badly damaged third molar. The size of the two teeth suggests that they might belong to the same species. Both teeth are selenodont and somewhat high crowned, and possess the poor styelar development, feeble costae and prismatic lobes which usually characterize the dentition of Recent Bovoidea. The enamel is very finely wrinkled. In the upper molar (Mb.228.49), the external styles are indicated by weak, vertical ribs. In the lower molar (Mb.242.49), there is a median, external accessory tubercle which is small, but of prismatic habit, and a feeble cingulum is developed across the anterior wall of the protoconid. There seems to be little doubt that both teeth are best placed in the family Bovidae. Their exact systematic position cannot be determined, although the closest resemblances are to the *Strepsicerotini* and *Antilopini* of Simpson's classification (1945). The dimensions of the lower tooth are: length 10.9 mm., breadth 7.0 mm. Those of the upper tooth are: length 10.8 mm., breadth 10.6 mm.

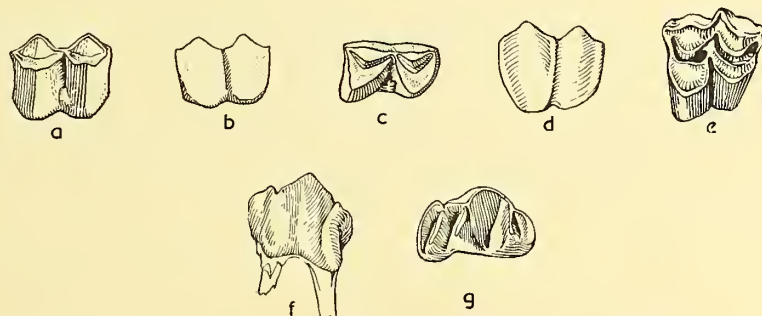


FIG. 10. Indeterminate Bovidae. (*a*) Lateral, (*b*) medial, (*c*) occlusal aspect of right  $M_2$  (Mb.242.49), (*d*) lateral, (*e*) occlusal aspect of isolated left upper molar (Kb.783.52), (*f*) lateral, (*g*) occlusal aspect of isolated left  $P_4$  (Kb.781.52). All approximately  $\times \frac{5}{4}$ .

The protoconid and entoconid of the lower molar (Mb.242.49) are linked, thereby isolating the hypoconid and metaconid. In this, and in general pattern, the lower tooth closely resembles the larger teeth from Maboko Island which MacInnes (1936) associated with his holotype of *Climacoceras africanus*. MacInnes based this species on fragments of non-deciduous "antlers" from the Maboko Miocene, and placed *Climacoceras* in the family Cervidae. Pilgrim (1941*a*) preferred to regard *Climacoceras* as a giraffoid genus, an opinion which Simpson (1945) has accepted, provisionally, in his classification of mammals. The teeth which MacInnes referred to *C. africanus* were not found in immediate association with any of the "antler" fragments,

and the fossiliferous beds at Maboko have yielded a considerable variety of pecoran, and other mammalian, remains. The "*Climacoceras*" teeth, described by MacInnes, are typically bovid in their pattern, being somewhat hypsodont and prismatic, with fused roots, and possessing neither stylids nor pronounced cingula. For these reasons, their association with the velvet-covered "antlers" of *Climacoceras* is questionable. It seems better to treat them as a distinct, but indeterminate, group of bovid material. An isolated fourth lower premolar (Kb.781.52, Text-fig. 10f, g) also from Maboko Island, may belong to this same bovid group. In its unworn condition, it is rather high crowned, with internally open basins and both intermediate crests well developed. The enamel is finely corrugated. The dimensions are: length 13.0 mm., breadth 6.8 mm.

Another isolated upper molar of the left side from Maboko Island (Kb.783.52, Text-fig. 10d, e) also resembles Recent strepsicerotine and antilopine teeth. It is rather high crowned and prismatic, but bears four roots, of which the inner pair are fused. There are no internal styles or cingula, and the parastyle and metastyle are very weak. The mesostyle is prominent, but represented by a narrow, compressed rib. The paracone possesses an ill-defined, median costa upon its labial face. The surface of the enamel is thrown into fine, vertical corrugations. The dimensions are: length 13.0 mm., breadth 12.0 mm., height at outer margin 11.0 mm. It is possible that this tooth belongs to the same species as the lower molars which MacInnes (1936) originally referred to *Climacoceras africanus*.

Finally, there is a badly damaged, left upper molar from Maboko Island (Kb. 784.52) which is very similar to the tooth described in the preceding paragraph. It is, however, larger, with more faintly wrinkled enamel and a stronger parastyle. The dimensions are: length 14.8 mm., breadth 14.5 mm., external height greater than 11.0 mm. This tooth also may belong to the same species as those described by MacInnes (1936).

No new generic or specific names are proposed for any of this scanty bovid material, which may be of later date than the more normal representatives of the Rusinga-type Miocene fauna (see p. 48).

## PECORA Incertae Sedis

### *PROPALAEORYX* Stromer, 1926, emend.

DIAGNOSIS.—Pecora of medium size, with shallow mandible and rather brachyodont, selenodont lower cheek teeth, closed from  $P_2$  to  $M_3$ ;  $P_1$  isolated by very short diastema. Enamel wrinkled. Lower molars with very strong meta-stylid and entostylid; pronounced median rib on lingual surface of metaconid, similar rib on entoconid; accessory stylid in median, external valley developed to varying degree.

TYPE SPECIES.—*Propalaeoryx austro-africanus* Stromer, 1926; Lower Miocene, South-west Africa.

AFFINITIES.—The lower cheek teeth in *Propalaeoryx* are brachyodont, with well-formed roots, and the molars show a pronounced tendency towards the development



of cingula and styliids. All these features are characteristic of Cervidae, but it is rather abnormal to find any of them developed in Bovidae (Loomis, 1925; Frick, 1937). Indeed, in everything, except size, the lower molars of *Propalaeoryx* are precisely like those of *Micromeryx* from the Miocene of Europe. Arambourg (1933) has already drawn attention to what he termed the unmistakable cervid affinities of *Propalaeoryx*. On the isolated evidence of the teeth, there would be little reason to question his opinion.

The East African Miocene deposits have also yielded a number of isolated ruminant limb bones which, from their size and pecoran character, may belong to *Propalaeoryx nyanzae*. The distribution of these bones among the fossiliferous localities is similar to that of dental material referred to *P. nyanzae*. Limb bones of this size are listed under Group 3 in a subsequent section devoted to associated post-cranial material (p. 39). Two specimens represent the distal portion of the cannon-bone, but only one (1635.50, Text-fig. 11b) belongs with certainty to a hind limb. Despite damage, this posterior cannon-bone clearly exhibits a bovid condition in the housing of the extensor tendon (see p. 23), while retaining a remarkably cervid-like development of the shaft. The bone cannot be assigned to *Propalaeoryx* with absolute certainty, but its occurrence in association casts grave doubts on the supposed cervid affinities of that genus, and indeed suggests that early Bovidae may have differed little in their dental characteristics from contemporaneous cervids. *Propalaeoryx* is undoubtedly a pecoran genus, but its exact systematic position within the Pecora remains uncertain.

*Propalaeoryx nyanzae* sp. nov.

(Text-fig. 12)

DIAGNOSIS.—A species of *Propalaeoryx* with lower molar series ( $M_{1-3}$ ) measuring about 45 mm. in length. All lower molars have prominent accessory tubercle in median, external valley. Teeth rather lower crowned than in type species, *P. austroafricanus*.

DISTRIBUTION.—Type area and formation, Lower Hiwegi Beds (Miocene) of Rusinga Island, western Kenya.

HOLOTYPE.—Fragment of left mandibular ramus (324.47) with  $M_{1-2}$ , from Lower Hiwegi Beds, Rusinga Island.

LOWER DENTITION.—The inferior molars are moderately low-crowned and of selenodont pattern. The second molar possesses somewhat angular protoconid and hypoconid, slightly compressed from front to rear; a slender, conical styloid is developed in the median valley between them. There is no *Palaeomeryx*-fold. The metaconid and entoconid are compressed transversely; the former does not overlap the latter to any appreciable extent. There is a very prominent metastyloid at the rear of the metaconid, which is separated from the metaconid by a deep, funnel-shaped depression and is cut off from the anterior extremity of the entoconid by a marked cleft. In wear, the metastyloid forms a pronounced, projecting fold at the rear of the metaconid trace. A robust entostyloid, with which the posterior limb of the crescentic hypoconid trace is confluent, lies directly behind the entoconid, but is separated from the latter cusp by a deep sulcus. The metaconid possesses a strong, median-

lingual rib, the entoconid bears a similar, but slightly weaker, rib. At the anterior junction of the protoconid and metaconid, there is another small, accessory stylid,

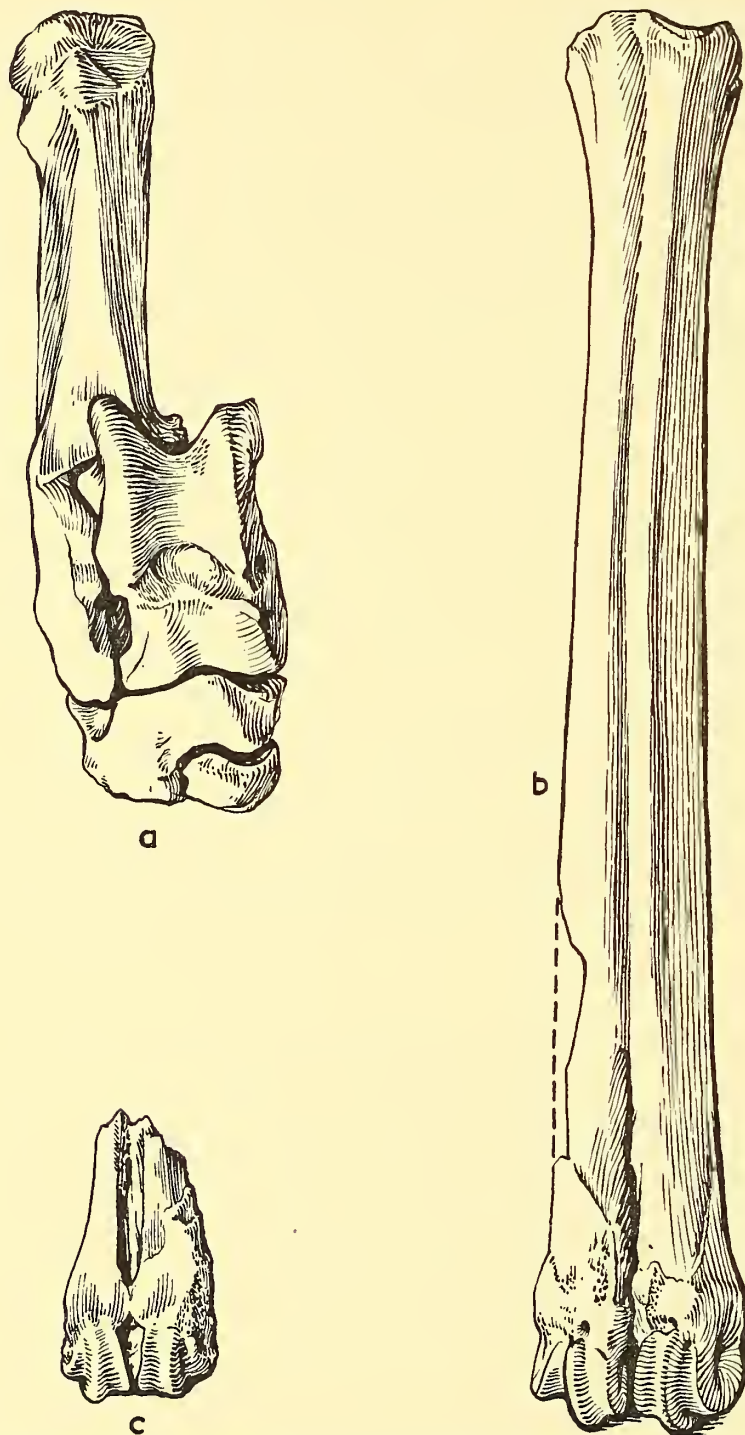


FIG. 11. (a) Anterior view of right tarsus (1632, 33, 34 and 36.50) and (b) anterior view of corresponding metatarsus (1635.50), both referred to size group 3 (see p. 39). (c) Anterior view of fragment of metatarsus (Sgr.232.49), referred to size group 4 (see p. 40). All natural size.

and a shelf-like cingulum is developed across the anterior face of the protoconid. A posterior cingulum is present, but it is usually less pronounced. A tiny, accessory styloid is sometimes found below the entostyloid. The two roots are broad and compressed from front to rear.

The first molar is very similar to the second, but slightly smaller. The third molar differs by the addition of a posterior third lobe, mounted on a single root. This third lobe consists of a postero-external main cusp, wearing into a crescentic trace, and a small, internal styloid, placed at the posterior limit of the crescent.

TABLE XI  
LOWER DENTITION OF *PROPALAEORYX NYANZAE*

| Catalogue No.        | Locality  | M <sub>1</sub> |     | M <sub>2</sub> |     | M <sub>3</sub> |     |
|----------------------|-----------|----------------|-----|----------------|-----|----------------|-----|
|                      |           | a.p.           | tr. | a.p.           | tr. | a.p.           | tr. |
| 324.47<br>(HOLOTYPE) | R.I       | 13.5           | 7.5 | 13.8           | 8.0 | —              | —   |
| 614.49               | R.IA      |                |     |                |     | —              | 8.5 |
| 1263.51              | Mfwanganu |                |     | 13.1           | 8.4 |                |     |
| 774.52               | R.I       |                |     | 13.8           | 8.8 | 18.1           | 8.8 |
| 780.52               | R.I2      |                |     |                |     | 20.0           | 8.2 |

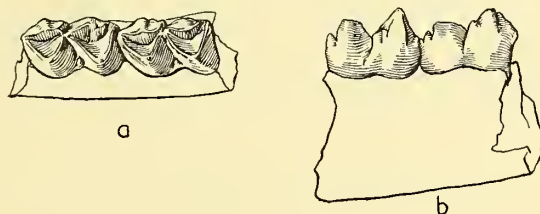


FIG. 12. *Propalaeoryx nyanzae*. Holotype (324.47). (a) Occlusal, (b) medial aspect of mandibular fragment with left M<sub>1-2</sub>. Natural size.

DISCUSSION.—The only specimens which Stromer (1926) referred to in his description of *Propalaeoryx austro-africanus* were the holotype (a right mandibular ramus with P<sub>2</sub> to M<sub>3</sub>; pl. 40, fig. 1), and a few isolated anterior teeth found in association. There can be little doubt that the Rusinga material must be assigned to the genus, *Propalaeoryx* Stromer, but it differs sufficiently from the holotype of *P. austro-africanus* to be distinguished by a new specific name. For example, the Rusinga teeth are smaller and lower crowned, the internal styloids of the molars are perhaps less pillar-like, and all the molars possess a prominent development of the median-external accessory tubercle which is restricted to the first lower molar of the holotype of *P. austro-africanus*. On the other hand, the holotype of *P. austro-africanus* may be atypical, since the Rusinga material seems to provide a condition intermediate between that specimen and the specimen which Stromer (1926, pl. 40, fig. 2) termed *Cfr. Strogulognathus* Filhol. There remains, therefore, a possibility that the two



groups of material described by Stromer and the Rusinga specimens may all represent a single species, *Propalaeoryx austro-africanus*, but this would be difficult to prove without further collecting at Stromer's sites in South-west Africa.

### *WALANGANIA* gen. nov.

DIAGNOSIS.—Small, lightly constructed Pecora. "Antlers" not known. Mandible shallow, with prominent angle and large, recurved coronoid process. Cheek teeth closed from  $P_2$  to  $M_3$ ;  $P_1$  lost from both jaws. Lower molars brachyodont, selenodont and somewhat narrow. Metaconid and entoconid compressed transversely, and only very slightly oblique to long axis of crown. Metaconid does not overlap entoconid lingually. Both inner cusps lack median, internal ribs. Metastylid feeble, entostylid moderately developed. Protoconid and hypoconid angular and compressed from front to rear, with slightly concave posterior wall. *Palaeomeryx*-fold absent. Slender, conical stylid developed in median external valley. Rather weak anterior and posterior cingula. Upper molars square, brachyodont and perfectly selendodont. Paracone possesses angular median external rib, metacone lacks external rib. Parastyle and mesostyle low and former a little bunoid; metastyle not developed. Mesostyle unites equally and symmetrically with paracone and metacone. Crescentic wear trace of protocone truncated by anterior limb of metaconule wear trace. Strong anterior and less pronounced postero-internal cingula. Enamel of cheek teeth usually smooth, sometimes shows very faint, vertical corrugations. Pelvis and rear limbs of advanced pecoran type.

TYPE SPECIES.—*Walangania gracilis* sp. nov.

#### *Walangania gracilis* sp. nov.

(Text-figs. 13-16)

DIAGNOSIS.—As for the genus.

DISTRIBUTION.—At present, only known by the holotype which was recovered from the Miocene of Walangani on the north-east coast of Mfwanganu Island, western Kenya.

HOLOTYPE.—Skeleton of a young individual (1334.51), with second molars erupting and epiphyses partly open. Most of the forelimbs and pectoral girdle, part of the vertebral column, and the upper part of the skull are missing. Since the skull is incomplete, and the specimen represents an immature individual of uncertain sex, it is impossible to determine whether *Walangania gracilis* possessed "antlers", or not. No fragments of "antlers" were found in association.

JAWS AND DENTITION.—The shallow mandible possesses a prominent angle which is preceded by a marked concavity in the inferior margin of the horizontal ramus. The coronoid process is large and recurved, as in Recent Pecora. The mandible bears a series of brachyodont cheek teeth, closed from the second milk molar to the partly erupted second permanent molar. The anterior milk molar, and presumably also the first premolar, was suppressed in both the upper and lower jaw.

The first lower molar is a selenodont, four-rooted tooth, with smooth enamel. It is rather narrow, relative to its length, and the posterior lobe is a little broader than the anterior. The internal cusps are somewhat compressed transversely, but possess a smoothly convex lingual face, lacking a central rib. Their wear traces lie almost parallel to the long axis of the crown, and the metaconid does not overlap the entoconid to any appreciable extent. The posterior extremity of the metaconid is prolonged into a very small metastylid, and a moderate entostylid is developed behind the entoconid. The protoconid and hypoconid are compressed from front to rear and possess a slightly concave posterior wall. Their wear traces are V-shaped, rather than crescentic, and incline a little towards the rear of the tooth. There is no *Palaeomeryx*-fold, but a conical stylid is developed in the median external valley, between the protoconid and hypoconid. There is a fairly strong anterior cingulum, and a less pronounced posterior cingulum.

The second milk molar is represented by two alveoli. The third is represented by the base of a long, narrow crown, also carried on two roots, and seems to have consisted originally of a prominent central cusp, with subordinate cusps placed one at the front and one at the rear of the crown. The fourth milk molar is precisely like a permanent molar, prolonged into a third anterior lobe. There are two posterior roots, a median external root, and probably a single anterior root. The anterior dentition of the lower jaw is not known.

The dimensions of the lower teeth are as follows:

|         | dM <sub>2</sub> |     | dM <sub>3</sub> |        | dM <sub>4</sub> |     | M <sub>1</sub> |     |
|---------|-----------------|-----|-----------------|--------|-----------------|-----|----------------|-----|
|         | a.p.            | tr. | a.p.            | tr.    | a.p.            | tr. | a.p.           | tr. |
| Left .  | c. 6.0          | —   | c. 8.0          | —      | c. 12.0         | 4.7 | 11.0           | 6.0 |
| Right . | c. 6.0          | —   | c. 8.0          | c. 3.0 | c. 12.0         | 4.7 | 11.0           | 6.0 |

The upper dentition is represented by a closed series of cheek teeth from the second milk molar to the second permanent molar, the latter being only partly erupted. The first milk molar was never developed. The first true molar is brachyodont, selenodont and four-rooted. The enamel is smooth. The paracone and metacone are strongly concave externally, and each bears a median angularity on its lingual face. The paracone also possesses a pronounced median external rib, but the metacone does not. The crescentic wear traces of the two outer cusps are confluent with a centrally-placed mesostyle which is rather low and a little compressed. There is a similar, but slightly more bunoid, parastyle at the antero-external angle of the crown. A metastyle is not developed. The protocone and metaconule are somewhat compressed from front to rear, and the V-shaped trace of the former terminates abruptly against the anterior wall of the metaconule. There is a pronounced cingulum across the anterior face of the protocone, as in *Palaeomeryx africanus*, and a weaker cingulum is developed around the base of the metaconule. The first molar of the left side seems to possess a very small, accessory crest which projects forward from the postero-external extremity of the protocone wear trace into the anterior fossette. The crest is not clearly developed in the corresponding molar of the right side.

The fourth milk molar of the upper jaw only differs from a permanent molar by possessing a very feeble median rib upon the outer face of the metacone. The third milk molar also resembles a true molar, but a posterior external rib is again developed, and the anterior half of the crown is rather long and narrow. There are

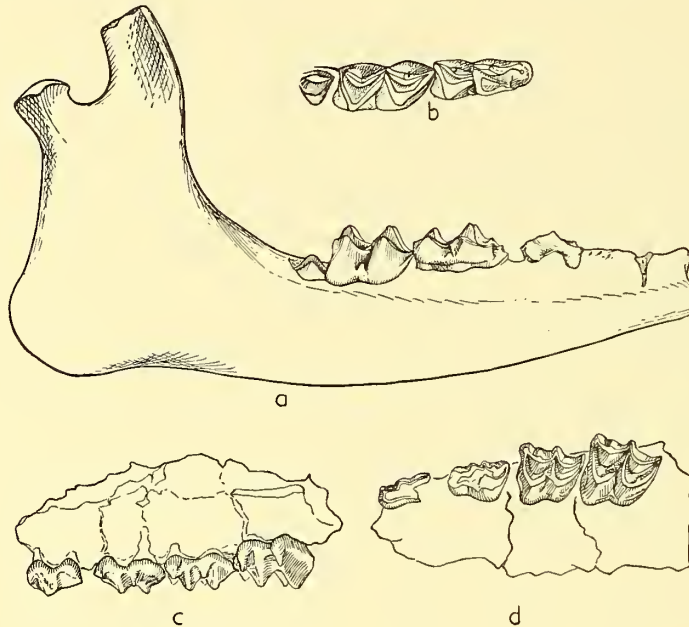


FIG. 13. *Walangania gracilis*. Holotype (I334.51). (a) Lateral view of immature right mandibular ramus with dM<sub>3</sub> to M<sub>1</sub> and part of M<sub>2</sub>, (b) occlusal aspect of right dM<sub>4</sub> and M<sub>1</sub>, (c) lateral and (d) palatal aspect of maxillary fragment with left dM<sub>2</sub> to M<sub>1</sub>. All natural size.

three roots, placed two beneath the rear of the crown and one in front. The second milk molar is a narrow tooth mounted on two roots, and closely resembles the corresponding tooth in Recent cervids. The dimensions of the upper teeth are as follows:

|         | dM <sup>2</sup> |     | dM <sup>3</sup> |        | dM <sup>4</sup> |     | M <sup>1</sup> |      |
|---------|-----------------|-----|-----------------|--------|-----------------|-----|----------------|------|
|         | a.p.            | tr. | a.p.            | tr.    | a.p.            | tr. | a.p.           | tr.  |
| Left .  | 8.5             | 4.7 | 9.7             | 6.5    | 9.0             | 8.7 | 10.5           | 10.2 |
| Right . | —               | —   | —               | c. 6.5 | 9.0             | 8.7 | 10.5           | 10.1 |

POST-CRANIAL SKELETON.—A small fragment of the atlas vertebra is preserved, and the anterior, ventral portion of the axis. The latter possesses the spout-like odontoid process, characteristic of Pecora. Only one thoracic vertebra is adequately preserved. This is an anterior thoracic, with small transverse process, faceted to receive the tuberculum of a rib. The opisthocoelous centrum possesses a strong, angular, median keel on its ventral surface. The right side of the neural arch and the



entire neural spine are missing, but the left pre- and post-zygapophyses are present. Nine isolated centra of graded size represent some cervical and some thoracic vertebrae. In addition, there are numerous fragments of at least twenty ribs. Some are thick, flat, double-headed, anterior ribs, others are single-headed, posterior ribs of rounded section. There is also a series of five lumbar vertebrae, probably the first to the fifth. This may be the original number, although the spacing of the anterior facets on the first sacral vertebra suggests that a sixth lumbar may have been present. They do not differ in any essential detail from the corresponding vertebrae in Recent Pecora. The opisthocoelous centra are low and broad at the rear of the series, becoming higher and narrower in the anterior lumbar region. The transverse processes are large, wide and inclined slightly forward and downward. The inward-inclined pre-zygapophyses are supported by stout metapophyses. The neural spines are low, broad in the antero-posterior direction and usually incline forward, although, in the first lumbar vertebra, the neural spine is approximately vertical. A complete series of four rapidly diminishing sacral vertebrae is represented. They are unfused and the dorsal portion of the first and second is missing, but they resemble very closely the corresponding vertebrae in Recent Cervidae. Five caudal vertebrae of pecoran type are included, and probably represent second to fourth and sixth and seventh. The first and fifth caudals seem to be absent, and, at the distal extremity of the tail, either two or three joints are lacking. Originally, there must have been about nine caudal vertebrae. The free portion of the tail projecting beyond the ischium was clearly very short.

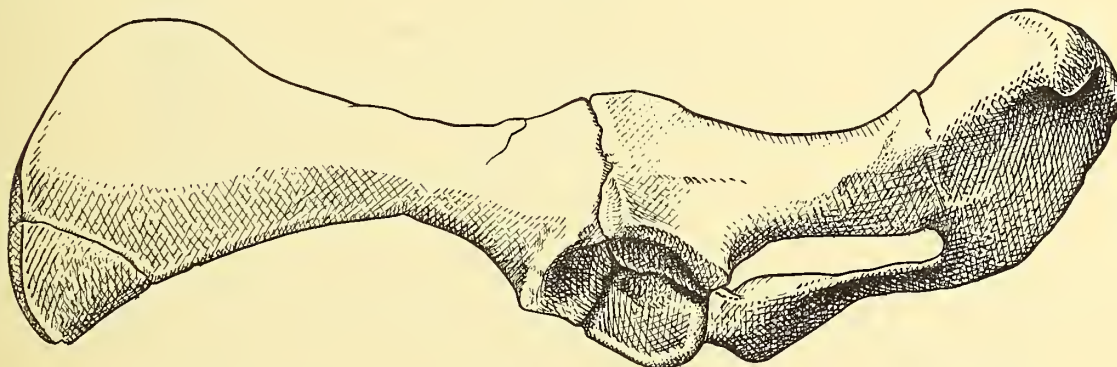


FIG. 14. *Walangania gracilis*. Holotype (I334.51). Lateral view of left innominate bone. Approximately natural size.

The pelvis (Text-fig. 14) is characteristically pecoran, and lacks any trace of the longitudinal bridge of bone which links the sacrum to the dorsal portion of the ischium in adult tragulids. The pelvis is elongate, and, in life, probably extended back from the sacrum at an acute angle to the horizontal, so that the entire pubic symphysis lay behind the acetabulum. Although the epiphyses are missing, the symphysis, in the adult condition, must have been long. The ilium is expanded and everted at its upper extremity, but not as much as in adult Pecora today. Immediately in front of the acetabulum, the ilium is greatly constricted. Although the pelvis has been a little distorted during burial, the anterior outlet seems to have been oval, and the posterior outlet a V-shaped channel with steeply dipping sides. The acetabular fossa

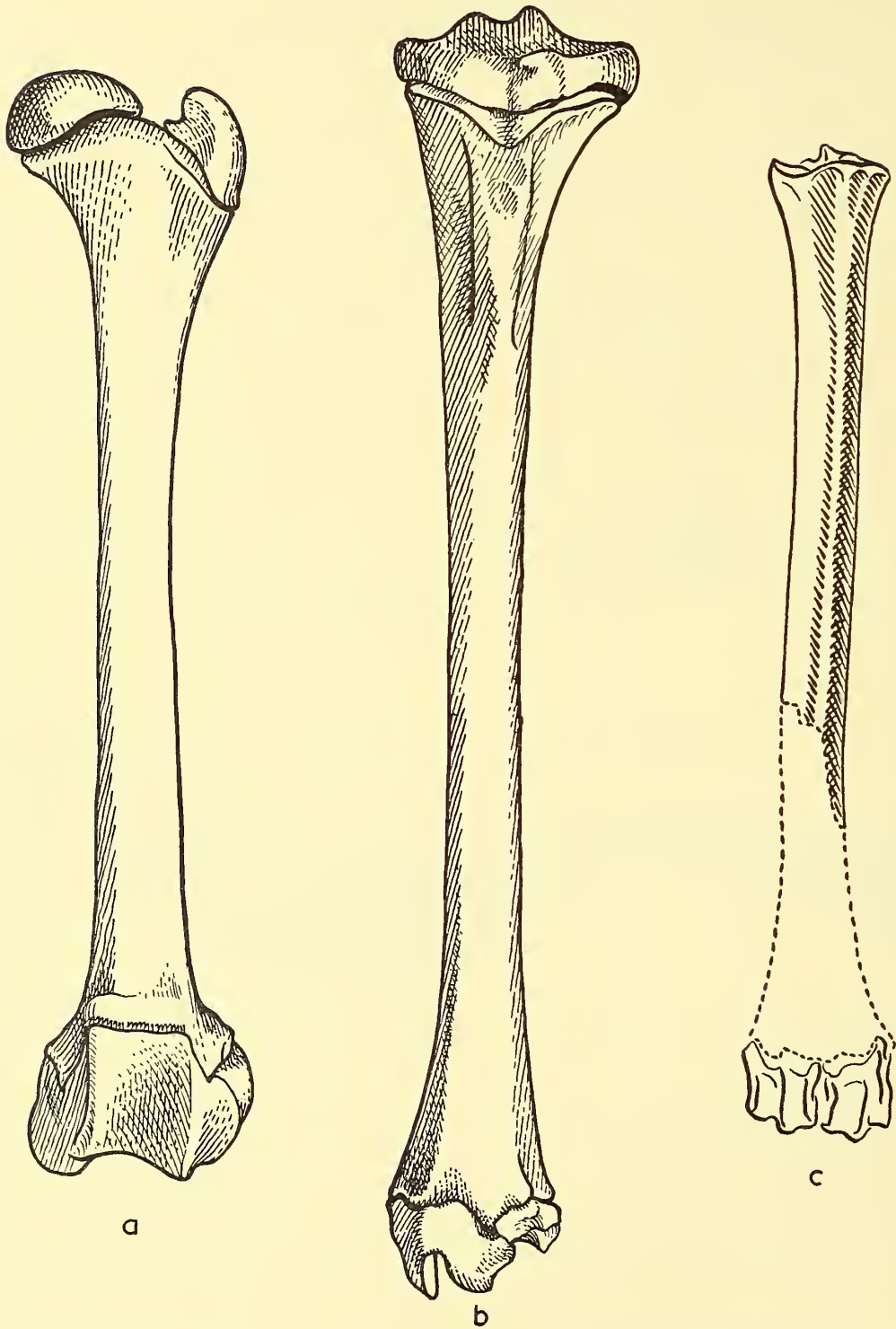


FIG. 15. *Walangania gracilis*. Holotype (1334.51). Anterior view of (a) left femur, (b) left tibia, (c) left metatarsus. All natural size.

is deep, narrow and well-formed, and the obturator foramen possesses a long, oval outline. The ischial tuberosities each carry a stout process on their outer side. The maximum length of the pelvis is about 135 mm.

The femur (Text-fig. 15a) is approximately 160 mm. in length. It is smaller and more delicately constructed than the femur of *Cervus elaphus*, but otherwise differs only in a manner related to its smaller size and immaturity. For example, the trochanters are relatively smaller, and the *linea aspera* is less pronounced. The position of the distal condyles indicates that the femur extended forward from the acetabulum at a marked angle to the vertical, as in Recent Cervidae and Bovidae, and in a manner quite foreign to Recent Giraffidae. The patella is wedge-shaped and is placed somewhat distally in relation to the femur. The tibia (Text-fig. 15b), which is about 190 mm. long, is indistinguishable from the corresponding bone in Recent cervids and bovids of similar size. The fibula is characteristically reduced to a small fragment of bone lying between the lower end of the tibia and the calcaneum.

The tarsus (Text-fig. 16) retains an independent internal cuneiform bone which is, proportionately, a little larger than in Recent Cervidae and Bovidae. For this reason, the facets uniting the tarsus and metatarsus differ slightly, but in all other respects, the tarsus is a reduced version of that found, for example, in *Cervus elaphus*. The dimensions of the holotypic tarsal bones of *Walangania gracilis* are as follows:

|                      | Greatest length<br>parallel to axis of<br>foot |       | Greatest breadth<br>transverse to axis of<br>foot |       |
|----------------------|--|-------|---|-------|
|                      | Left   | Right | Left  | Right |
| Calcaneum . . .      | 54.0 mm.                                       | 54.5  | 18.0  | 18.0  |
| Astragalus . . .     | 27.0   | 28.0  | 18.0  | 18.0  |
| Cubo-navicular . . . | 18.0   | 18.0  | 21.0  | 21.0  |
| Ext. cuneiform . . . | 5.5  | 5.5   | 11.0  | 11.0  |

The long, slender cannon-bone (Text-fig. 15c) is typically pecoran. It is strongly compressed laterally, and, although the component metatarsals are completely fused, it is deeply divided behind, as well as in front, by a longitudinal, median sulcus. In these two characters, it resembles the cervid, rather than the bovid, condition, although a similar, but less pronounced, condition is found in some small, delicately constructed antelopes. The distal keeling of the third and fourth metatarsals is strong, and extends fully on to the anterior surface of each condyle. The distal portion of the cannon-bone shaft is missing, and it is impossible to determine, from a study of the associated articular condyles, whether the lower extremity of the metatarsus was of cervid or bovid type (see p. 23). At a conservative estimate, the holotypic cannon-bone of *Walangania gracilis* measured not less than 140 mm. in length. Thus, the ratio, length of tibia and metatarsus to length of femur, was as great in *W. gracilis* as in many Recent deer and antelopes. There is no sign of lateral metapodials.

The anterior limbs and pectoral girdle are poorly represented. There are three isolated, distal epiphyses belonging to metapodial bones. Since they are a little



smaller than those associated with the metatarsals, they are presumed to belong to the anterior cannon-bones. The wrist joint is represented by isolated lunar, scaphoid and magnum of the right side. In addition, the distal trochlea of the right humerus is identifiable, and a proximal fragment of the right ulna, lacking the olecranon process. The glenoid portion of the left scapula is all that remains of the pectoral girdle. As far as can be determined, all these bones resemble the corresponding bones in Recent Cervidae and Bovidae. A number of isolated phalanges, indistinguishable from those found in Recent deer, are also preserved. Five are proximal phalanges, six are middle phalanges, and three are ungual phalanges. Finally, there are three isolated sesamoid bones, similar to those found in the limbs of Recent Pecora, and a quantity of indeterminate fragments of anterior limb bones. These remnants suggest that, in *Walangania gracilis*, the fore limbs were a trifle smaller, relative to the hind limbs, than they are, for example, in *Cervus elaphus*.

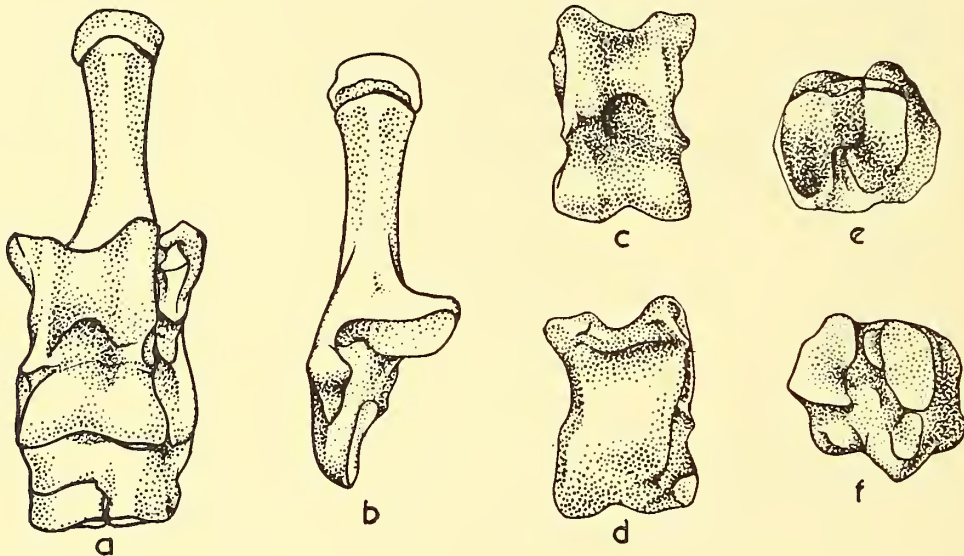


FIG. 16. *Walangania gracilis*. Holotype (I334.51). (a) Anterior view of left tarsus, (b) anterior view of right calcaneum, (c) anterior view of right astragalus, (d) plantar view of same, (e) proximal aspect of right cubo-navicular, (f) distal aspect of same. All natural size.

AFFINITIES.—The post-cranial skeleton of *Walangania gracilis* is of rather advanced pecoran type. In life, the pelvis seems to have extended almost horizontally from sacrum to posterior outlet with very little change of direction between its iliac and pubic portions, so that the symphysis and obturator foramen lay behind the acetabulum. In addition, the ischia were steeply inclined, in cervid fashion, on either side of the posterior outlet. The patella occupied a somewhat distal position in relation to the femur, indicating that the femur extended forward from the acetabulum. The tarsus retained independent external and internal cuneiform bones. The fully fused metatarsals are strongly compressed in a transverse direction, but the cannon-bone is deeply grooved by a longitudinal sulcatus on both its anterior and plantar surfaces. The condyle of each metatarsus possesses a pronounced keel which extends fully on to the anterior face of each condyle. The length of the cannon-bone and tibia is great when compared with the length of the femur. These features are

characteristic of the Recent cervid and bovid condition, particularly the former. In contrast, the pelvis of advanced Giraffidae (*Giraffa* and *Okapia*) exhibits a marked change of direction between the horizontal pubic portion and the steeply inclined ilia. Consequently, the pubic symphysis commences below, or even anterior to, the acetabulum. In addition, the ischia slope outwards at a low angle on either side of the posterior outlet which differs, therefore, from the narrow channel found in Cervidae and Bovidae. Wherever the tarsus of Giraffidae is known, the cuneiform bones have usually lost their independence, even in immature individuals. The tragulid pelvis and rear limbs also possess distinctive features which are entirely unrepresented in *Walangania*.

The molar teeth of *W. gracilis* are brachyodont, with early formed roots, and they show a tendency to develop cingula and accessory tubercles. The upper molars have a strong, rather angular, anterior external rib, but lack a posterior external rib. Each of these characters is more typical of Cervidae than of Bovidae. The upper molars also differ from the giraffid condition, in that the mesostyle unites equally and symmetrically with both paracone and metacone. The closest similarities to the dentition of *W. gracilis* are exhibited by the Miocene Blastomerycini of North America, although members of that tribe, described by Matthew (1908) and Frick (1937), seem to possess rather more primitive limbs than *Walangania*. Among Recent genera, the Asiatic musk-deer shows the strongest resemblance, but its teeth incline to greater hypsodonty.

It would be unwise to treat *Walangania* as a giraffoid genus, since *W. gracilis* possessed certain specialized features which characterize advanced Cervidae and Bovidae, but are not found in Giraffidae. To decide whether *Walangania* should be referred to the Cervidae or the Bovidae is a more difficult problem. The dentition of *Walangania gracilis* is typically cervid, and there would be little hesitation in placing *Walangania* within the family Cervidae, but for one factor. The East African Miocene has yielded diagnostically bovid cannon-bones which may conceivably belong to *Propalaeoryx nyanzae*, another ruminant species with deer-like dentition. The presence of such bones in the Miocene of Kenya is sufficient to cast doubt on the value of dental characters when distinguishing between the early African deer and antelopes. It is unfortunate that the distal portion of the posterior cannon-bone shaft is not preserved in the holotype of *Walangania gracilis*, and that no definite conclusions can be reached concerning its original condition. Thus, the only certain means of deciding whether it is to be considered a bovid or a cervid skeleton is lost. For the present, *Walangania* must be regarded as a pecoran genus of doubtful systematic position, although the available evidence may slightly favour inclusion with the Cervidae. If this latter interpretation is correct, it seems likely that *Walangania gracilis* represents a somewhat precocious cervid stock, which developed along similar lines to the North American Blastomerycini, but independently of that group.

#### MISCELLANEOUS LIMB BONES

The East African Miocene deposits have yielded very many isolated, and often fragmentary, limb bones. All examples listed here are of ruminant pattern, but only



in rare cases can they be linked with certainty to a particular dentition. Most of the specimens cannot be diagnosed accurately, although they have been divided into a number of groups, on the basis of size and form.

The astragalus is the bone most frequently preserved; it is represented by 276 specimens. About 80 of them are indistinguishable from the corresponding bone in Recent Cervidae and Bovidae, and clearly belong to the cervid and bovid species described in preceding sections of this paper. The remaining astragali are narrower relative to their length. Viewed from above, they show a pronounced bend in their long axis, being convex externally and concave internally (Text-fig. 17*d-g*). Fortunately, an astragalus of this type occurs as part of an intact tragulid tarsus and metatarsus (738.52), preserved in association with a dentition which has been referred to *Dorcatherium pigotti*.

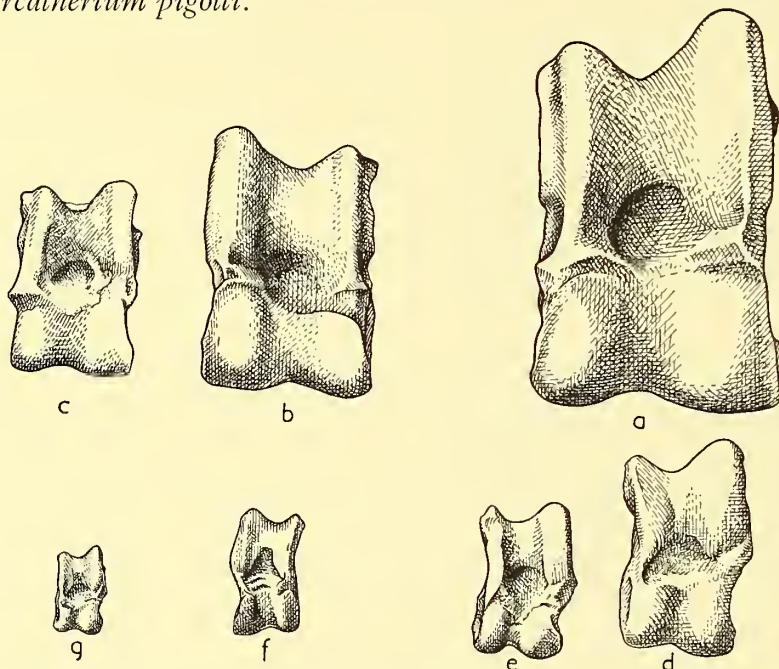


FIG. 17. Anterior view of seven isolated ruminant astragali from the Miocene of East Africa. (a), (b) and (c) three astragali of pecoran habit, representative of size groups 2, 3 and 4, respectively; (d), (e), (f) and (g) four astragali of tragulid pattern, representative of size groups 5, 6, 8 and 7, respectively (see pp. 38-42). All natural size.

The astragali of pecoran type exhibit a well-defined trimodal distribution with respect to size. Similarly, the tragulid astragali fall into four clear-cut size groups, one of them being further differentiated by its restriction to the Songhor site. These seven groups of astragali form the basis of the principal subdivisions adopted here (Text-fig. 17). In most cases, isolated cubo-navicular bones can be referred to their correct astragalus group by a combination of size and distinctive tragulid or pecoran pattern, but other limb bones are extremely constant throughout the Ruminantia. Consequently, some of the groups listed below may contain limb bones drawn from different genera, or even from distinct families. It is possible, for example, that tragulid bones, other than astragali, may be included with bovid and cervid bones in group 4, since Tragulidae, Cervidae and Bovidae of similar size are present in the



East African Miocene. On the other hand, some indication of the size relationship between dentitions and corresponding limb bones is provided by the holotypic skeleton of *Walangania gracilis* (1334.51), and by the associated tarsus (738.52) of *D. pigotti*, mentioned above.

GROUP 1.—An unknown ruminant of very large size, represented by an isolated left magnum from Kirimon (Kir.37) and a right lunar from Maboko Island (Kb.1934). Both bones are about one and a half times larger than the corresponding bones in an adult red deer, but their form is very similar.

GROUP 2.—A large ruminant with individual bones similar in pattern and dimensions to the corresponding units in the skeleton of *Cervus elaphus*. Material of this size group comprises four scaphoids, two lunars, three magna and one unciform; part of a left humerus, portions of a left femur, and a right tibia, a patella and a right fibula; ten astragali (Text-fig. 17a), portions of three calcanea, one cubo-navicular and an isolated sesamoid bone; portions of four cannon-bones and six isolated distal condyles of same; three proximal, twelve second and seven ungual phalanges. All the cannon-bone fragments seem to belong to anterior limbs and it is impossible to determine whether they are cervid, or bovid, or represent both families. The distribution, by numbers of specimens was:

| Rusinga | Karungu | Muruorot | Mfwanganu | Ombo | Maboko |
|---------|---------|----------|-----------|------|--------|
| 35      | 8       | 10       | 3         | 4    | 2      |

Some of these isolated limb bones may represent the same species as the mandibular fragment from Rusinga, described previously (p. 24) as ?*Palaeomeryx* sp.

It is possible that another group, intermediate in size between groups 1 and 2, could be split off. There are two astragali (Kb.-A-1934 and Om. 29-6-42), two proximal phalanges (Kb.-A-36 and Mt.10.51) and part of a cannon-bone (Mw.2) included in group 2, which are appreciably larger (approx.  $\times 5/4$ ) than the corresponding bones forming the bulk of that group. Since the absence of material of intermediate size may be due to inadequate sampling, this larger material is retained, provisionally, in group 2.

GROUP 3.—A ruminant of medium size, perhaps *Propalaeoryx nyanzae*, with limb bones approximately equal to those of an adult fallow deer. The following items are included here. Skeleton of a right foot, lacking the digits and the internal cuneiform bone, and portion of an associated right femur (1631-36.50, Text-fig. 11a, b) from Kathwanga, Rusinga Island. The cannon-bone (1635.50) is about 188 mm. long and possesses strongly keeled distal condyles. The shaft is slender and completely fused, but is deeply grooved on both the anterior and plantar surfaces. This condition is common in Cervidae, but of rarer occurrence in Bovidae. Nevertheless, the lower portion of the shaft seems to lack the canal which, in Cervidae, transmits the tendon of the long digital extensor muscle. The distal portion of another right metatarsus (Karungu, 14-7-37) is also included in group 3. It is of unmistakable bovid type, with an open groove for the passage of the long digital extensor tendon. In addition, there are remnants of two scapulae and one ulna; three scaphoids, one unciform, two magna and one cuneiform; fragments of two femora and three tibiae, and an

isolated left patella and fibula; twenty-five astragali (Text-fig. 17*b*), six cubo-naviculars, one external cuneiform bone and two isolated distal condyles of metapodial bones; eight proximal, twelve second and four ungual phalanges. An isolated thoracic vertebra from Maboko may also belong here. The distribution, by numbers of specimens, was:

| Rusinga | Karungu | Muruorot | Ombo | Maboko |
|---------|---------|----------|------|--------|
| 28      | 23      | 6        | 1    | 15     |

The internal cuneiform bone of the tarsus seems to have been proportionately larger than it is, for example, in *Cervus*, and, consequently, the posterior facet between the cubo-navicular and the cannon-bone is not so well developed as it is in that genus. Nevertheless, all the bones listed above are very similar to the corresponding bones in Recent Cervidae or Bovidae.

GROUP 4.—A ruminant of small-medium size, represented by portions of three scapulae, eight humeri and five radii; nine scaphoids, two lunars, two cuneiforms, one unciform and one magnum; fragments of seven femora and seven tibiae, with two patellae and one fibula; forty-nine astragali (Text-fig. 17*c*), parts of twenty-two calcanea, five cubo-naviculars, three external cuneiforms and remains of ten cannon-bones; eighteen proximal, twenty-seven second and twelve ungual phalanges. The distribution, by numbers of limb bone units, was:

| Rusinga | Karungu | Mfwanganu | Maboko | Songhor | Koru |
|---------|---------|-----------|--------|---------|------|
| 97      | 1       | *1        | 20     | 73      | 2    |

(\*Excluding holotypic skeleton of *Walangania gracilis*)

The astragali and cubo-navicular bones are all of pecoran type. Only one posterior cannon-bone (Sgr.232.49, Text-fig. 11*c*) is sufficiently preserved for conclusive identification. It is of characteristic cervid pattern. The distal portion of another cannon-bone, collected at Rs.18, Rusinga, is preserved, but seems to represent a metacarpus. It might be either cervid or bovid. There is also the proximal portion of a right cannon-bone (F.2103.41) from Rusinga which retains vestiges of the lateral metapodials. It is impossible to determine whether this example is cervid or bovid, and whether it represents a front or rear limb.

The bones allotted to this group indicate creatures about the size of roe deer, or even smaller. Some of the material may belong to *Walangania gracilis*, but the majority probably belongs to the commoner species, *Palaeomeryx africanus*. Certain of the less diagnostic limb bones included in group 4 may represent *Dorcatherium chappuisi* which seems to have attained a size similar to that of the two pecoran species, *W. gracilis* and *P. africanus*.

GROUP 5.—A large tragulid, probably *Dorcatherium chappuisi*, represented by thirty-five astragali (Text-fig. 17*d*), similar in size to the pecoran astragali of group 4.

They suggest that *D. chappuisi* was approximately equal in size to a roe deer, a conclusion which is in accordance with the evidence of jaws and dentitions referred to that species. With the astragali are grouped three cubo-navicular bones from Rusinga, which are of comparable size. The external cuneiform bone is retained in intimate association with one of the cubo-naviculars, and seems to have remained an independent unit in the tarsus of *D. chappuisi*. Nevertheless, the characteristic tragulid condition, in which the cuneiform-metatarsal union occurs at a higher level than the cuboid-metatarsal union, is indicated by the abnormally deep step between the distal surfaces of the navicular and cuboid portions of the cubo-navicular bone. The material forming this group was distributed numerically as follows:

| Rusinga | Karungu | Mfwanganu | Maboko |
|---------|---------|-----------|--------|
| 32      | 3       | 2         | 1      |

GROUP 6.—A medium-sized tragulid, *Dorcatherium pigotti*, represented by the following material: seventy astragali (Text-fig. 17e), nine cubo-naviculo-cuneiforms and parts of three cannon-bones, all of tragulid pattern. Associated on the basis of size are one magnum, one scaphoid, parts of two scapulae, two humeri, one radius and six femora, a complete tibia (644.51) about 135 mm. long, and fragments of five others, portions of thirteen calcanea, and ten proximal, twenty-one second and six ungual phalanges, all of ruminant pattern. The material was distributed numerically as follows:

| Rusinga | Karungu | Mfwanganu | Maboko | Ombo | Muruorot |
|---------|---------|-----------|--------|------|----------|
| 97      | 14      | 4         | 33     | 1    | 2        |

The tarsus of *D. pigotti* (Text-fig. 6) is practically indistinguishable from that of Recent tragulids. The ectocuneiform is fused with the cuboid and navicular, but the internal cuneiform bone remains independent. At the upper end of the posterior cannon-bone, the individual metatarsals are somewhat angular and fully fused, but retain separate medullae. They are divided on their anterior surface by a deep, median valley. Their plantar surface is flat, with a narrow, impersistent, median cleft. The distal portion of the metapodial bones is unrepresented. Individual bones in group 6 are about twice as large as those of Recent tragulids.

GROUP 7.—A small tragulid, almost certainly *Dorcatherium parvum*, represented by a group of seventy-six astragali (Text-fig. 17g), together with a quantity of less diagnostic ruminant limb bones of corresponding size. All the bones are of uniform pattern, but there is an appreciable variation in their size, some being a trifle larger than the equivalent bones in Recent tragulids, others being a little smaller. Despite this variation, the bones form a homogeneous assemblage. In addition to the astragali, there are parts of seven humeri, six radii, one ulna, seventeen femora, four tibiae, five cubo-naviculo-cuneiforms, two calcanea, two cannon-bones and



seventeen isolated phalanges. The distribution of this material, by numbers of limb bones, was:

| Rusinga | Karungu | Mfwanganu | Maboko | Songhor | Muruorot |
|---------|---------|-----------|--------|---------|----------|
| 99      | 16      | 1         | 10     | 8       | 3        |

None of the material from Songhor is diagnostically tragulid, and the Songhor specimens are only included on the basis of size.

In *D. parvum* the ectocuneiform is fused into a single compound bone with the navicular and cuboid. Proximal and distal portions of cannon-bones are represented by two separate specimens from Rusinga Island. The lower half (517.48) is rounded anteriorly and flat behind. The individual metapodials are divided in front by a deep, median furrow. They are incompletely fused and preserve independent medullae. They are also free for a much greater distance above the distal condyles than is usual in Pecora, and the keeling of the condyles is feeble. It is uncertain whether this fragment belongs to a rear or fore limb. The proximal portion of the cannon-bone (370.49) represents a metatarsus. It is more drastically compressed in a transverse direction than is specimen 517.48. The medullae of the two principal metatarsals remain separate, although they are less distinctly divided than in *D. pigotti*. The proximal articular surfaces of the bone are diagnostically tragulid. A small splint attached to the upper, internal margin of the third metatarsal may be a persistent vestige of the second metatarsal bone. The transverse diameter of the cannon-bone shaft is about 6.7 mm. in specimen 370.49 and about 7.5 mm. in 517.48.

GROUP 8.—A small quantity of ruminant limb bones from Songhor, comprising parts of one humerus, three radii, one femur, one tibia, one cannon-bone, seven astragali (Text-fig. 17f) and two second phalanges. The astragali are of tragulid type. In size, they fall between groups 6 and 7, and it is presumed that they belong to *Dorcatherium songhorensis*. The cannon-bone fragment (Sgr.212.48) is doubtfully tragulid and may, in fact, belong to some unknown pecoran species.

### ISOLATED RUMINANT INCISORS AND CANINES

A number of isolated ruminant incisors and canines have been collected from the Miocene beds of East Africa. Exact identification is rarely possible.

GROUP 1.—Four isolated incisor teeth from Maboko Island and Songhor (Mb.73 and 74.49, Mb.22.51 and Sgr.33.49) which are clearly the lower, anterior incisors of a large tragulid or a small pecoran. They are almost identical in size and pattern (Text-fig. 18a) with the corresponding teeth in small individuals of *Cervus capreolus*. It is possible that they belong to one of the larger species of *Dorcatherium* (in which case, the first, lower incisor of these early tragulids was less specialized than in their Recent relatives), or to *Palaeomeryx africanus*, or to both species. The dimensions of the teeth are as follows:

|           | Maximum diameter of crown | Total length of tooth |
|-----------|---------------------------|-----------------------|
| Mb.73.49  | 6.0 mm.                   | 16.7 mm.              |
| Mb.74.49  | 5.5                       | 14.0+                 |
| Mb.22.51  | 6.0                       | 15.2                  |
| Sgr.33.49 | c. 6.0                    | 16.8                  |

GROUP 2.—An isolated lower tooth (1036.47) from Rusinga, probably a lateral incisor of the ?left side, belonging to either *Palaeomeryx africanus*, or one of the larger species of *Dorcatherium*. The crown is narrow and styliform, and originally possessed enamel on all its faces. The maximum diameter of the crown is 3.6 mm., the height of the crown, from the inferior border of the enamel to the terminal wear-surface, is about 7.0 mm. Only a part of the root is preserved, but this is compressed in a direction at right angles to the greatest diameter of the crown.

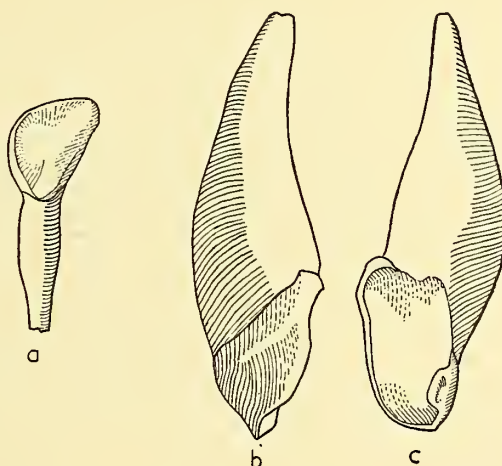


FIG. 18. Isolated anterior teeth. (a) Lingual aspect of a first lower incisor of the right side (Mb.22.51), (b) lateral, (c) occlusal aspect of a left upper ?canine (770.47). All  $\times 2$ .

GROUP 3.—A small, isolated tooth (1034.47) from Rusinga, perhaps a left, upper canine. The root is stout, of slightly compressed section and gently curved in its long axis. The crown is small and, viewed from the labial aspect, is of triangular outline. Enamel is developed on all sides of the crown. This is clearly a lateral, anterior tooth of the upper jaw and bears some resemblance to the upper canine found in *Cervus elaphus*. It is also similar to the upper canine found in the Recent female chevrotain. The dimensions of specimen 1034.47 are: height of crown 4.0 mm., antero-posterior diameter of crown 5.0 mm., length of root about 14.0 mm. and maximum diameter of root 6.0 mm.

GROUP 4.—Fragment of a tusk-like upper canine of the left side (777.52) from R.3, Rusinga. The external surface of the crown is flat to slightly convex, whereas, in *Dorcatherium*, the male canine usually possesses a concave labial surface. The

crown in specimen 777.52 is also deflected laterally near its extremity, as in *Moschus*. The maximum antero-posterior diameter of the crown is about 7.4 mm. It is possible that the upper tooth (1034.47), described immediately above, is a female canine of *Palaeomeryx africanus*, and that specimen 777.52 is the corresponding male tusk.

GROUP 5.—Five isolated teeth from Rusinga and Songhor (F.3197, 770.47, 150.49, 1042.49 and Sgr.44.49), identical in pattern with the upper ?canine (1034.47) referred to above, but approximately one and a half times larger. These teeth may belong to the large ruminant described on page 24 as ?*Palaeomeryx* sp. The crown of a typical specimen (770.47, Text-fig. 18*b, c*) measures 6.0 mm. in height and 9.0 mm. in its antero-posterior diameter. The length of crown and root together is 28.6 mm.

GROUP 6.—Part of a right upper canine from Maboko (Mb.79.49), exactly like the male tusk in *Dorcatherium pigotti*, but a little larger. The antero-posterior diameter of the blade-like crown measures 5.9 mm. The tooth may have belonged to an individual of *D. chapuisi*.

GROUP 7.—An isolated, third incisor or incisiform, lower canine (Sgr.168.48) from Songhor, possessing a long, slender, leaf-like crown. It resembles the corresponding teeth in small Cervidae, and in some small Bovidae, such as the duiker. The dimensions are: breadth of crown 4.0 mm., height of crown about 9.0 mm. and total length of root and crown greater than 19.0 mm.

GROUP 8.—Four isolated teeth from Maboko (Mb.71, 76, 77 and 78.49) very similar to the lower incisors and canines of small Bovidae like the kudu. These teeth may belong to the small, indeterminate bovid, also represented at Maboko Island by the isolated molars, Mb.228 and 242.49 (p. 25). The dimensions of the teeth are:

|  | Maximum diameter<br>of crown | Total length<br>of tooth |
|--|------------------------------|--------------------------|
| Mb.71.49 (I <sub>2</sub> or I <sub>3</sub> ) | 5.1 mm.                      | 13.6 mm.                 |
| Mb.76.49 (I <sub>2</sub> or I <sub>3</sub> ) | 5.5                          | 12.8                     |
| Mb.77.49 (C)                                 | 3.8                          | 14.0                     |
| Mb.78.49 (I <sub>1</sub> or I <sub>2</sub> ) | 5.5                          | 14.3                     |

GROUP 9.—A number of teeth of varying size and possessing strongly wrinkled enamel (548.51, 778.52 and 779.52 from Rusinga, and Mb. 69.49) which are similar to the median incisors in large Cervidae.

GROUP 10.—A group of isolated teeth (1801 and 1802.50 from Rusinga; Mb.72.47, Mb.75.47 and Mb.782.52) of varying size which resemble the lower incisors and canines of large Bovidae.

### III. GENERAL DISCUSSION

1. One of the most striking features of this East African ruminant fauna is its pronounced Eurasian affinity. The most abundant dental material can be referred



to two genera characteristic of the European Tertiary, *Dorcatherium* and *Palaeomeryx*. On the other hand, *Dorcatherium* and *Palaeomeryx* seem to attain their European acme in Vindobonian times (although they persisted into Sarmatian and Pontian times, and may be found more rarely in Burdigalian strata), whereas the East African species are concentrated in beds commonly regarded as Burdigalian, and perhaps, according to Arambourg (1933), belonging to the lowest Burdigalian. The European distributions of *Dorcatherium* and *Palaeomeryx* suggest either, that East African rocks rich in these genera may be a little younger than the early Miocene dating normally assigned to them, or, that these two genera reached their zenith in Africa earlier than in Europe. The dating of the East African Miocene fauna is based upon rather flimsy evidence. Andrews (1914) originally proposed a Burdigalian age for the fossil fauna of Karungu, principally because the anthracotheres from Karungu showed a similarity to those characterizing authentic Burdigalian deposits in Europe. Later, Hopwood (1929) confirmed Andrews's conclusions and extended the Burdigalian dating to other fossil sites in East Africa. He also quoted the association of *Deinotherium* and *Creodonta* in the East African beds as confirmatory evidence of their early Miocene age. Le Gros Clark & Leakey (1951) have recently referred to the possibility of a later dating for the principal East African sites, and have drawn attention to various genera which, elsewhere, extend far above the Lower Miocene. Moreover, these genera are not restricted to the higher members of the Miocene sequence in Kenya. *Palaeomeryx* and *Dorcatherium* can be added to the list, and it is clear that the question of geological age may have to be reviewed when the description of the East African fossils is completed.

2. The Miocene fauna of Kavirondo provides the first indisputable evidence of pre-Pleistocene deer in Africa. It is true that, at present, only one cannon-bone (Sgr.232.49), which can be diagnosed as cervid, has been recovered; but it is significant that this metatarsus was found at Songhor, in association with numerous remains of the dentition of *Palaeomeryx africanus*, a species which possesses a number of cervid-like dental features. Other ruminant limb bones establish equally the presence of Bovidae in the East African Miocene. Indeed, it is probable that the Bovidae were already numerous in parts of Africa at that time, but may have differed little from contemporaneous Cervidae in the development of their teeth. This last statement, however, is largely speculative, and it would be unwise, at this juncture, to emphasize the obvious implications concerning the ancestry of the Bovoidea.

It should be added that these African species of Miocene ruminants were probably immigrants. Up to the present, no ruminants have been recorded in the pre-Miocene rocks of Africa, although ancestral ruminants, such as *Archaeomeryx* (Matthew & Granger, 1925; Colbert, 1941) and *Eumeryx* (Matthew & Granger, 1924), have been found in the early Tertiary of Asia.

3. It has been customary to treat the entire Miocene fauna of East Africa as a single unit, disregarding the dispersion of the various sites from which material has been collected. No very serious attempt has been made either to prove or to disprove the implied assumption of close contemporaneity between all principal sites. Le Gros Clark & Leakey (1951) have merely expressed the opinion that a preliminary study of the fossils provides no evidence of significant differences in the age of the

various sites. The distributions of ruminant species at Rusinga Island and Songhor raise the possibility that a real distinction can now be drawn between the fossiliferous deposits of these two localities. For example, a giant chevrotain, *Dorcatherium chapuisi* is abundant in the Miocene beds of Rusinga, absent from the Miocene of Songhor, and re-appears far beyond Songhor at the Losodok site of northern Kenya. *Pro-palaeoryx nyanzae*, another rather large ruminant, is also found at Rusinga, but is unrepresented at Songhor. It is significant that no limb bones which could be assigned to either of these two species have been found at Songhor, whereas limb bones of appropriate size and pattern are plentiful at Rusinga. *Palaeomeryx africanus*, on the other hand, is equally common at both sites, and limb bones which may belong to this species show a similar distribution. Table 12 indicates the concentration (by numbers of specimens) of each species of the Miocene mammal fauna at the various fossiliferous sites in East Africa, and provides additional differences between the faunules of Songhor and Rusinga. For example, there is a difference in the balance of the two limnophilic species, *Limnopithecus legetet* and *L. macinnesi*. The former is more common at Songhor, the latter, a larger form, is more common at Rusinga. The lagomorph, *Kenyalagomys*, is very abundant at Rusinga and totally unrepresented at Songhor. The Rusinga anthracothere, *Hyoboops africanus*, is also absent from Songhor. *Megalohyrax championi* is exceedingly common at Rusinga, represented by one doubtful specimen at Songhor, and recurs at Losodok. *Myohyrax oswaldi* is most profuse at Karungu, fairly common at Rusinga, and entirely absent from Songhor. The Miocene insectivore material, which has been described by Butler (1956) and Butler & Hopwood (1957), is perhaps too scanty to provide a completely reliable distributional picture, but what material there is seems to confirm the distinctness of the Rusinga and Songhor assemblages.

A study of the distributions summarized in Table XII establishes a genuine difference between two representative fossil assemblages. This difference usually takes the form of an absence from Songhor of species which are well represented at Rusinga. The faunal discrepancies at Songhor must be explained either by differences in the geological age of the deposits at Songhor and Rusinga, or by synchronous differences in environment at these two localities. The former possibility is unlikely, but cannot be ruled out entirely, since the Miocene at Songhor rests directly on a surface of appreciable relief cut into Pre-Cambrian rocks (Shackleton, 1951), whereas the base of the Miocene sequence is not seen at Rusinga. However, the alternative explanation, that the two faunas represent different environments, seems to be more probable. Numerous mammalian species of uncertain habit are common to both localities, and it is significant that species absent from Songhor, but well represented at Rusinga, are usually of plains-dwelling habit. The fossil assemblage at Rusinga seems to be a representative savannah fauna, and it has been suggested elsewhere (Whitworth, 1953) that in early Miocene times Rusinga was principally an area of parkland and steppe. At Songhor, we are probably dealing with the fauna of an associated, but more restricted, habitat, perhaps analogous to the isolated, tree-clad jebels which rise, here and there, above the Recent African savannahs, and support a mammal fauna distinct from that of the surrounding parklands. It is unfortunate that published accounts of the fossiliferous Miocene deposits of Songhor (Kent, 1944; Shackleton, 1951) provide no very clear lithological confirmation of a profound facies change.



TABLE XII  
DISTRIBUTIONS OF MIOCENE MAMMALS IN KENYA  
BY NUMBERS OF INDEPENDENT SPECIMENS

(From Le Gros Clark & Leakey, 1951; Le Gros Clark & Thomas, 1952; MacInnes, 1951, 1953; Whitworth, 1954.)

|  | Karungu | Mfwanganu | Rusinga | Ombo | Maboko | Songhor | Koru | Muruorot | Losodok |
|--|---------|-----------|---------|------|--------|---------|------|----------|---------|
| <i>Dorcatherium chappuisi</i> . . . . .    |         | 1         | 82      |      | ?      |         |      |          | 1       |
| <i>Dorcatherium pigotti</i> . . . . .      | 2       | 5         | 85      | 2    | ?      |         |      |          |         |
| <i>Dorcatherium parvum</i> . . . . .       | 12      |           | 189     |      | 1      |         |      | 1        |         |
| <i>Dorcatherium songhorensis</i> . . . . . |         |           |         |      |        | 45      | 2    |          |         |
| <i>Palaeomeryx africanus</i> . . . . .     |         |           | 71      |      |        | 56      | 1    | 2        |         |
| <i>Palaeomeryx</i> sp. . . . .             |         |           | 5       |      |        |         |      |          |         |
| Bovidae indet. . . . .                     |         |           |         |      | 5      |         |      |          |         |
| <i>Climacoceras africanus</i> . . . . .    |         |           |         |      | Few    |         |      |          |         |
| <i>Propalaeoryx nyanzae</i> . . . . .      |         | 1         | 4       |      |        |         |      |          |         |
| <i>Walangania gracilis</i> . . . . .       |         | 1         |         |      |        |         |      |          |         |
| <i>Proconsul africanus</i> . . . . .       |         |           | 23      |      |        | 11      | 1    |          |         |
| <i>Proconsul nyanzae</i> . . . . .         |         |           | 55      |      | 2      | 10      | 1    |          |         |
| <i>Proconsul major</i> . . . . .           |         |           | ?       |      |        | 5       |      |          |         |
| <i>Sivapithecus africanus</i> . . . . .    |         |           | 1       |      | 1      |         |      |          |         |
| <i>Limnopithecus legetet</i> . . . . .     |         |           | 8       |      |        | 32      | 1    |          |         |
| <i>Limnopithecus macinnesi</i> . . . . .   |         |           | 21      |      |        | 13      |      |          |         |
| <i>Progalago dorae</i> . . . . .           |         |           | 5       |      |        | 6       |      |          |         |
| <i>Progalago robustus</i> . . . . .        |         |           | 1       |      |        | 3       |      |          |         |
| <i>Progalago minor</i> . . . . .           |         |           | 1       |      |        | 1       |      |          |         |
| <i>Kenyalagomys rusingae</i> . . . . .     |         |           | 321     |      |        |         |      |          |         |
| <i>Kenyalagomys minor</i> . . . . .        |         |           | 24      |      |        |         |      |          |         |
| <i>Hyobooops africanus</i> . . . . .       | 1       |           | 5       | Few  |        |         |      |          |         |
| <i>Brachyodus aequatorialis</i> . . . . .  |         | Few       | 5       |      | ?      |         |      |          |         |
| <i>Megalohyrax championi</i> . . . . .     | 1       |           | 139     |      | 1      | ?       |      |          | 2       |
| <i>Megalohyrax</i> sp. . . . .             | 1       |           | 4       |      |        |         |      |          |         |
| <i>Bunohyrax</i> sp. . . . .               |         |           |         |      |        | 1       |      |          |         |
| <i>Myohyrax oswaldi</i> . . . . .          | 120     |           | 18      |      |        |         |      |          |         |
| <i>Meroëhyrax bateae</i> . . . . .         |         |           | 2       |      |        |         |      |          |         |

The Table refers only to dental material, and does not include associated units of the post-cranial skeleton. If these were added, the distributional differences between Songhor and Rusinga would be greatly accentuated.

4. The unique occurrence at Maboko Island of isolated teeth which exhibit an advanced bovid condition deserves special mention. At no other locality in East Africa, have bovid teeth of prismatic habit been found in association with normal representatives of the Rusinga-type fauna. These Bovidae are not the only abnormal element in the Maboko fauna. The strangely shaped "antlers" of *Climacoceras* seem to be peculiar to Maboko, and Hopwood (1951) has drawn attention to the presence of advanced (?Helvetian) mastodonts there. It is unlikely that the diversity of the Maboko fauna can be explained in terms of partial derivation from older strata, since well rolled fossils are unknown at Maboko. For several years, I have suspected that



the Maboko assemblage may be the result of haphazard collecting from two distinct, but unrecognized, series. Recently, L. S. B. Leakey has cut trenches across the poorly exposed Maboko sites, and claims (in a personal communication) to have demonstrated the presence of two independent deposits, separated by a pronounced unconformity. It is possible, therefore, that the characteristically Rusinga-type fossils were collected from a lower group of beds which can be termed, provisionally, Burdigalian, and that the prismatic bovid teeth and other exotic items came from an upper series of appreciably younger, perhaps Vindobonian or even Pontian, age.

5. The salient points in the preceding discussion can be summarized as follows. The Miocene ruminant fauna of East Africa shows similarities to the Middle Miocene ruminant fauna of Europe, and undoubtedly includes the fossilized remains of deer. The Miocene deposits of Rusinga and Songhor are probably of similar age, but the fossil faunas which they contain differ, and may represent distinct environments. Finally, the Maboko fossil assemblage includes forms collected from two discrete series of beds, one series being equivalent in age to the fossiliferous Miocene deposits of Rusinga, the other being of later date.

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