THE LOWER MIOCENE RUMINANTS OF
GEBEL ZELTEN, LIBYA

BY

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CONTENTS

SYNOPSIS

RUMINANTS from the Lower Miocene (Burdigalian) deposits of Gebel Zelten, Libya, are described. The skull and dentition of a new giraffoid—*Zarafa zelteni*— are described in detail. This genus exhibits dental characteristics which ally it to the palaeomerycids; however details of the cranial anatomy indicate a close relationship to the palaeotragines. *Zarafa* is classified as a palaeotragine and its palaeomerycid features are interpreted as evidence of a common ancestry for the two groups. The Palaeotraginae and Giraffinae are grouped in the Giraffidae.

The skull and dentition of *Prolibytherium magnieri* indicate that it is a member of the Sivatheriidae and primitive features of the skull suggest the divergence of the two families soon after the origin of the Giraffoidea in the late Oligocene.

The different evolutionary trends exhibited by the Giraffidae and the Sivatheriidae are related to the different fighting methods used in intra-specific combat. In the Giraffidae an elongation of the neck and limbs was possible while in the Sivatheriidae selective pressures existed tending to maintain the short neck and limbs.

The other Gebel Zelten ruminants are poorly represented but a new genus and species—*Canthumeryx sirtensis*—is described and identified as a palaeomerycid. A new tragulid species—*Dorcatherium libiensis* and three bovid species—*Gazella sp.*, *Protragocerus sp.* and *Eotragus sp.* are present in the fauna.

A further study of the ruminants from the Miocene of East Africa, enables the species *Palaeomeryx africanus* and *Walangania gracilis* to be synonymized as *Walangania africanus* and the upper dentition of *Propalaeoryx nyanzae* is described. A new species—*Gelocus whitworthi*—is described, this is the first recorded occurrence of the Gelocidae in Africa.

The influence of these new discoveries upon the accepted classification of the giraffoids is discussed.

I. INTRODUCTION

The fossil vertebrate fauna of Gebel Zelten, Libya was discovered by Arambourg (1961a and b) who published preliminary notes on some new elements in the fauna. Further collections were made by R. J. G. Savage of Bristol University between 1964 and 1968. Many crania of *Prolibytherium magnieri* were collected and as some of these were of superior quality to the holotype, described by Arambourg (1961a); a full and detailed study of this species has been made. The presence of a second giraffoid—*Zarafa zelteni*—was not known until 1968 when M. White of Bristol University, completed the preparation of a skull which had been discovered, enclosed in a sandstone block. These two species form the basis of this work but as the study proceeded its scope was expanded to include the other ruminants of the area and finally a revision of some elements of the East African Miocene fauna was made.

Gebel Zelten

Gebel Zelten lies about 200 km south of the Gulf of Sirte, Libya. It consists of an elongate mesa running northwest-southeast for about 140 km at 19° 30′–20° 30′E. 28°–29°N. The ESSO Company oil camp of Zelten lies to the north of the gebel and the Oasis Oil Company of Libya camp lies to the south; the road between these camps crosses the gebel at its narrowest point where it is only 8 km. wide. In the west the gebel rises 40–60 m above the Zelten Rambla; it dips gently to the east and blends with the Calenscio Serir at its eastern end. The plateau is capped by marine sandstone which is Lower Miocene in age and the edges are dissected by steep walled wadis up to 3 km in length (Savage and White 1965). It is in these wadis that many of the vertebrate remains are found though some of the sites are on areas of washout from the wadis.

Detailed geological studies of the area have been published by Magnier (1962) and Selley (1968 and 1969); a detailed study of the geology with reference to the vertebrate sites is in preparation (Savage pers. comm.). The vertebrate remains are found in fluviatile deposits which probably originated in a coastal, alluvial flood plain (Selley 1969). The conditions at the time of deposition are interpreted as those of the savannah by Desio (1935) and again by Savage and White (1965).

Desio (1935) indicated that the Zelten deposits are Burdigalian and Helvetian in age and he stated that the deposits on the south side of Gebel Zelten are of Aquitanian

age. Arambourg and Magnier (1961) and Arambourg (1961a and b, 1963a and b.) have consistently placed the deposits in the Burdigalian, and Arambourg (1963b) states that the Gebel Zelten deposits rest on Oligocene marine beds and are overlain by Helvetian marine beds. Savage and White (1965) indicate a Burdigalian age and this was later refined (Savage in Selley 1969) to Early Burdigalian or Late Aquitanian.

Terminology

In most anatomical details the terminology used follows that of Sisson and Grossman (1953). The nomenclature applied to the dentition (Text fig. 1) is mainly after Arambourg (1947). In the upper molars the postero-lingual cusp, termed the hypocone by Arambourg (1947) is here termed the metaconule after Weber (1928). In the lower molars I have treated the antero-lingual corner as if the paraconid has been entirely lost, thus the antero-lingual cuspid is the metaconid with an anterior mesostylid. The '*Palaeomeryx* fold' is used to define any fold of enamel which runs vertically down the postero-labial face of the protoconid into the median valley.
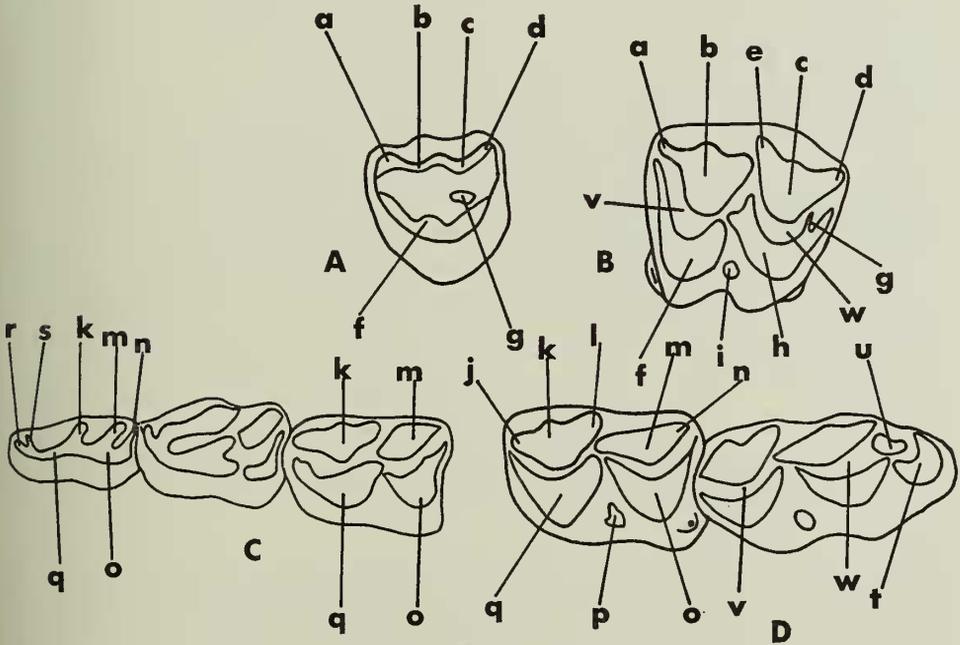
FIG. 1. Ruminant molar and premolar cusp nomenclature. (A) Third upper premolar. (B) First upper molar. (C) Second, third and fourth lower premolars. (D) Second and third lower molars. *Upper dentition*. a: parastyle. b: paracone. c: metacone. d: metastyle. e: mesostyle. f: protocone. g: accessory crest. h: metaconule. i: entostyle. *Lower dentition*. j: mesostylid. k: metaconid. l: metastylid. m: entoconid. n: entostylid. o: hypoconid. p: ectostylid. q: protoconid. r: parastylid. s: paraconid. t: hypoconulid. u: entoconulid. v: anterior fossette. w: posterior fossette.

The abbreviations used in reference to the dentition follow the convention in general use in Britain and America.   I, C, P and M represent incisor, canine, premolar and molar respectively; the tooth is then defined by a number added above or below the line to indicate presence in the upper or lower jaw; thus P_4 is the lower, fourth premolar which is in contact with M_1 the first lower molar.   The deciduous cheek teeth are referred to as D^1, D_1 etc.   The external side of the tooth is labial and the internal side is lingual.   Anterior and posterior with reference to the dentition, indicate those directions which apply if the mandible or maxilla is in the horizontal position.

Frontal Appendages

In current usage the term 'horn' can refer to any cranial appendage but in this work a restriction of the term is applied.   In the ruminants the type of frontal appendage is some times the main criterion on which the classification of a genus is based as stated by Pilgrim (1941):

> '. . . the varying types of frontal appendage—horns—constitute one of the most important distinctions between the different families of the Pecora.'

In this situation it is clearly desirable that separate terms be applied to the different types of frontal appendage.   Voorhies (1969) listed four types of frontal appendages in the living artiodactyls as:

> '1. the unshed true horns growing on the bony core in the Bovidae, 2. the deciduous antlers of the Cervidae, 3. the annually-shed horny sheath growing over a permanent, vascular bony core in the Antilocaprinae, and 4. the bony core permanently covered by skin ('velvet') in the Giraffidae.'

The first three of these appendages are referred to as; 'horns', 'antlers' and 'horn-cores' respectively but no widely accepted term exists for the giraffid appendage. Lankester (1907) used the term 'ossicone' to refer to this appendage and defined ossicones as:

> '. . . independently ossifying bony cores which are found in *Okapia* and *Giraffa* on the frontal and parietal areas and in the giraffe also in the median position.'

A slight widening of the application of this term was made by Ginsburg and Heintz (1966) who applied the term to the palaeomerycid appendage and its application to all giraffoid cranial appendages is desirable.

Abbreviations

The prefix 'M' refers to specimens in the collections of the British Museum of Natural History, London: 'B.U.' in the Department of Geology, University of Bristol and 'P' in the Institut de Paléontologie, Paris.   Specimens described in chapter 4 are the property of the National Museum, Nairobi, Kenya and are defined by the prefix 'K'.

Classification

The system of classification used in this work differs slightly from that of Simpson (1945), this is mainly due to alterations within the Giraffoidea and primitive Cervoidea.   The Palaeomerycidae is treated as a family of the Giraffoidea and follow-

ing the suggestion of Ginsburg and Heintz (1966), those genera of the family Palaeomerycidae which lack frontal appendages, are removed to the separate family Dremotheriidae. The family Blastomerycidae is grouped with the Dremotheriidae in the Dremotherioidea. The position of the Dromomerycidae is uncertain and requires further study, but in this work the family is treated as a group probably originating in the nearctic region and having no direct relationship to the Palaeomerycidae.

The family Giraffidae has been split by the establishment of the Sivatheriidae as a separate family.

II. SYSTEMATIC DESCRIPTIONS

Family **TRAGULIDAE** Milne-Edwards 1864

DIAGNOSIS: Small primitive ruminants; lacking frontal appendages. Dentition primitive but with upper incisors reduced or absent. Upper canines large, especially in the male. Molars bunodont but showing selenodonty in advanced forms. Limbs showing features of advanced ruminants but with varying degrees of fusion exhibited by the metacarpals and metatarsals. Navicular and cuboid fused. (After Milne-Edwards 1864).

Genus *DORCATHERIUM* Kaup 1833

DIAGNOSIS: This genus was defined by Whitworth (1958 p. 3) whose diagnosis is followed here.

TYPE SPECIES: *Dorcatherium naui* Kaup 1833.

Dorcatherium libiensis sp. nov.

DIAGNOSIS: A small species of *Dorcatherium*. Length of lower tooth row P_3–M_3 about 39 mm.

REMARKS: This species is established on a size basis and further work in the Gebel Zelten area may reveal wide variation in the species; however as the species is very rare at Gebel Zelten and as collecting in the area has been terminated it was decided, with some hesitancy, to establish the species on the basis of a single specimen.

HOLOTYPE: M.26684. A fragmentary right mandible with P_3 to M_2 and the alveoli of P_1 and P_2 preserved.

LOCALITY: The Lower Miocene (Burdigalian) deposits of Gebel Zelten, Libya.

Lower Dentition. The molars are heavily worn but the main details of their anatomy are visible (pl. 1, fig. 1). M_1 is complete though badly cracked posterior to the median valley and the postero-lingual corner of M_2 is missing. The molars are bunodont as in *D. chappuisi* and *D. naui* and strong anterior and posterior cingula were present on M_1 and M_2. The posterior face of the protoconid bears a strong fold similar to a 'Palaeomeryx fold' but more lingually situated and similar to that of *D. chappuisi*. The postero-lingual region of the metaconid carries a deep vertical groove on both molars, as in *D. naui* and *D. chappuisi* this fold seems to be characteristic of the genus *Dorcatherium*. A small ectostylid is present in the median valley as in *D. naui*, this stylid is usually absent in *D. chappuisi*.

The anterior end of P_3 is missing but P_4 is complete. The premolars are elongate and similar to those of *D. chappuisi* and *D. naui*. The dentition of *D. libiensis* is thus similar to that of *D. chappuisi* and is distinguished from this species and *D. pigotti* on a size basis only.

The presence of this mandible in the Gebel Zelten fauna serves to establish the presence of the genus in North Africa at this time but gives no indication of the relative abundance of tragulids at Gebel Zelten, as specimens of this size and smaller, are relatively rare in the collection (Savage and White 1965).

TABLE I

	D. libiensis M.26684		D. chappuisi (Whitworth)		D. pigotti (Whitworth)	
	Length	Width	Length	Width	Length	Width
P_3	10·0 mm	3·6 mm	13·5 mm	5·1 mm	8·4 mm	3·1 mm
P_4	9·6 mm	4·0 mm	12·3 mm	6·0 mm	7·9 mm	3·8 mm
M_1	9·3 mm	5·8 mm	11·7 mm	7·2 mm	8·2 mm	4·8 mm
M_2	11·0 mm	6·6 mm	12·9 mm	9·0 mm	8·9 mm	5·3 mm

Superfamily **GIRAFFOIDEA** Simpson 1931

DIAGNOSIS: Medium to large sized ruminants. Cheek teeth brachyodont or occasionally hypso-brachyodont. Enamel of cheek teeth usually rugose. Ossicones present in male and sometimes female. Metapodials fully fused.

COMMENTS: This is a well defined group of ruminants which is probably related more closely to the Cervoidea than the Bovoidea and is in many respects more primitive than either group.

Family **PALAEOMERYCIDAE** Lydekker 1883

DIAGNOSIS: A group of primitive giraffoids exhibiting features that may indicate a close relationship to the cervoids. Ossicones are present and in some species these have a long proximal region and a whorl of short tines distally. The mandible is shallow with brachyodont selenodont molars which have lightly rugose enamel. P_1 may be present. Metastylid and entostylid usually very prominent and strong cingula are present anteriorly and posteriorly. A '*Palaeomeryx* fold' is often present. Labial ribs of the upper molars prominent. Accessory crests often present in the fossettes and entostyle usually present in the median valley.

Genus *CANTHUMERYX* nov.

DIAGNOSIS: A medium sized ruminant, about as large as the fallow deer, *Dama dama*. Lower dentition similar to *Propalaeoryx* but lacking P_1. Lower molars relatively high with weaker mesostylid and a stronger more flexed metastylid than is usual in the palaeomerycids. Strong anterior and weak posterior cingula on M_1 and M_2. Premolars elongate similar to usual palaeomerycid pattern but strong entostylid on P_4.

TYPE SPECIES: *Canthumeryx sirtensis* sp. nov.

DIAGNOSIS: As for genus.

DERIVATION OF NAME: The generic name is from Canthus a character of Greek mythology: according to Appollonius:

'Fate had decreed that he and the great seer Mopsus should wander to the ends of Libya to be destroyed.' (Rieu 1959).

The trivial name refers to the Sirte basin in which the specimens were discovered.

HOLOTYPE: A mandibular fragment with D_3 to M_3, the last molar being only partially erupted. M_3, P_4 and P_2 have been dissected out.

LOCALITY: The Lower Miocene (Burdigalian) of Gebel Zelten, Libya.

MATERIAL:

M.26682   Holotype.

M.26683   A right mandibular fragment with D_4 and M_1 erupted. P_3 and P_4 dissected out.

B.U.20111   An isolated lower right M_3 showing moderate wear.

Lower Dentition. The lower dentition forms a closed series from P_2 to M_3 and P_1 is absent as in *Palaeomeryx* but in contrast to *Propalaeoryx*. The enamel of the molars is finely rugose and the molars are higher and more elongate than in *Palaeo-*

meryx but lower and slightly wider than in *Propalaeoryx*. The metaconid of M_1 is transversely flattened with a weak mesostylid, a strong lingual rib and a strong metastylid which is flexed more lingually than in *Palaeomeryx* and is longer and more slender than in *Propalaeoryx*. The entoconid has a strong lingual rib, the cuspid is almost parallel to the axis of the molar as in *Propalaeoryx* whereas in *Palaeomeryx* it has a more diagonal orientation. The posterior end of the entoconid is reduced and rounded in M_1 (pl. 1, fig. 2). The hypoconid is isolated until very late in wear and the anterior fossette would be entirely worn away before the hypoconid wear trace joined that of the protoconid. The hypoconid is much lower than the protoconid, but due to the increased overall height of the tooth, this difference is less marked than in *Palaeomeryx*. The posterior end of the hypoconid is produced lingually forming the posterior end of the tooth and causing the posterior fossette to open lingually in M_1 (pl. 1, fig. 3).

M_2 is very similar to M_1 but the posterior end of the entoconid bears a strong keel, causing it to extend further posteriorly and tending to close the posterior fossette which opens at the postero-lingual corner of the tooth; this contrasts with *Propalaeoryx* in which the entoconid of M_2 is rounded posteriorly and the posterior fossette opens lingually as in M_1. In *Palaeomeryx* the posterior end of the entoconid usually bears a strong crest in M_1 and M_2.

M_3 has a feeble mesostylid and a strong metastylid. The entoconid is transversely flattened and its anterior region consists of a strong crest of enamel which meets the anterior face of the protoconid. The posterior region of the entoconid consists of a strong crest and from its posterior end the long mentoconulid curves posterolabially, to blend into the middle of the lingual face of the hypoconulid. The protoconid joins the posterior end of the metaconid closing the fossette even in the unerupted condition; this region is very variable in *Palaeomeryx* but in *Propalaeoryx* it is similar to *Canthumeryx*. The posterior end of the hypoconid is short, it meets the hypoconulid but fails to reach the entoconulid. The crescentic hypoconulid is lower than the hypoconid. The molars each have a strong ectostylid in the median valley (pl. 1, fig. 4) and M_3 has a small stylid in the posterior valley. A strong anterior cingulum is present on each molar and feeble posterior cingula are present on M_1 and M_2.

The P_4 of *Canthumeryx* is generally similar to that of *Palaeomeryx* or *Propalaeoryx*. The metaconid is the highest part of the tooth, it is strongly swollen anteriorly (pl. 1, fig. 5) and produces a strong wing posteriorly, these features are similar in *Palaeomeryx* but in *Propalaeoryx* the anterior and posterior projections are absent. The protoconid is joined to the metaconid by a strong ridge of enamel as in *Palaeomeryx*. The entostylid is very strong in *Canthumeryx* (pl. 1, fig. 5), curving across the whole posterior face of the tooth as in *Propalaeoryx* and in contrast to *Palaeomeryx* in which it is reduced lingually. The entoconid of *Palaeomeryx* usually curves postero-lingually at its lingual end but there is no indication of such a curvature in *Canthumeryx* or *Propalaeoryx*. The paraconid and parastylid are very strong and widely divided in *Canthumeryx* (pl. 1, fig. 5) and *Propalaeoryx* whereas in *Palaeomeryx* they are usually weaker and less widely divided. The labial face of the P_4 is swollen labially in *Palaeomeryx* but in *Canthumeryx* and *Propalaeoryx* this swelling is absent

and the wall is vertical. A strong groove on the labial wall separates the hypoconid from the protoconid, this groove is very strong in *Palaeomeryx* weaker in *Canthumeryx* and weaker again in *Propalaeoryx*.

P_3 is more elongate than P_4; the metaconid is lower than in P_4 and it has no posterior fold or anterior swelling, it is also situated further posteriorly than on the P_4 (pl. 1, fig. 5). The posterior region consists of a hypoconid and an entoconid as in the P_4 but the entostylid is joined to the posterior face of the entoconid from which it curves postero-lingually and does not join the hypoconid (pl. 1, fig. 5); this is probably an individual variation which is also found in *Palaeomeryx* and *Walangania* and in these genera it is more usual for the posterior region of the P_3 to resemble that of the P_4.

The P_2 of *Canthumeryx* is relatively simple with a single, conical, primary cuspid in the central region from which an unforked anterior crest is produced; this curves lingually at its anterior end. A posterior swelling and a postero-lingual crest are produced from the primary cuspid. The posterior region is much lower than the primary cuspid, it consists of a single transverse crest which falls away posteriorly. Strong anterior and posterior cingula are present on all the premolars.

The D_4 is heavily worn in both specimens. It is elongate and trilobed; its anterior end is narrower than the posterior end and the anterior, median and posterior fossettes are joined (pl. 1, fig. 2). The anterior fossette is bounded by a strong labial cuspid and a narrow lingual cuspid, the anterior end is closed by a small stylid. In both specimens the anterior region is very heavily worn and very little surface detail is visible. The metaconid is high and selenodont as in the molars (pl. 1, fig. 2), it has a strong metastylid which communicates with the high entoconid.

The posterior region of the entoconid is shortened as in the M_1 and the posterior fossette opens lingually (pl. 1, fig. 2). The protoconid is stout and crescentic, in the heavily worn condition its wear trace is joined to the antero-labial cuspid. The hypoconid is higher than the protoconid but this may be a wear factor. The D_4 has a very strong ectostylid in the median valley. The posterior cingulum is strong and the anterior cingulum continues along the labial face as far as the anterior valley, in which there is a weak cingulum.

The D_3 is elongate narrowing anteriorly. The primary cuspid lies in the middle of the tooth and has a feeble lingual cuspid. The anterior region is similar to that of P_3 with a long crest giving rise to antero-lingual and lingual branches. The posterior region has a single central hypoconid which is joined by a crest to the primary cuspid. The hypoconid produces a posterior branch which curves lingually at its posterior end and a lingual branch which curves posteriorly, a large enamel island is produced between these branches.

The D_2 is known from the alveoli only (pl. 1, fig. 4); these are single, anterior and posterior and indicate that D_2 was slightly less elongate than the D_3. The absence of a D_1 indicates that P_1 was also absent.

The dentition of *Canthumeryx* resembles that of *Propalaeoryx* more closely than any other ruminant, and both resemble *Palaeomeryx*. Differences of the metastylid, entoconid, height and width serve to distinguish the molars of *Canthumeryx* from those of *Palaeomeryx* and *Propalaeoryx* and many details of the fourth premolars

present differences between these genera.   The absence of a P_1 in *Canthumeryx* is an important difference distinguishing it from *Propalaeoryx*.

TABLE 2

The Lower Dentition of *Canthumeryx*

| | M.26682 | | M.26683 | | B.U.20111 | |
	Length	Width	Length	Width	Length	Width
D_3	16·3 mm	5·7 mm	—	—	—	—
D_4	22·2 mm	—	23·0 mm	11·1 mm	—	—
P_2	13·6 mm	5·3 mm	—	—	—	—
P_3	—	—	18·7 mm	8·6 mm	—	—
P_4	15·8 mm	7·5 mm	19·0 mm	9·8 mm	—	—
M_1	19·5 mm	11·0 mm	20·1 mm	14·0 mm	—	—
M_2	20·3 mm	13·6 mm	—	—	—	—
M_3	29·2 mm	13·3 mm	—	—	31·2 mm	13·7 mm

Palaeomeryx sp.

The presence of a species of the genus *Palaeomeryx* in the Gebel Zelten fauna is indicated by two fragmentary molars; M.26691 and B.U.20112.   The specimens are both third molars of which the former is the more complete.

The metaconid is broken off but its postero-labial region indicates that it was joined to the protoconid and entoconid.   The entoconid is transversely compressed and its posterior region is shortened, thus the posterior fossette opens lingually in contrast to *Canthumeryx*.   The protoconid is crescentic and very stout, a 'Palaeomeryx fold' may have been present but the posterior face of the protoconid is very heavily worn.   The anterior end of the hypoconid is produced anteriorly and its posterior end which joins the entostylid is much longer than in *Canthumeryx*.   The hypoconulid is stout and curves around the posterior end of the tooth, joining the entostylid and enclosing a posterior enamel island in contrast to *Canthumeryx* in which the posterior enamel island would not be formed in this position.   A strong ectostylid is present in the median valley and a feeble stylid is present in the posterior valley of B.U.20112.

These specimens are distinguished from *Canthumeryx* by details of their dental anatomy and also by their smaller size; they resemble *Prolibytherium* closely in size but are more brachyodont and differ in anatomical details from this genus.

TABLE 3

The Lower Molars of *Palaeomeryx* sp

M_3	M.26691	B.U.20112	K.R.442.51
Length	24·2 mm	—	28·1 mm
Width of anterior lobe	11·5 mm	—	12·5 mm
Width of posterior lobe	11·0 mm	11·0 mm	13·0 mm
Width of accessory lobe	6·6 mm	6·7 mm	6·7 mm

Palaeomerycidae Indet.

A single pair of ossicones M.26690 (pl. 1, fig. 6), cannot be definitely assigned to any group of the Giraffoidea. These ossicones diverge at an angle of 40° and slope posteriorly at an angle of about 50° from the vertical. The bone surface has many fine vertical striations which fade out well above the base and it is unlikely that a horny sheath could have been present. The ossicones were very centrally positioned on the cranium and the region between them curves smoothly with no sign of a median suture. The small area of cranium that is preserved, indicates that the animal was slightly larger than *Prolibytherium*.

The cervid genus *Dicrocerus* has long pedicles which are comparable in form with this specimen but in *Dicrocerus* the pedicles were supra-orbitally situated and were less divergent. The ossicones of *Climacoceras* diverged at an angle of about 60° (MacInnes 1936), their internal structure is similar to ordinary bone with a core of vesicular structure; this agrees with M.26690. MacInnes (1936) also states that the shaft of *Climacoceras* was nearly straight throughout its length. The ossicones of *Climacoceras* may represent a condition derived from ossicones similar to M.26690.

Family **GIRAFFIDAE** Gray 1821

DIAGNOSIS: Giraffoids in which the neck and limbs are usually lengthened. Ossicones small, consisting of a single tine. Degree of facial flexion small. Cheek teeth brachyodont; upper molars with strong mesostyle. Paracone and metacone having a diagonal orientation on the molar. Lower premolars exhibiting molarization. On the fourth lower premolar, the metaconid is strong and the hypoconid and entoconid are separated from the protoconid. '*Palaeomeryx* fold' usually absent.

COMMENTS: This group previously included the Sivatheriidae which is here treated as a separate family of the Giraffoidea.

Subfamily **PALAEOTRAGINAE** Pilgrim 1911

DIAGNOSIS: Primitive, medium sized giraffids, usually with one pair of supra-orbital, frontal ossicones. A second pair of ossicones may be present on the anterior extremities of the frontals. Skull usually elongate. Cheek teeth brachyodont. Limbs and neck slightly elongate. (After Colbert 1935a.)

Genus **ZARAFA** nov.

DIAGNOSIS: A very primitive palaeotragine with flattened, laterally expanded frontals and frontal sinuses in the supraorbital region. Supraorbital ossicones present. Paired lacrymal foramina present on the anterior edge of the orbit. Basicranial and basipalatal planes almost parallel. Maxilla very shallow. Cheek teeth primitive and very brachyodont. A strong accessory crest present on the posterior region of the metaconule.

Zarafa zelteni sp. nov.

DIAGNOSIS: As for genus.

DERIVATION OF NAME: The generic name is from the Arabic for 'giraffe'. The trivial name is from Gebel Zelten, the area from which the type specimen was collected.

HOLOTYPE: An almost complete but edentulous skull (M.26670). The premaxilla and anterior region of the maxilla are missing and only the proximal region of the nasals is preserved. The lingual wall of the third molar is the only dental fragment preserved.

LOCALITY: The material is all collected from the Lower Miocene (Burdigalian) deposits of Gebel Zelten, Libya.

MATERIAL:

M.26670   Holotype. An almost complete skull of an adult individual.

M.26671   A right maxillary fragment with P^4 to M^3. The dentition exhibits medium wear.

M.26672   A left maxillary fragment with D^2 to D^4. The first two permanent molars are dissected out.

M.26673   A cranial fragment consisting of the supra-occipital and parietal region.

M.26674   A cranial fragment with the frontal-parietal suture and the anterior part of the frontals preserved.

M.26675   A fragment of right mandible with M_3 showing light wear. The ascending ramus and condyle are preserved, though badly shattered.

M.26676   A heavily worn M_3.

M.26677   A lightly worn M_2.

Skull. The skull was found enclosed in a large sandstone nodule from which it was removed by the standard acetic acid preparation method. The postorbital region is in an excellent state of preservation but much of the preorbital region is missing. Slight crushing has occurred in the preorbital region. The specimen is from a mature individual but the acid preparation has opened and defined the sutures; these are not visible in areas prepared by hand.

Maxilla. It is likely that the maxilla was very shallow and probably resembled that of the juvenile giraffe. The postero-lateral region of the maxilla is missing but its shape is indicated as an internal cast (pl. 2). The facial tuberosity lies above M^2. The palatine process of the maxilla is badly broken and interpretation of the surface features is difficult. The surface is shallowly convex, its posterior edge extends to the maxillary tuberosity and into the orbit where it contributes to the lacrymal bulla. The anterior palatine foramen lies on the palatine-maxillary suture opposite the anterior end of the M^2; more posteriorly than in *Okapia* but similar to *Giraffa*. The anterior part of the bone is missing from the level of the anterior edge of P^2. The maxilla extends behind the third molar, forming a large maxillary tuberosity which is badly broken in the specimen.

Nasal. A small part of the nasal is preserved on the antero-dorsal edge of the

prelacrymal vacuity. The bone is very flattened in the same plane as the frontal, as in *Palaeotragus microdon*.

Lacrymal. The large lacrymal forms the posterior edge of the prelacrymal vacuity and extends into the orbit. The antero-lateral face of the bone is concave in contrast to *Okapia* in which it is plane or *Giraffa* in which it is convex. The concavity in *Zarafa* results from the lateral expansion of the frontal bones. The lacrymal is expanded dorsally between the orbit and the prelacrymal vacuity. This dorsal expansion is more marked than in the other giraffids and may be due to the expansion of the frontals but a large lacrymal is also found in *Dremotherium*. A small lacrymal tubercle stands on the antero-dorsal edge of the orbit as in *Okapia* and paired lacrymal foramina are present behind the edge of the orbit. The maxillary foramen lies posterior to the lacrymal tubercle in the same position as in *Okapia*. The lacrymal bulla is badly broken posteriorly.

Jugal. The jugal forms the ventral and postero-ventral edges of the orbit and contributes about half of the postorbital bar; as in *Okapia* a strong ridge forms the ventral edge of the orbit. The lateral face of the jugal is concave and the ventro-lateral region of the bone is badly eroded. The facial region is large and elongate resembling the cervids rather than *Okapia*.

Palatine. Two parallel depressions run antero-posteriorly along the palatine. The bone is badly eroded posteriorly but it is preserved as a vertical plate in the pterygo-palatine fossa which is shallower but otherwise similar to that of *Okapia*.

Frontal. The orbital region of the frontal is concave with the orbital opening of the supraorbital canal lying in the most dorsal part. The ethmoid foramen lies ventro-medial to the supraorbital canal. The frontal-parietal suture runs dorsally from the alisphenoid to the top of the skull and medially across the dorsal face to the median suture (pl. 3). The temporal region of the frontal is very small its concave ventro-lateral face resulting from the great expansion of the posterior supraorbital crest. A strong postorbital ridge runs transversely between the supraorbital process of the frontal and the squamosal bone. The frontal forms the dorsal edge of the preorbital vacuity and dorso-lateral to this the bone thickens forming a high supraorbital crest. As in *Okapia* the supraorbital foramen is directly above the orbital opening of the supraorbital canal; a shallow concavity lies anterior to the foramen but there is no supraorbital groove in *Zarafa*. Lateral to the foramen the bone rises sharply to a peak and a process has been broken off revealing an extensive supraorbital frontal sinus which indicates the presence of a supraorbital ossicone. Ossicones are found in a similar position in *Palaeotragus microdon* and *Samotherium sinense* (Bohlin 1926) and this is probably the primitive position of ossicones in the Giraffidae. Postero-medial to this region is a strong lateral ridge which continues on the parietal.

Parietal. The temporal face of the parietal is dorso-laterally inclined with a convex anterior region and a concave posterior region. The parietal crest crosses the dorsal part of the temporal region and probably continued as far as the edge of the nuchal crest but the posterior region is missing. The dorsal face of the parietal is shallowly concave with raised lateral and medial ridges.

Occipital. The mastoid foramen lies on the postero-lateral face of the supra-

occipital region and the occipital forms its ventro-medial wall (pl. 4, fig. 1).   The shape of the nuchal crest was probably similar to that of *Okapia* but the supra-occipital region is broken dorsally (pl. 4, fig. 1) and most of the nuchal crest is missing.   The occipital condyles and foramen magnum are large in *Zarafa* and dorso-medial to the edge of the condyle the bone surface is concave but it is produced as a large swelling over the foramen magnum, a similar swelling is present in *Palaeotragus microdon* but is less pronounced in *Okapia* and absent in *Giraffa* and *Prolibytherium*.   Dorsal to the swelling the bone is excavated as insertion for the semispinalis capitis muscle; these excavations are shallower than in *Okapia*.   A weak median occipital crest stands between the excavations but the external occipital protuberance is not preserved.

The paroccipital process projects ventrally to the level of the ventral edge of the condyles (pl. 4, fig. 1) as in *Okapia*.   The basioccipital region has a pair of anterior occipital swellings between which the bone surface is concave, a median keel begins at the anterior end of this concavity and continues on the basisphenoid (pl. 4, fig. 2). The lateral face of the basioccipital is concave, this concavity giving way anteriorly to the paired basilar tubercles.   The occipital-basisphenoid suture is closed.   In *Okapia* the anterior swellings of the occipital condyles are much stronger than in *Zarafa* and the median keel is lost; in contrast a median depression runs posteriorly from the basioccipital—basisphenoid suture.   The basilar tubercles are stronger and more elongate in *Okapia* than in *Zarafa*.   The tubercles of the basioccipital provide insertion for the rectus capitis ventralis muscle which acts to flex the head downwards.

Sphenoid.   The posterior region of the orbitosphenoid is concave with the optic foramen lying at its posterior end.   Behind the optic foramen is a large foramen at the base of the alisphenoid.   This foramen results from the fusion of the foramen rotundum and the foramen lacerum anterius (Colbert 1933) and through it emerge cranial nerves III, IV, VI and part of V, it is here referred to as the foramen rotundum.   Behind the foramen rotundum the pterygosphenoid is produced as a ventral process (pl. 2) with convex lateral and concave medial faces.   The ridge runs posteriorly from the posterior edge of the pterygosphenoid and forms the medial wall of the formen ovale through which the mandibular branch of cranial nerve V emerges.   The foramen ovale is elongate in *Zarafa* as in *Okapia* and *Giraffokeryx* but in contrast to the giraffines and sivatheriids in which the foramen is circular (Colbert 1935b).   Postero-lateral to the foramen ovale a groove runs along the edge of the basisphenoid and dorsal to the auditory bulla as far as the eustachian canal and the foramen lacerum medius.   The basisphenoid is transversely convex with a strong median keel fading out anteriorly.   The basisphenoid of *Okapia* does not bear a median keel but is otherwise very similar to that of *Zarafa*.

Squamosal.   In *Zarafa* the squamosal surface is concave lateral to the foramen ovale.   The temporal condyle of the glenoid gives way laterally and posteriorly to a glenoid cavity.   The post-glenoid process is a strong, high, transverse ridge extending further laterally than in *Okapia* or *Giraffa*.   The anterior edge of the glenoid region is formed by a strong ridge which begins at the alisphenoid tuberosity and continues laterally as far as the zygomatic arch.   The squamosal is convex dorsally and con-tributes about half of the temporal wall of the skull, it is also produced laterally as

part of the zygomatic arch. Over the ear region the squamosal forms a strong lateral tuberosity which contributes the postero-dorsal third of the external auditory meatus. The anterior edge of the tuberosity is produced into the temporal crest which runs anteriorly as far as the post-glenoid process. The squamosals of *Zarafa* and *Okapia* are similar.

Ear Region. In *Zarafa* the external auditory meatus is very ventrally situated, it is a postero-laterally directed tube formed by the petrosal and squamosal bones. The antero-lateral face of the external auditory meatus is concave with a strong hyoid process lying lateral to the bulla.

The bulla has a relatively thick wall, it is almost spherical in shape and is larger than that of *Okapia*. A large bulla is a primitive feature of the giraffids (Colbert 1938). The inner ear was partly exposed on the left side of the specimen; it is more elongate than that of *Prolibytherium* but appears to be similar in the main features of its ventro-lateral face. The fossa tensor tympani is very deep as in *Prolibytherium*. The bone surface is swollen postero-ventrally and above the swelling is a shallow concavity which leads anteriorly to the hiatus falloppii. These are the only parts of the inner ear visible.

The temporal canal opens between the ear region and the paroccipital process. Lateral to this the petromastoid suture runs dorsally between the squamosal and occipital regions. The petromastoid forms the postero-lateral part of the nuchal crest and has a concave posterior face.

Mandible. Only the posterior part of the mandible is known in *Zarafa*. The mandibular foramen is very large (pl. 4, fig. 3) and is situated more anteriorly in *Zarafa* than in *Okapia*. A deep depression runs from the foramen towards the condyle and from the ventral edge of the mandibular foramen a shallow groove runs antero-ventrally, this groove accommodates the lingual nerve and below it the face of the mandible is concave as far as the angle which was probably weak. Ventro-medial to M_3 the surface of the mandible is swollen and convex. The condyle is expanded laterally and medially with a slightly curved articular surface as in *Okapia*. The lateral face of the mandible is slightly convex and in the region behind M_3 the bone surface rises medially, forming a sharp medial ridge.

The Skull as a whole. The dorsal view of the skull (pl. 3) is dominated by the laterally expanded frontals but the extent, to which the lateral expansion of the frontals has effected the individual bones of the facial region, is difficult to assess. It is likely that the ancestral giraffids possessed a lacrymal fossa similar to that of the cervids; this assumption is made more probable by the condition of *Prolibytherium* and the concavity in *Zarafa* may represent a stage in the reduction of the fossa, however it is more likely that the expansion of the anterior supraorbital crest formed the concavity of the lacrymal. The dorsal expansion of the lacrymal in *Zarafa* may also be a primitive feature as *Dremotherium* has a large lacrymal bone but the lateral expansion of the frontals has probably influenced the lacrymal causing it to expand dorsally. The facial region of *Zarafa* exhibits some features that are certainly primitive; the paired lacrymal foramina, elongate jugal bones, shallow maxilla and large maxillary tuberosity are all features found in the cervids and palaeomerycids but absent in adult giraffids.

B

The main parameters of the gross cranial anatomy in the giraffids were studied by Colbert (1938) who used seven features of the skull in an attempt to establish the primitive features of *Okapia*.   Owing to the broken nature of the skull of *Zarafa* only four of Colbert's parameters can be used (table 5).   The degree of facial flexion is given as the angle between the basipalatal and basicranial axes; this angle is similar in *Dremotherium, Okapia, Zarafa* and *Palaeotragus microdon* and in these genera it is less than in advanced giraffids.   The degree of facial flexion is usually treated as a measure of the evolutionary stage reached by the genus under consideration and on this basis *Zarafa* is as primitive as *Dremotherium* or *Palaeotragus microdon*.   The angle between the basipalatal axis and the line joining the anterior edge of the orbit to the anterior border of the M1, indicates that the orbit of *Zarafa* is more anteriorly situated than in the other giraffids except *Okapia* in which the orbit is in a similar position to that of *Dremotherium*.   An anteriorly situated orbit is usually regarded as a primitive feature.   The nasals are flat in *Zarafa* and *Palaeotragus microdon* but in the other giraffids and in *Dremotherium* the nasals are more flexed relative to the skull roof and the basipalatal axis.   The condition of the primitive giraffid skull is discussed below and it is postulated that a wide, flattened skull roof is probably primitive for the giraffids.

In general shape of the skull, position of the ossicones and features of the basi-

TABLE 4

Zarafa zelteni. Measurements of the skull and dentition

The Skull

	M.26670	M.26673
Height above M3	88 mm	
Postorbital length. (From anterior edge of orbit to occipital condyle)	187 mm	
Maximum width of frontals	179 mm	
Maximum width across occipital region	103 mm	
Width of occipital condyles	57 mm	
Maximum height of occipital region	78 mm	77 mm

The Upper Dentition

	M.26671		M.26672	
	Length	Width	Length	Width
P4	15 mm	20 mm	—	—
M1	19 mm	—	21 mm	19 mm
M2	22 mm	24 mm	23 mm	22 mm
M3	22 mm	23 mm	—	—
D2	—	—	17 mm	8 mm
D3	—	—	18 mm	13 mm
D4	—	—	18 mm	15 mm

The Lower Dentition

	M.26675		M.26676		M.26677	
	Length	Width	Length	Width	Length	Width
M2					25 mm	17 mm
M3	33 mm	17 mm	32 mm	15 mm		

(All dental measurements are maximum.)

TABLE 5

Gross cranial features of *Zarafa zelteni*

(Measurements for *Okapia, Palaeotragus microdon, Giraffa* and *Giraffokeryx*, after Colbert 1938)

	Dremotherium	*Zarafa*	*Okapia*	*P. microdon*	*Giraffa*	*Giraffokeryx*
Angle between basipalatal and basicranial axes	5°	2°	4°	6°	17°	13°
Angle between basipalatal axis and line joining the anterior edge of the orbit to the anterior border of M1.	82°	75°	82°	69°	71°	52°
Angle between basipalatal axis and superior border of nasals	18°	10°	17°	10°	31°	13°
Ratio of height of maxilla to premolar-molar length (Pm—M length = 100.)	68	59	105	94	130	93

cranial region *Zarafa* resembles the genus *Palaeotragus* and in particular the species *P. microdon*.

Upper Dentition. The deciduous dentition of *Zarafa* forms a closed series it is therefore likely that the permanent cheek teeth also formed a closed series from P^2 to M^3. The molars are more brachyodont than those of *Palaeotragus*, resembling in degree of brachyodonty the molars of *Palaeomeryx*. The enamel is finely rugose and the molars are four rooted with the lingual roots fused.

M^1 is almost square with the posterior half of the tooth displaced labially relative to the anterior half. The parastyle is strong and its labial rib is stronger than that of *Palaeotragus*. The paracone has a strong labial rib, similar to that of *Palaeomeryx* and stronger than that of *Palaeotragus*. The posterior end of the paracone lies lingual to the mesostyle which is the most labial part of the tooth. The metacone of M^1 is the same height as the paracone, its selene has a diagonal orientation on the tooth (pl. 5, fig. 1) and owing to the reduction of the labial rib it is more smoothly curved than the paracone. A weak metastyle forms the postero-labial corner of the tooth. The protocone is stout with a weak labial swelling which lends slight angularity to its crescentic shape, the posterior extension of the protocone terminates in the median valley without meeting the anterior face of the metaconule (pl. 5, fig. 1). The metaconule is higher than the protocone, its anterior region curves labially between the paracone and the metacone and from the anterior face of this region a small crest is produced into the median valley. A conule in the anterior fossette joins this crest and also joins the protocone and metacone giving an 'h' shaped wear trace (pl. 6, fig. 1). The metaconule has a stronger labial swelling than the protocone and behind this the height of the cusp is rapidly reduced. A long narrow accessory crest is produced from the metaconule and runs antero-labially to meet the base of the metacone (pl. 5, fig. 1). M^1 has strong anterior and posterior cingula. The M^1 of M.26672 (pl. 5, fig. 1) has a strong entostyle in the median valley, this arises from the base of the metaconule and does not join the protocone. M.26671 (pl. 6, fig. 1) has strong cingula in the median valley region but an entostyle is not developed. M^2 and M^3 are similar in the main features of their anatomy to M^1.

P^4 is three rooted and brachyodont with finely rugose enamel and anterior and posterior cingula which do not join as a lingual cingulum (pl. 6, fig. 1). The parastyle has a strong labial rib (pl. 6, fig. 2) as in *Palaeomeryx* but in contrast to *Palaeotragus* in which the labial rib of P^4 is feeble. The strong labial rib of the paracone curves anteriorly and carries a deep groove on its anterior face. The paracone of the *Palaeomeryx* P^4 is similar to that of *Zarafa* but in *Palaeotragus* the labial rib is reduced and the cusp is more compressed transversely than in the other two genera. The metacone has a weak swelling posterior to the paracone rib in *Zarafa* whereas in *Palaeomeryx* the labial rib of the paracone is clearly fused to the metacone rib, a groove indicating the line of fusion and in *Palaeotragus* a single rib is present with no posterior swelling. The protocone of the P^4 is stout and more regularly crescentic than in the molars; the anterior region joins the parastyle at an early stage of wear. On the posterior region of the protocone a weak accessory crest joins the base of the metacone and anterior to this crest a weaker parallel crest runs into the fossette

but does not join the base of the metacone (pl. 6, fig. 1). This region of the P^4 differs from both *Palaeomeryx* and *Palaeotragus* but this crest is probably an individual variation of *Zarafa*.

D^4 is molariform (pl. 5, fig. 1), the parastyle is stronger than in the permanent molars with a strong labial rib. The paracone is thicker transversely than in the molars and in the anterior fossette there are a number of small conules (pl. 5, fig. 1). The mesostyle is stronger than in the molars, remaining as an independent style until late in wear. The metacone has a weak labial rib and the metastyle is stronger than in M^1 or M^2. The metaconule of D^4 is similar to that of the molars, a strong fold is produced from its anterior region into the median valley producing a forked anterior wear trace as in the molars. A strong accessory crest is produced from the posterior region of the metaconule and runs antero-posteriorly in contrast to the molars in which it runs antero-labially. A small entostyle is produced from the antero-lingual face of the metaconule into the median valley as in the molars. A cingulum stretches over the antero-lingual region of the protocone and a small cingulum covers the postero-lingual corner of the tooth.

D^3 is triangular with a single anterior root and a posterior pair. The enamel is smooth except on the lingual faces of the paracone and metacone where it is rugose. The parastyle is strong, existing as a separate style until late in wear, it lies near the anterior end of the tooth and the wear trace of the paracone branches labially to meet it. The paracone has a very strong labial swelling with an anterior groove. The metacone and its anterior and posterior styles are similar to those of D^4 or the molars. The protocone is elongate, its anterior region joins the protostyle which forms the anterior end of the tooth. A small crest is produced into the fossette opposite the parastyle and opposite the paracone a stronger crest is produced (pl. 5, fig. 1). The posterior end of the protocone joins the lingual part of the metaconule and there is no median valley. The metaconule of D^3 is similar to that of D^4, it is crescentic and in the anterior region it is produced between the paracone and metacone (pl. 5, fig. 1). A strong crest is produced from the anterior region of the metaconule into the posterior fossette, this crest runs posteriorly across the base of the metacone terminating near the middle of the fossette. An accessory crest is produced from the posterior region of the metaconule, this also runs to the middle of the fossette but does not join the anterior crest. A lingual cingulum runs along the base of the protocone ending in the middle of the tooth and a short cingulum is produced at the postero-lingual corner.

D^2 is very heavily worn and few surface features are visible. The parastyle is strong as in D^3 and joins a weak protostyle anteriorly. The paracone is high and more anteriorly situated than in D^3, it has a strong labial swelling. The metacone is elongate with a weak labial swelling. The protocone is small and its anterior region joins the protostyle and the parastyle, behind this is a weak crest as in D^3. There are three fine accessory crests on the posterior region of the metaconule (pl. 5, fig. 1). D^2 has a weak lingual cingulum which runs around the base of the metaconule and the posterior region of the protocone. The anterior region of D^2 resembles that of D^3 but the posterior region does not show any molariform features.

Lower Dentition. The lower dentition of *Zarafa* is known from a single M_2 and

two third molars. These teeth are identified as *Zarafa* on the basis of their size, giraffoid features, height and enamel features.

M_2 resembles *Canthumeryx* in height and is lower than *Palaeotragus rouenii*. The mesostylid is weaker than in *Canthumeryx* or *Palaeotragus* and the metaconid rib is weak (pl. 5, fig. 3). In *Palaeomeryx* and *Canthumeryx* this rib is strong but in *Palaeotragus* it consists of a slight swelling of the surface. The entoconid has a weaker lingual swelling than in *Canthumeryx* or *Palaeomeryx* and resembles *Palaeotragus*. The posterior region of the entoconid is shortened but expands as a crest at some distance above the crown (pl. 5, fig. 3); a similar expansion is present in *P. rouenii* (M.8367) but in *Canthumeryx* the posterior crest is very strong throughout its height. The posterior fossette opens lingually (pl. 5, fig. 2). The anterior fossette is very shallow and widens at its anterior end (pl. 5, fig. 2); a similar widening occurs in *Palaeotragus* but not in *Canthumeryx*. The anterior cingulum is weaker in *Zarafa* than in *Canthumeryx* and the posterior cingulum is very short and small (pl. 5, fig. 2). M_2 has no ectostylid.

The metaconid of M_3 (pl. 5, fig. 4) is similar to that of M_2 (pl. 5, fig. 2) and is more nearly parallel to the axis of the tooth than in *Palaeotragus* or *Canthumeryx*. The metaconid rib is weak as in M_2 and the metastylid is also weak. The entoconid is similar to that of M_2 but in its posterior region it expands backwards to join the strong entoconulid (pl. 5, figs. 4 and 5) thus closing the posterior fossette. The protoconid and anterior end of the hypoconid are similar to those of M_2 but the posterior end of the hypoconid is flattened.

The accessory column consists of a stout hypoconulid which curves around the posterior end of the tooth, its antero-labial end abuts on the posterior end of the hypoconid and its lingual end curves anteriorly and joins the entoconulid (pl. 5, fig. 5). A strong ectostylid is present in the median valley and a weaker stylid stands in the posterior valley.

The cheek teeth of *Zarafa* show resemblances to both *Palaeomeryx* and *Palaeotragus* so that in some respects *Zarafa* may be regarded as intermediate between these genera. The labial ribs of the paracone and parastyle are weaker than is usual in *Palaeomeryx* though slightly stronger than in *Palaeotragus*. The mesostyle is strong in *Zarafa* as in *Palaeomeryx* but the smoothly curved general shape of the metacone and reduction of the labial metacone rib are very similar to *Palaeotragus* and contrast with *Palaeomeryx*. The protocones are similar in *Zarafa* and *Palaeotragus* and lack the strong postero-lingual spur which is present in *Palaeomeryx*. The cingula are more reduced in *Zarafa* than in *Palaeomeryx* but less reduced than in *Palaeotragus*. The upper molars of *Zarafa* are more hypsodont than in *Palaeomeryx* but are still much lower than in *Palaeotragus*. On the P^4 of *Zarafa* the labial ribs of the paracone and parastyle are stronger than in *Palaeotragus* though weaker than in *Palaeomeryx*, with this exception the P^4 is very similar in all three genera though a lingual cingulum is sometimes present in *Palaeomeryx* only.

The lower molars of *Palaeomeryx* are low crowned and wider relative to their length than in *Zarafa*, *Canthumeryx* or *Palaeotragus*. The lingual faces of the lower molars carry weak ribs in *Zarafa* and *Palaeotragus* whereas in *Palaeomeryx* these ribs are much stronger. A very weak '*Palaeomeryx* fold' is present in M.26675, this fold

rarely occurs in *Palaeotragus* but it is usual and often strong in *Palaeomeryx*. The lower molars are higher crowned in *Zarafa* than in *Palaeomeryx* though lower than in *Palaeotragus*.

The upper and lower cheek teeth of *Zarafa* show features in which they resemble *Palaeotragus* and as these features are more advanced than the primitive ruminant condition they are interpreted as indicative of true relationship between the genera.

Post-cranial material. The Gebel Zelten collection includes a considerable amount of post-cranial material but owing to the conditions of preservation none of this material was found in association with the cranial elements. Specimens may be assigned to one or other of the ruminant genera with varying degrees of confidence, highest in the case of *Zarafa* which is the largest ruminant found at Gebel Zelten. In cranial features *Zarafa* is sufficiently like the other palaeotragines for the assumption to be made that the post-cranial elements must also show affinities with this group.

MATERIAL: B.U.20115—An almost complete right femur. B.U.20116—A complete right tibia. B.U.20117—A complete right metatarsal. B.U.20118—A complete left calcaneum. B.U.20119—A right calcaneum. B.U.20120—A right astragalus. B.U.20121—A left astragalus. B.U.20122—A left astragalus. B.U.20123—A left scapular fragment. B.U.20124—The distal end of a left humerus. B.U.20125—A right olecranon region. B.U.20126—The proximal end of a left radius. B.U.20127 —The distal end of a left radius. B.U.20128—A fragment of a right metacarpal. B.U.20129—An anterior phalange. B.U.20130—A posterior phalange. B.U.20143 —An anterior phalange. B.U.20144—A posterior phalange. B.U.20145—A posterior phalange. B.U.20146—The proximal end of a left tibia. B.U.20147—An axis. B.U.20148—An axis. B.U.20149—A seventh cervical vertebra. B.U.20150 —A thoracic vertebra, probably the eighth. B.U.20151—A fourth lumbar vertebra. B.U.20152—A sixth lumbar vertebra.

The pectoral girdle

Scapula. The glenoid is shallowly concave and almost elliptical with a deep glenoid notch lying postero-lateral to the coracoid process (text fig. 7c). The coracoid process is strongly developed and projects further from the body of the bone than the tuber scapulae. In *Okapia* and *Giraffa* the tuber scapulae is very strongly developed and has grown over the coracoid process whereas in *Zarafa* the tuber scapulae is weak, consisting of a swelling lateral to the coracoid process. The surface of the tuber scapulae is heavily sculptured as the origin for the biceps brachii muscle. The spine of the scapula is shifted anteriorly and the supraspinous region is very narrow as in *Okapia*. The base of the spine indicates that it rises smoothly and an acromion process was probably present as in *Palaeotragus* and in contrast to *Okapia* and *Giraffa* in which this process is entirely absent. The absence of the acromion process appears to be related to the development of the tuber scapulae as in *Equus*, *Camelus* and large species of *Bos* the acromion process may be lost, in which case the tuber scapulae is of a size comparable to that of *Giraffa*. A strong tuber scapulae presumably indicates a greater development of the biceps brachii muscle and similarly reduction or absence of the acromion process indicates a reduction in the importance of the acromial part of the deltoideus muscle. The infraspinatus region

is wide with a thickened posterior edge resulting in the concavity of the infraspinous fossa, the posterior edge is also concave as in *Giraffa*.   The subscapular fossa is concave distally but the subscapular face of the neck is slightly convex.   The shape of the neck of the scapula indicates that the blade was as elongate as that of *Okapia*. The anterior shift of the spine is also similar to *Okapia*.

Humerus.   The distal end of the humerus is known from a single badly shattered specimen.   The coronoid fossa is shallow with a deeply pitted surface and lateral to this the bone is expanded as a very strong lateral epicondyle similar to *Okapia* and *Giraffa*.   The lateral condyle is wide with a concave surface and the medial condyle is also wide.   The olecranon fossa is very deep.   The distal end of the humerus is similar to that of *Okapia* and *Giraffa*.

Radius.   The lateral tuberosity of the radius is weaker than in *Okapia* or *Giraffa* and the medial tuberosity is concave.   These tuberosities provide attachment for the ligaments of the elbow and the smaller size of the lateral tuberosity indicates a weaker ligament; this is possible in a small relatively light animal such as *Zarafa*. The distal end of the radius has the usual three articular facets.   The scaphoid facet is relatively wide; a concavity at the anterior end of the facet acts as a stop preventing over extension; this concavity is about the same depth in *Okapia* and shallower in *Giraffa*.   The lunar facet has deep anterior and posterior depressions which also act as stops.   The cuneiform facet is more oblique than the other two facets and its postero-medial region consists of a vertical concavity.   The dorsal face of the bone has two strong ridges as in *Okapia*.   The shaft of the bone, although incompletely known, appears to have been more slender than in *Okapia*.

Ulna.   The olecranon process of the ulna is the only region preserved.   The semilunar notch is transversely narrow and the edges of the facet are rounded giving it a transversely convex shape which agrees closely with that of *Giraffa*.   In *Okapia* the semilunar facet is transversely plane which greatly restricts the lateral mobility of the elbow.   The semilunar region is produced disto-laterally as a strong process articulating partly with the lateral condyle of the humerus and partly with the posterior face of the radius; this facet is similarly developed in *Giraffa*.   The olecranon process is short and transversely flattened with a concave medial face. The distal end is heavily sculptured for the insertion of the triceps muscle.

Metacarpal.   The facets of the proximal end are similar to those of *Okapia* and on the postero-medial face of the proximal end the surface of the bone is heavily sculptured as in *Okapia* but there is no indication of metacarpal V.   The presence of this metacarpal is variable in *Giraffa* (Fraser 1951) and may also have been variable in *Zarafa*.   The shaft of the metacarpal is more slender than that of *Okapia;* its cross-section is flattened as is usual in the ruminants, with a deep channel on the posterior face to accommodate the flexor tendons.   The distal head has the usual paired condyles converging slightly as in *Giraffa*.   The keel of the condyle is very strong and in the posterior region it extends proximally as a strong ridge over the articular face and beyond this onto the body of the bone.   The strength of this keel resembles the cervid condition.   In both *Okapia* and *Giraffa* the condyle is expanded in the interdigital region which reduces the apparent strength of the keel. The distal head of the metacarpal is much wider than the shaft in *Zarafa*, *Giraffa*

and the cervids but in *Okapia* it is only slightly wider as the shaft is thickened.

Phalanges. The phalanges are very slender. Their postero-proximal epicondyles are very short whereas in *Okapia* and *Giraffa* they are elongate, covering about one third of the posterior face of the phalange. The interdigital face has a weak tuberosity in the distal region to which the interdigital ligament attaches. The distal articular face consists of a central depression flanked by two expanded areas which extend over the end of the bone; this facet is slightly oblique which causes the second phalange and hooves to move towards each other when weight is placed on the foot.

Five phalanges are identified with *Zarafa*, these include two larger and three small ones. The difference in size between these groups is approximately the same as the size relationship between the anterior and posterior phalanges of *Okapia*; for this reason the larger are identified as anterior and the smaller as posterior. The smaller phalanges will not be described separately with the description of the pelvic limb.

The Pelvic Limb

Femur. The head of the femur is small relative to the length of the bone; its articular surface extends onto the neck and around the lower side of the head as in *Okapia*. The neck of the femur is long and the head is displaced further medially than in *Okapia* or *Giraffa*. In both *Okapia* and *Giraffa* certain tendencies towards a graviportal condition of the limbs are evident, these tendencies are most apparent in the rotation of the articulations into the line of the shaft. The greater displacement of the articulations or curvature of the shaft of the limb bones in *Zarafa* indicates a lighter animal. The trochanter minor is weak and is not displaced as far medially as it is in *Okapia* or *Giraffa*; as a result the trochanteric ridge appears stronger in *Zarafa* than in the extant giraffids.

The distal region of the femur is of the usual ruminant pattern. On its anterior face the medial ridge is high and expanded but is less swollen than that of *Okapia* or *Giraffa*, this indicates that the 'stifle joint' was less effective than in *Okapia* or *Giraffa* as expected in a smaller lighter animal (Shuttleworth 1943). The medial and lateral epicondyles are very strong but are less transversely expanded than those of *Okapia*. The shaft of the femur is slender and slightly curved anteriorly (posterior face concave) as in the medium sized cervids and in contrast to *Okapia* and *Giraffa* in which the shaft is straight and relatively stout. The supracondyloid fossa is more elongate than in *Okapia*, this is probably due to the generally narrower nature of the distal region in *Zarafa*.

The femur of *Zarafa* is much more slender than that of *Okapia* and both extremities are narrower. The curvature of the shaft indicates a lightly built animal and features such as the position of the trochanter minor are similar to the cervid condition.

Tibia. The proximal head of the tibia is narrow transversely as in the cervids and in contrast to *Okapia* or *Giraffa* in which the head is relatively wide. The cnemial crest is high and blends gradually into the shaft over the proximal quarter of its length; this crest is similar in the medium sized cervids but in *Okapia* it occupies the proximal third of the anterior face. The antero-proximal region of the cnemial crest forms a large triangular tuberosity bounded laterally by the sulcus muscularis

and medially by a shallow depression through which the middle patellar ligament passes. A small tubercle is produced posterior to the spine, this is similar to that of *Okapia* and provides attachment for the posterior cruciate ligament.

The distal end of the tibia is much narrower in *Zarafa* than in *Okapia* and in general features it resembles the cervid tibia. The shaft is slightly curved posteriorly as in the cervids and in contrast to *Okapia* in which the shaft is straight. The tibia of *Zarafa* is relatively shorter than that of *Capreolus* but longer than that of *Okapia* or *Giraffa*. It is similar in its main features to the tibia of *Giraffa* which is more primitive than that of *Okapia*.

Calcaneum. The tuber calcis is very long and similar to *Capreolus* or *Palaeomeryx* whereas in *Palaeotragus* and *Samotherium* it is slightly shortened and in *Okapia* and *Giraffa* it is extremely shortened. The tuber calcis is more flattened than in *Okapia*. The posterior face of the sustentacular process is plane whereas in *Okapia* and *Samotherium* it is concave. The lateral face of the calcaneum bears an area of heavy sculpturing occupying most of the antero-proximal region, posterior to this is a small oval facet to which the lateral ligament of the ankle attaches. The fibular facet is of the usual primitive form with a raised convex posterior region and a concave anterior region as in *Palaeomeryx* and in contrast to *Okapia* in which this facet is specialized by the loss of the anterior region. The facet in *Zarafa* indicates that the fibula was probably similar to that of *Capreolus*. The sustentacular facet is wide and transversely convex, it does not show any reduction of the proximo-medial corner, such as is found in *Okapia* and *Giraffa* as a specialization facilitating greater flexion of the ankle. The calcaneum is generally more like that of the cervids than the extant giraffids, this is however partly due to the specialization of the ankle in *Okapia* and *Giraffa*.

Astragalus. This is more elongate than in *Okapia* or *Giraffa* and compares very closely in all its main features with the astragalus of *Palaeomeryx*.

Metatarsal. The proximal facets of the metatarsal are similar to those of *Okapia*. A deep notch lies on the lateral edge of the bone between the facets, this probably housed metatarsal V which appears to have been well developed in contrast with the extant giraffids in which it is represented as a thin ribbon of bone, entirely fused to the lateral face (Fraser 1951). A strong tubercle lies between and medial to the facets, this is metatarsal II and is stronger than in *Giraffa* or *Okapia*; it continues on the medial face as a wide ribbon of bone fused to the shaft and continuing much further distally than in *Giraffa*.

The shaft of the metatarsal is very long and slender in *Zarafa*, it has a deep cross-section as in *Giraffa*, *Samotherium* and *Palaeotragus*, this is narrower transversely than in *Okapia*. The two condyles of the distal extremity are similar to those of *Giraffa* but the ridges of the condyles are stronger as on the metacarpal. A deep channel runs down the anterior face of the bone, this channel is open for its whole length as in *Okapia*, *Giraffa* and the bovids whereas in the cervids the channel is roofed over in the distal region.

Vertebrae

Axis. The axis of *Zarafa* is smaller and more elongate than that of *Okapia*. The

neural spine has a high posterior tubercle (text fig. 2a) from which it slopes down-
wards anteriorly and projects over the odontoid process as in *Okapia*. The odontoid
process is similar to that of *Giraffa* and the anterior articular facet has a depression
near to and around the base of the odontoid process as in *Giraffa* but in contrast to
Okapia in which the facet blends into the odontoid process. The anterior articular
facet slopes almost vertically as in *Giraffa*. The intervertebral foramen (text fig.
2a) is in the same position as that of *Okapia*, it has a deep postero-ventral channel
which joins it to the anterior channel of the vertebrarterial canal. This canal begins
near the middle of the bone and emerges on the posterior face, dorso-lateral to the
articulation. The posterior articular process is less pronounced than in *Okapia*, its
articular facet is almost circular and faces postero-ventrally. The transverse
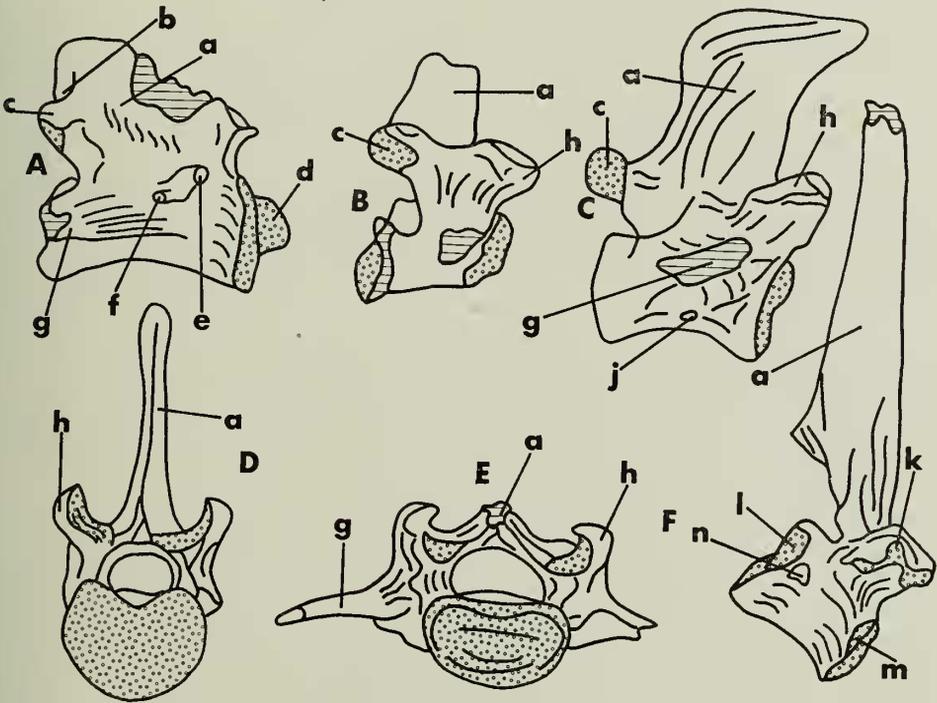
FIG. 2. The vertebrae of *Zarafa*. (Half natural size.). (A) Lateral view of the axis
(B.U.20148). (B) Lateral view of the seventh cervical vertebra (B.U.20149). (C) Lateral
view of the fourth lumbar vertebra (B.U.20151). (D) The anterior face of the fourth
lumbar vertebra (B.U.20151). (E). Anterior face of the sixth lumbar vertebra (B.U.20152).
(F) Lateral view of the eighth thoracic vertebra (B.U.20150). a: neural spine. b:
posterior tubercle. c: posterior articular process. d: odontoid process. e: inter-
vertebral foramen. f: vertebrarterial canal. g: transverse process. h: anterior
process. j: nutrient foramen. k: tubercular facet. l: posterior facet for the head of
the rib. m: anterior facet for the head of the rib. n: tuberosity.

process is more slender than that of *Okapia* and is more dorsally situated; lying at the same level as the top of the centrum (text-fig. 2a).   The posterior articular face of the centrum is concave as in *Okapia*; and in *Zarafa* it is more nearly vertical than in *Okapia*.

Cervical vertebra.   The seventh cervical vertebra (text fig. 2b) is similar to that of *Okapia* with no signs of the specialization found in *Giraffa* (Lankester 1908).   The centrum is thicker than in *Okapia* and both anterior and posterior articulating faces of the centrum are more nearly vertical in *Zarafa* than in *Okapia;* in this feature the vertebra is similar to that of *Giraffa*.   The anterior articulating processes are more widely divergent than in *Okapia* but the articulating facets are orientated at the same angle in both genera.   The posterior articular processes are lateral only with no indication of the medial articulation such as occurs in *Okapia* (Lankester 1910). The facets are elongate which indicates that there was considerable freedom of movement of the lower neck region.

Thoracic region.   A single thoracic vertebra (B.U.20150) agrees closely with the eighth thoracic vertebra of *Okapia*.   The anterior face of the centrum is shallowly convex and the facet extends ventrally as it does in *Okapia*.   The facet for the head of the rib (text fig. 2f) is more closely blended with the centrum face than in *Okapia*. The ventral ridge is strong with a tubercle in the postero-dorsal corner of the concave lateral face (text fig. 2f), this is equally well developed in *Okapia*.   The posterior face of the centrum is concave with the facets for articulation with the rib situated high up at the dorso-lateral corners of the face (text fig. 2f).   The transverse process is well developed with a tubercular facet running antero-dorsally from its ventro-lateral region.   The mamillary process is only weakly developed and is more laterally situated than in *Okapia*.   Both anterior and posterior articular processes are deformed as only the left side is developed in each case and the facets on this side have undergone compensatory size increases.   The neutral spine is very slender and its posterior region is only slightly thickened; the spine was probably higher than in *Okapia* and more posteriorly inclined.

Lumbar vertebrae.   The fourth lumbar vertebra (B.U.20151) is more elongate than in *Okapia* or *Giraffa* with a strong ventral ridge and ventro-lateral concavities as in *Okapia*.   A large nutrient foramen lies lateral to the ventral ridge, just anterior to the middle of the centrum (text fig. 2c); in *Okapia* and *Giraffa* many small foramina are found in this region.   The anterior face of the centrum is shaped as shown (text fig. 2d) and the posterior face is expanded slightly transversely as in the other giraffids.   The anterior articular process is strong and high with a medially concave articular facet as is usual in the lumbar region of the ruminants.   The posterior articular process is short and resembles *Giraffa* as it faces ventro-laterally, rather than laterally as it does in *Okapia*.   The posterior articular process is not produced as far posteriorly as it is in *Okapia*.   The neural spine is stout and high; it is expanded anteriorly in the distal region which is also thickened and has an excavated surface for the insertion of the longissimus dorsi muscle.

The sixth lumbar vertebra (B.U.20152) is free with a transversely expanded centrum (text fig. 2e) bearing a strong ventral ridge in the anterior region only. The anterior articular process has an elongate articular facet directed postero-

ventrally as in *Giraffa* and not ventrally as in *Okapia* which indicates a greater freedom of movement at this joint in *Zarafa* and *Giraffa* than in *Okapia*. The transverse process (text fig. 2e) is slender and slopes slightly ventrally as in *Giraffa*. The facet of the posterior articular process is elongated antero-posteriorly but is not as long as that of *Giraffa*. The neural spine is more anteriorly situated in *Zarafa* than in *Giraffa* and the posterior part of the centrum is slightly elongated.

Functional Interpretations. The forelimb and vertebral column of *Zarafa* are poorly known and it is not possible to make any meaningful functional interpretations of these regions. Fortunately the hind-limb is almost completely known and it has been used to assess the degree of cursorial adaptation attained.

The main recent study of functional features of the limbs of mammals is that of Smith and Savage (1956) who in their section on the hind limb deal only with the muscles originating on the pelvis. In *Zarafa* the pelvis is not known and therefore this group of muscles cannot be studied but the mechanical advantage of the biceps femoris and semi-tendinous muscles, which insert on the cnemial crest, can be estimated using the formula:

$$\text{Mechanical advantage of biceps femoris and semitendinous muscles} = \frac{\text{Height of cnemial crest}}{\text{Total length of lower leg}}$$

In this equation it is assumed that the femur and pelvis are rigid which they are not; but the accuracy of the figures obtained is sufficiently high as the formula is used for comparative purposes rather than to obtain absolute measurements. The height of the cnemial crest of the tibia is measured from the posterior face of the tibial spine and the length of the lower leg is measured vertically from the knee to the ground.

If the mechanical advantage of the locomotory muscles is high then a slow powerful action is indicated as found in graviportal animals. A low mechanical advantage of the locomotory muscles indicates a weak but rapid action and is characteristic of cursorial animals, thus the mechanical advantage of a group of muscles may be used to measure the degree of cursorial adaptation attained. Table 7 indicates that *Giraffa* has a lower mechanical advantage for the biceps femoris than the other genera and *Giraffa* is more cursorially adapted than these genera. In degree of cursorial adaptation, as measured using the muscles inserting on the cnemial crest *Zarafa* lies between *Okapia* and *Capreolus*.

The mechanical advantage of the gastrocnemius muscle which inserts on the end of the tuber calcis can be estimated using the formula:

$$\text{Mechanical advantage of gastrocnemius muscle} = \frac{\text{Length of tuber calcis}}{\text{Length of ankle and pes}}$$

As may be expected *Giraffa* again exhibits considerably greater cursorial adaptation than the other genera and *Zarafa* again lies between *Okapia* and *Capreolus* (table 7).

The osteological features of *Zarafa* indicate a lightly built animal and this is borne out by features of the limbs which taper rapidly and are very slender, thus the low degree of cursorial adaptation, as measured from the mechanical advantages of the muscles, must be interpreted as a primitive feature of *Zarafa*.

TABLE 6

Measurements of *Zarafa zelteni* post-cranial elements

Vertebrae

	B.U.20147	B.U.20148	B.U.20149	B.U.20150	B.U.20151	B.U.20152
Length of centrum	69 mm	65 mm	32 mm	34 mm	47 mm	37 mm
Total height of vertebra	63 mm	68 mm	72 mm	131 mm	91 mm	47 mm
Depth of centrum	20 mm	19 mm	23 mm	24 mm	23 mm	21 mm
Width of anterior end of centrum	52 mm	49 mm	19 mm	28 mm	35 mm	37 mm
Width of posterior end of centrum	35 mm	34 mm	34 mm	36 mm	39 mm	48 mm

Scapula

	B.U.20123
Width of neck of scapula (Min.)	36 mm
Depth of neck of scapula (Min.)	19 mm
Width of glenoid (Ant-post)	47 mm
Depth of glenoid (Transverse)	39 mm

Humerus

	B.U.20124
Distal end	
Width across epicondyles	59 mm
Antero-posterior depth of distal articular surface	27 mm

Radius

	B.U.20126	B.U.20127
Width of proximal articular surface	49 mm	
Depth of proximal articular surface:		
Minimum	29 mm	
Maximum	18 mm	
Width of distal articular surface		44 mm
Depth of distal articular surface		29 mm

Metacarpal

	B.U.20128
Length	317 mm
Width of distal end	46 mm
Depth of distal end	25 mm

Phalanges

	B.U.20129	B.U.20143	B.U.20144	B.U.20145	B.U.20130
Length	70 mm	68 mm	63 mm	62 mm	58 mm
Width of proximal end	21 mm	21 mm	20 mm	19 mm	20 mm
Depth of proximal end	23 mm	25 mm	23 mm	24 mm	23 mm
Width of distal end	16 mm	18 mm	16 mm	16 mm	17 mm
Depth of distal end	14 mm	15 mm	12 mm	13 mm	12 mm

Femur

	B.U.20115
Total length (Maximum)	341 mm
Width of proximal end	84 mm
Depth of articular head	36 mm
Width of distal end	66 mm
Depth of distal articular head:	
Maximum	83 mm
Minimum	58 mm

TABLE 6 (*cont.*)

Tibia

	B.U.20116	B.U.20146
Length	349 mm	—
Width of proximal end	68 mm	69 mm
Depth of proximal end	76 mm	72 mm
Width of distal end	46 mm	—
Depth of distal end	35 mm	—

Calcaneum

	B.U.20118	B.U.20119
Total length	108 mm	115 mm
Length of tuber calcis	74 mm	76 mm
Width across sustentaculum	34 mm	32 mm
Depth of tuber calcis	28 mm	27 mm
Maximum depth of bone	41 mm	42 mm

Astragalus

	B.U.20120	B.U.20121	B.U.20122
Maximum length	49 mm	41 mm	53 mm
Minimum length	40 mm	40 mm	41 mm
Width proximally	29 mm	30 mm	32 mm
Width distally	29 mm	29 mm	30 mm
Maximum depth	23 mm	23 mm	25 mm

Metatarsal

	B.U.20117
Length	349 mm
Width of proximal end	39 mm
Depth of proximal end	41 mm
Width of distal end	42 mm
Depth of distal end	29 mm

TABLE 7

Measurements used for functional interpretation of the *Zarafa* hind limb

	Giraffa	*Okapia*	*Zraafa*	*Capreolus*
Height of cnemial crest of tibia	10·5 mm	5·7 mm	6·5 mm	3·5 mm
Total length of lower leg	179·0 mm	87·5 mm	87·0 mm	45·5 mm
Length of tuber calcis	15·9 mm	8·6 mm	8·7 mm	5·0 mm
Length of ankle and pes	110·0 mm	51·0 mm	50·0 mm	26·0 mm
Mechanical advantage of biceps femoris muscle	0·059	0·065	0·075	0·077
Mechanical advantage of gastrocnemius muscle	0·163	0·166	0·174	0·192

Family SIVATHERIIDAE nov.

DIAGNOSIS: Large giraffoids with strongly expanded frontal bones and pneumatized skull roof. On the frontal and parietal bones a pair of large, flattened, variably branched ossicones is produced. A great increase in overall body size occurs in advanced genera but elongation of the limbs and neck does not occur.

REMARKS: This group has previously been treated as a subfamily of the Giraffidae but the presence of *Prolibytherium* and *Zarafa* in deposits of early Miocene age indicates a division which extends back into the Oligocene. A more natural grouping results if the Palaeotraginae and Giraffinae are grouped together in the Giraffidae and the Sivatheres are placed in a separate family the Sivatheriidae.

Genus *PROLIBYTHERIUM* Arambourg 1961

DIAGNOSIS: A primitive sivatheriid of small size. The cranium is narrow and exhibits very little facial flexion. The frontals support large, aliform ossicones which extend anteriorly in the supraorbital region and posteriorly over the parietal and occipital region. The occipital condyles are large with very thickened bone. A lacrymal fossa and paired lacrymal foramina are present.

Prolibytherium magnieri Arambourg 1961

DIAGNOSIS: As for genus.

HOLOTYPE: A cranium with badly shattered ossicones, described by Arambourg (1961a).

LOCALITY AND HORIZON: The material is all collected from the Lower Miocene (Burdigalian) deposits of Gebel Zelten, Libya.

REMARKS: Specimens in l'Institut de Paléontologie, Paris, include dentitions of *Prolibytherium* but these were not found with the type material and were not described by Arambourg.

MATERIAL: Specimens in l'Institut de Paléontologie are defined by capital letters.

M.21901	An almost complete skull; the ossicones, cranium and left maxilla are complete. The upper dentition is heavily worn and lacks P^3.
M.21899	A right mandible with heavily worn dentition.
M.26678	An endocranial cast that was dissected out of a skull.
M.26679	A fragment of cranium, with ossicones and bearing the only large lacrymal fragment.
M.26680	An edentulous mandible which has a complete diastema.
M.26681	An isolated lower third molar, lightly worn.
P.M. A.	An almost complete mandible with P_2 to M_3 exhibiting slight wear.
P.M. B.	A mandibular fragment with almost unworn M_1 to M_3.
P.M. C.	A mandibular fragment with heavily worn M_1. The P_4 was displaced to the side during life and is thus virtually unworn.
P.M. D.	A mandibular fragment with heavily worn M_1 to M_3.
P.M. E.	P_3 and P_4, both lightly worn.
P.M. F.	A badly shattered M^3. The paracone and antero-labial region is missing but the metacone is complete.
B.U.20175	A right mandible with heavily worn P_3 to M_3.
B.U.20176	A cranium with the external auditory meatus preserved.

THE SKULL AND DENTITION

The Skull.   The skull roof is entirely covered by large ossicones (pl. 7) which are completely fused to the frontal and parietal bones without any visible suture.   The facial region is incompletely known as the premaxillary and nasal bones are not preserved and the jugal is known from a single small fragment.   A complete lacrymal has not been discovered but several large fragments of the lacrymal are known. With these exceptions the cranial elements are almost completely known from well preserved specimens.

Maxilla.   The maxilla of M.21901 is broken near the postero-labial alveolus of M^3, the break continuing antero-dorsally along the maxillary jugal suture (text fig. 3a). The maxilla is complete dorsally as far as the maxillary-nasal suture and anteriorly it is broken along what is probably the maxillary-premaxillary suture (pl. 8).   The lateral surface of the maxilla is convex with a feeble facial crest which joins the weak facial tuberosity at its posterior end.   The infraorbital foramen is slightly larger than the lingual alveolus of P^3; it is deeply inset below the curve of the maxilla above P^2 as in *Sivatherium* and *Capreolus* (text fig. 3b).   In *Okapia* and *Giraffa* the infraorbital foramen is more anteriorly situated than in *Prolibytherium*; this difference may be due to the expansion and increased height of the maxilla in the extant giraffids.   The molars and P^4 have a diagonal orientation relative to the main contours of the maxilla which results in strong juga alveolaria on the surface of the maxilla (pl. 8).   Above the facial tuberosity the surface of the maxilla is deeply concave indicating the presence of a lacrymal fossa (pl. 8), this region agrees closely with that of *Capreolus* and differs from *Okapia* and *Giraffa*.   Above this region the maxilla forms the antero-ventral border of the preorbital vacuity (text fig. 3a), this edge is similar to that of *Capreolus* (text fig. 3b).

The palatine process of the maxilla is shallowly concave with the median suture raised above the bone surface.   The anterior palatine foramen is level with the antero-lingual corner of M^2 and the palatine groove runs anteriorly from it (pl. 9).   Behind M^3 is a large maxillary tuberosity as in *Palaeomeryx* and *Zarafa*.

The maxilla of *Prolibytherium* is very shallow in the region under the orbit, as in *Zarafa*.   The maxillae of *Prolibytherium* and *Capreolus* agree closely in shape (text fig. 3b); this agreement is less close in the posterior region where the maxilla is reduced in *Capreolus* and the jugal is expanded ventrally.

Lacrymal.   The orbital face of the lacrymal is concave and the border of the orbit is sharp.   Paired lacrymal foramina are present, the dorsal foramen lies behind the lacrymal tubercle and in *Prolibytherium* both foramina lie behind the edge of the orbit whereas in *Capreolus* they are situated on the edge of the orbit.   The anterior face of the lacrymal is very concave and the bone is thin ventrally.   Although the ventral part of the lacrymal is not known, the concavity of the dorsal region and the reduction in thickness of the bone agree with the concavity of the dorsal part of the maxilla and indicate the presence of a deep lacrymal fossa.   A lacrymal fossa is absent from all giraffids and the other sivatheriids but is present in cervids and in some bovids.   In the cervids this fossa houses the facial gland which produces a secretion used in territorial marking.   The establishment and maintenance of a territory involves a certain amount of intraspecific combat and the occurrence of this

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in *Prolibytherium* is also indicated by the large ossicones.   The presence of a lacrymal fossa in *Prolibytherium* the cervids and *Dremotherium* could result from parallel development but in this instance it is more likely that its presence is a primitive feature.

Jugal.   A fragment of the jugal is preserved attached to the maxilla (text fig. 3a). The dorsal edge of this fragment runs postero-ventrally and is probably the suture with the lacrymal.   The flattened antero-dorsal face of the jugal is continuous with the lacrymal fossa.

Palatine.   The palatine is transversely concave and the depth of this concavity increases posteriorly (pl. 9).   The anterior palatine foramen opens on the anterior suture.   The median suture is slightly raised as on the maxilla and the posterior end of the palatine is deeply indented forming the edge of the pterygo-palatine fossa (pl. 9); here the bone is vertical with a lateral face which is continuous with the maxillary tuberosity.   The lateral face of the palatine is penetrated by the posterior palatine foramen which is similarly situated in *Capreolus* but is higher in *Okapia*.
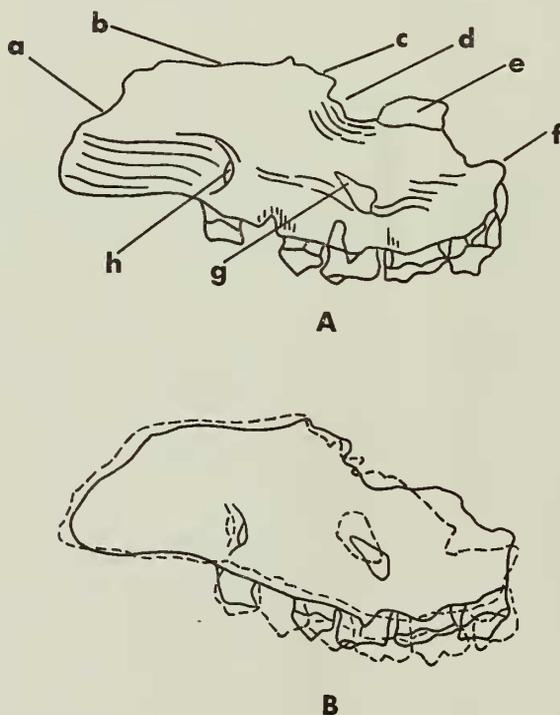
FIG. 3.   The maxilla of *Prolibytherium* (B.M.21901).   (Half natural size).   (A) Lateral view of the maxilla.   a: maxillary-premaxillary suture.   b: maxillary-nasal suture.   c: border of preorbital vacuity.   d: lacrymal fossa.   e: fragment of jugal bone.   f: maxillary-jugal suture.   g: facial tuberosity.   h: infraorbital foramen.   (B) Comparative outlines of the maxilla in *Prolibytherium* and *Capreolus*.   *Prolibytherium* ——————:   *Capreolus* - - - - - - - - - - - - - - -

Frontal. The orbital region of the frontal is concave and the orbital opening of the supraorbital canal is in the dorsal region of this concavity; probably as a result of the thickening of the bone, this opening is situated more medially than in *Okapia* or *Giraffa.* From its orbital opening the supraorbital canal runs dorso-medially for a short distance before turning sharply anteriorly, it continues in this direction as far as the dorsal face, thus opening much more anteriorly than is usual in the ruminants. The medial edge of the supraorbital process forms a strong ridge which continues medially as far as the alisphenoid tuberosity. The temporal region of the frontal is convex dorso-ventrally and blends into the ossicone in its dorsal region. The supraorbital foramen is anterior to the highest part of the orbit and the deep supraorbital groove runs anteriorly from the foramen to the lateral end of the frontal-nasal suture (text fig. 4). The supraorbital crest is formed by the thickening of the frontal along the edge of the orbit. Behind the supraorbital foramen the bone forms a triangular depression bounded antero-laterally by the supraorbital crest and medially by the median suture which is raised into a crest running posteriorly as far as the frontal eminence (text fig. 4).

Parietal. The lateral face of the parietal is convex and the dorsal region fuses with the ossicone. In front of the occipito-parietal suture the dorso-lateral face of the bone is concave with a strong parietal crest which blends into the ossicone anteriorly. The opening of the large temporal canal is visible on the broken edge of the bone (pl. 7).

Ossicones. The ossicones fuse completely with the expanded frontal and parietal bones, they are large and aliform and have been arbitrarily divided into anterior and posterior palmations for the purposes of description (text fig. 4). From the frontal eminence a strong crest runs antero-laterally forming the posterior edge of the triangular supraorbital concavity of the frontal (text fig. 4); this crest continues laterally as the leading edge of the anterior palmation. Another crest runs postero-laterally from the frontal eminence and forms the thick posterior edge of the posterior palmation. Lateral to these crests the ossicones become much thinner with concave dorso-lateral faces.

The dorsal and ventral surfaces of the ossicone bear a large number of fine, radiating grooves (pl. 7). Immediately dorsal to the supraorbital process is a small foramen on the leading edge of the anterior palmation, a deep groove originates from this foramen and runs postero-laterally across the lateral concavity of the ossicone, giving off many smaller branches over the surface.

The ventral surface of the ossicone is convex antero-posteriorly and shallowly concave transversely. A large groove begins postero-lateral to the supraorbital process and runs postero-laterally nearly to the edge of the ossicone where it forks, one branch follows the lateral edge of the anterior palmation and the other follows the edge of the posterior palmation. Above the glenoid cavity a large foramen, at the base of the ossicone, gives rise to a deep groove which divides into many fine grooves radiating over the lateral surface of the ossicone. A medial foramen is situated above the occipital region, at the base of the ossicone, lateral to this is a stout column beyond which is a larger lateral foramen (pl. 10, fig. 2) many fine grooves radiate from this foramen.

Occipital. The dorsal surface of the supraoccipital region is convex as far as the nuchal crest. In the palaeotragines the supraoccipital region is reflected over the condyles but in *Prolibytherium* it is vertical or slopes slightly anteriorly as in *Capreolus*. The mastoid process forms the lateral wings of the nuchal crest and the supra-occipital forms the dorsal part of the crest (pl. 10, fig. 2). The medial edge of the mastoid foramen is formed by the occipital bone. On the posterodorsal face of the supraoccipital region are paired depressions providing insertion for the semispinalis capitis muscles—the chief extensors of the head and neck. The external occipital protuberance lies medio-ventral to these pits (pl. 10, fig. 2), its surface is deeply sculptured (pl. 10, fig. 2) for attachment of the nuchal ligament. The ventral part of the external occipital protuberance is produced ventrally as a strong median crest. The occipital condyles have sharp keels on their lateral faces (pl. 10, fig. 1). The condyles are set very close to the skull; they are relatively large and the bone is
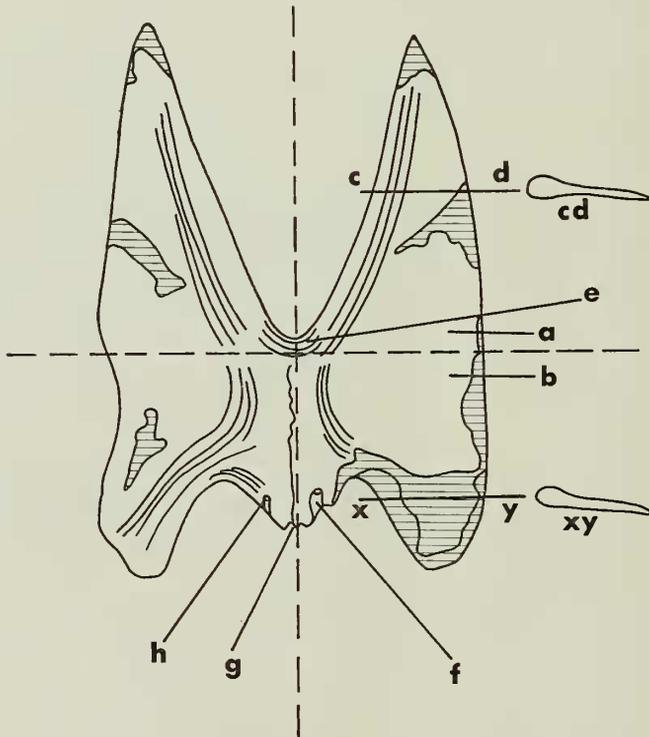

FIG. 4. Dorsal view of the ossicones of *Prolibytherium* (B.M.21901) (One sixth natural size.). a: posterior palmation. b: anterior palmation. c–d: cross-section of the ossicone. e: position of frontal eminence. f: supraorbital groove. g: fronto-nasal suture. h: dorsal opening of supraorbital canal. x-y: cross-section of the ossicone.

greatly thickened. The foramen magnum is small relative to *Okapia* or *Giraffa* and the incisura intercondyloidea, which is strong is the giraffids, is reduced to a small notch on the ventral edge of the foramen magnum.

The basioccipital region is extremely thickened with a pair of large anterior swellings produced from the anterior region of the occipital condyles (pl. 10, fig. 1). Weaker swellings are present in *Okapia* and *Giraffa*. Mead (1906) found that these anterior swellings are present in all horned ruminants, in which they act to strengthen the atlanto-occipital joint during combat and according to Webb (1965) they also act to prevent over flexion of the joint during grazing. The great weight of the ossicones in *Prolibytherium* would increase the requirement for such swellings for both functions. The median keel originates at the anterior end of the basioccipital and runs posteriorly, merging into the condyles between the swellings (pl. 10, fig. 1). Paired basilar tubercles lie in front of the swellings (pl. 10, fig. 1); they have sculptured surfaces and fade anteriorly into slight concavities. The tubercles provide insertion for the rectus capitis ventralis muscles which act to flex the head and to incline it laterally. The eustachian canal follows the lateral edge of the basioccipital region.

The paroccipital process is stout, with a thickened anterior face providing origin for the digastric muscle. The posterior face of the process is concave and is the area of insertion of the rectus capitis lateralis muscle. The anterior face of the process is sculptured for attachment to the meatus region of the squamosal.

Sphenoid. The optic and ethmoid foramina are more ventrally situated in *Prolibytherium* than they are in *Giraffa* or *Okapia* and the ethmoid foramen is more anteriorly situated in *Prolibytherium*. Behind the optic foramen is the large foramen rotundum (pl. 10, fig. 1) and behind this is the foramen ovale which is circular in *Prolibytherium*, as in *Giraffa* and *Sivatherium* and in contrast to *Zarafa* and the other palaeotragines in which it is oval. The orbitosphenoid is concave in front of the optic foramen. The alisphenoid has a plane lateral face and a concave ventral face, with a strong alisphenoid tuberosity at the junction of these faces. The pterygoid groove follows the edge of the basisphenoid ventro-medial to the foramen rotundum and the foramen ovale, it is roofed over at its posterior end by the temporal process of the sphenoid; this process has two longitudinal grooves on its surface, the medial one of these carries the eustachian tube and the other is continuous with the pterygoid groove. Only the posterior end of the pterygo-sphenoid is preserved. The basisphenoid is cylindrical widening slightly at the posterior end, near the suture with the basioccipital (pl. 10, fig. 1).

Squamosal. The cranial surface of the squamosal is overlapped by a downward process of the parietal and is not visible. The lateral face is convex and the post-glenoid foramen is directed dorso-laterally. In front of the postglenoid foramen the bone surface is convex as far as the squamosal-alisphenoid suture. The glenoid cavity is transversely convex and the postglenoid process is slightly concave on its anterior face, the process is elongate transversely as in *Zarafa* (pl. 10, fig. 1). The temporal condyle is shallowly convex and its anterior edge forms a strong crest as far as the alisphenoid. The bone is concave medial to the glenoid cavity and a groove runs postero-laterally around the postglenoid process. The zygomatic arch is missing as the bone is broken immediately lateral to the glenoid cavity. The lateral

tuberosity of the squamosal is stronger than in *Okapia*, it has a concave posterior face which is deeply sculptured.   The antero-ventral face has a deep groove running laterally across it, this is the postero-dorsal part of the tube of the external auditory meatus.

Petrosal.   The tympanic bulla is not preserved but the region which surrounded the bulla indicates that it was about the same relative size as that of *Okapia* or *Zarafa*.   The petrosal contributes most of the meatus, with a small contribution from the squamosal in the postero-dorsal region.   The meatus opens laterally as in *Okapia* or *Giraffa* and in contrast to *Capreolus* in which it slopes dorso-laterally from the bulla.   The stylomastoid foramen lies postero-lateral to the meatus.   Antero-ventral to the meatus is a strong hyoid process.

The inner ear is figured in ventro-lateral and medial views (text figs 5a and b). In ventro-lateral view (pl. 11, fig. 3) the most prominent region is the fossa tensor tympani, a large deep depression housing the tensor tympani muscle which inserts on the malleus.   Anterior to this fossa is a deep, narrow channel, the hiatus falloppii, which carries the superficial petrosal nerve, a branch of cranial nerve VII.   Posterior to the fossa tensor tympani is a small foramen which is continuous with a deep, ventrally running groove—the aquaeduct falloppii, this in turn is continuous with the stylomastoid foramen (text fig. 5a).   Cranial nerve VII enters the petrosal via the
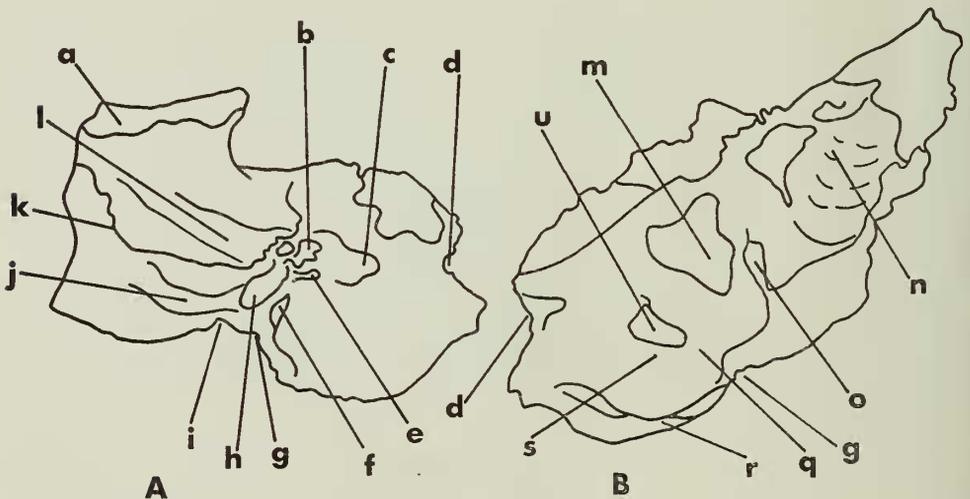
FIG. 5.   The right petrosal of *Prolibytherium* ($1\cdot25$ × natural size).   (A) Ventro-lateral view.   (B) Dorso-medial view.   a: lateral tuberosity of the squamosal bone.   b: aquaeduct falloppii.   c: fossa tensor tympani.   d: hiatus falloppii.   e: fenestra ovalis.   f: fenestra rotunda.   g: aquaeduct cochlea.   h: chorda tympani.   i: groove of the foramen lacerum posterius.   j: petrosal wall of the stylomastoid foramen.   k: squamosal-petrosal suture.   l: squamosal region of the ear.   m: floccular fossa.   n: wall of the temporal canal.   o: aquaeduct vestibularis.   q: crus commune.   r: groove of the sulcus venus basilaris cranii.   s: position of the semicircular canals.   u: internal auditory meatus.

internal auditory meatus and after running along the aquaeduct falloppii leaves by way of the stylomastoid foramen. Postero-ventral to the fossa tensor tympani is a large opening—the fenestra rotunda, above which is the smaller fenestra ovalis (text fig. 5a). Posterior to and partly overhanging the fenestra ovalis is the stapedial promontory which provides origin for the stapedial muscle. The whole ventro-lateral face of the petrosal is very similar in *Prolibytherium* and *Capreolus*.

The medial view of the petrosal (pl. 11, fig. 4) is dominated by the internal auditory meatus which has the shape shown (text fig. 5b). Cranial nerve VII enters the petrosal posteriorly and cranial nerve VIII enters anterior to this; separate openings for the nerves are visible inside the meatus. Above and slightly behind the meatus is the wide, shallow floccular fossa which houses the floccular lobe of the cerebellum. Between the floccular fossa and the internal auditory meatus the bone is swollen by the crus commune. The semi-circular canals lie ventral to the internal auditory meatus, these were located by X-raying the petrosal but owing to the size of the specimen this technique could not be used to discover any further details of the internal anatomy.

The aquaeduct vestibularis and aquaeduct cochlea carry small veins. The medial region of the petrosal in *Prolibytherium* differs only slightly from that of *Capreolus*, the main difference being that the region around the floccular fossa and the fossa itself are more concave and larger in *Capreolus*. The petrosal of *Okapia* differs from *Prolibytherium* as the ventral part of the petrosal is expanded and the floccular fossa is relatively smaller in *Okapia*.

Brain. A single endocranial cast of *Prolibytherium* was available (pl. 12, fig. 1 and 2); this was formed from large calcite crystals and was dissected out of an almost complete cranium. The rhinal sulcus is situated very high on the lateral face of the brain (text fig. 6a); this reflects the greater importance of the rhinencephalon relative to the neopallium and is a primitive feature which is also found in *Dremotherium*, while in *Capreolus* and *Okapia* the rhinal sulcus is more ventrally situated. The anterior and posterior rhinal sulci meet each other at an angle of about 150°; this agrees with the angle given by Sigogneau (1968) for *Dremotherium*. In both *Prolibytherium* and *Dremotherium* the two regions of the rhinal sulcus join with a smoother curve whereas in *Capreolus* the anterior and posterior regions bend sharply upwards before joining. The anterior rhinal sulcus runs slightly ventrally and its anterior end is lost, due to an imperfection of the cast.

The olfactory lobes are produced anteriorly and a part of the olfactory peduncle is visible in dorsal view (text fig. 6b); this is similar to *Amphitragulus* and is more primitive than *Dremotherium* or *Capreolus* in which the olfactory peduncle is shorter and the lobes are flexed ventrally, lying under the neopallium. Posterior to the lateral fissure the brain is expanded laterally which results in a great widening of the posterior region; this is similar to *Dremotherium* but in *Capreolus* the posterior region is not expanded and in *Okapia* the brain is uniformly very wide.

The cerebellum and vermis are relatively large and lie at the same level as the neopallium; this is a primitive feature also found in *Dremotherium*. The neopallium is flattened in the vertical plane and its dorsal surface is almost flat as in *Okapia* whereas in *Capreolus* this region is curved antero-posteriorly and transversely.

The parts of the suprasylvian sulcus are clearly defined (text fig. 6a). The anterior branch curves medially with a very small descendant branch, whereas in *Capreolus* the inward curvature is more marked and a large descendant branch is produced running just in front of the sylvian sulcus. The central part of the suprasylvian sulcus is shallowly convex dorsally, this convexity is similar to *Dremotherium* but is less marked than in *Capreolus*. In *Okapia* (Clark 1939) the posterior and central parts of the suprasylvian sulcus are separated and overlap extensively. In *Prolibytherium* the posterior branch of the suprasylvian sulcus extends posteriorly almost as far as the cerebellum, it does not bifurcate whereas in *Dremotherium* a weak descendant branch is produced. A long posterior extension of the suprasylvian sulcus indicates an advance over the tragulid condition in which the posterior
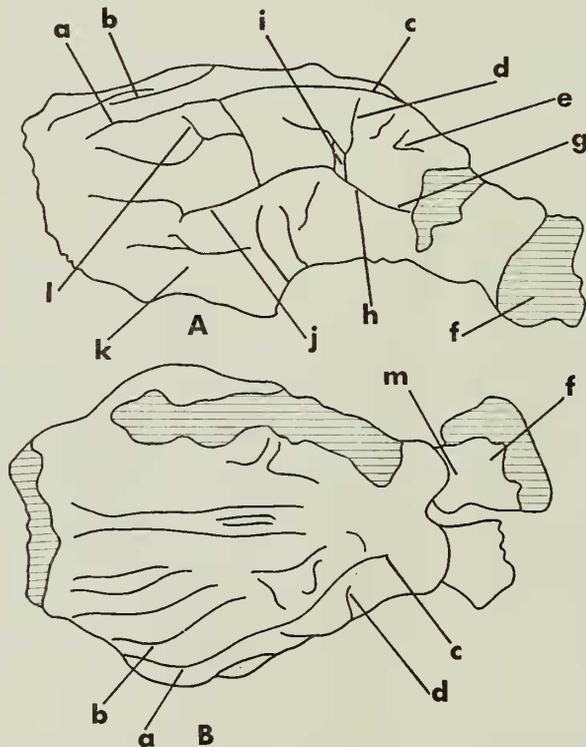
Fig. 6.　The brain of *Prolibytherium* (B.M.26678) (Natural size × 0·7). (A) Right lateral view of the endocranial cast. (B) Dorsal view of the endocranial cast. a: posterior suprasylvian sulcus. b: lateral groove. c: anterior suprasylvian sulcus. d: sylvian sulcus. e: gamma sulcus. f: olfactory lobe　g: anterior rhinal sulcus　h: anterior ectosylvian sulcus　i: lateral fissure　j: posterior rhinal sulcus and posterior ectosylvian sulcus　k: piriform lobe　l: delta sulcus　m: olfactory peduncle.

region of the sulcus is very short. The presence of a well marked descending limb of the suprasylvian sulcus, is stated by Black (1915) to be a giraffid feature and its absence in *Prolibytherium* is therefore a primitive feature.

The ectosylvian and rhinal sulci are separate near the lateral fissure but fuse completely at a short distance from the fissure both anteriorly and posteriorly, as in *Dremotherium*. This feature is primitive and in *Capreolus* and *Okapia* the rhinal and ectosylvian sulci are separate over their whole length. The lateral fissure is triangular and large (text fig. 6a) as in *Dremotherium* and *Capreolus*. The sylvian sulcus is produced from the dorsal region of the lateral fissure, this sulcus runs antero-dorsally and almost reaches the suprasylvian sulcus (text fig. 6b); this feature is similar to the cervids rather than the giraffids Clark (1939). Behind the sylvian sulcus is a deep groove which is more nearly vertical in *Capreolus* but is absent in *Dremotherium*. In *Dremotherium* the sylvian sulcus is more vertical than in *Capreolus* or *Prolibytherium*. The posterior region, between the suprasylvian and ectosylvian sulci, is occupied by the 'delta' sulcus (Sigogneau 1968); this sulcus is forked anteriorly and curves ventrally in its posterior region. The 'gamma' sulcus is very deep and much shorter in *Prolibytherium* than in *Dremotherium*.

The brain as a whole compares closely with that of *Dremotherium* but details of the sulci and olfactory lobes indicate that it was more primitive in *Prolibytherium*. The long sylvian sulcus is a cervid rather than a giraffid feature; however in *Amphitragulus* the sylvian sulcus is very short, this casts some doubt upon the importance of this feature in establishing relationships in early ruminants. As *Prolibytherium* is an early sivatheriid it is very unfortunate that no brain casts of sivatheriids were available. Agreement between the brain casts of *Prolibytherium* and the sivatheriids would probably be greater than the agreement between *Prolibytherium* and the giraffids.

Mandible. The ascending ramus is high with a concave medial and a plane lateral face in the dorsal region. The mandibular foramen is at the same level as the tooth row, it is elongate antero-posteriorly and a shallow channel runs anteriorly from it. The lower part of the ascending ramus is concave laterally and provides insertion for the masseter muscle. The horizontal ramus is convex dorso-ventrally on both sides. The ventral edge of the ramus is curved with the deepest region below M_2 (pl. 11, fig. 2). The bone surface slopes dorso-medially behind the M_3 and a sharp ridge is formed which continues dorsally as the leading edge of the ascending ramus. A small posterior mental foramen lies ventral to P_2 (pl. 11, fig. 2) in both specimens in which it is preserved. The anterior mental foramen is double in M.26680, it lies at the level of the posterior end of the symphysis and the two foramina communicate internally. The diastema of *Prolibytherium* is about the same length as the distance P_2 to M_2, which is the same as in *Capreolus* but is much shorter than in *Giraffa* or *Okapia* in which the diastema is longer than the tooth row.

Upper Dentition. The molars are generally similar in form; they are brachyodont with finely rugose enamel. M.21901 is so heavily worn that the crown of M^1 is almost completely worn away and the only remaining feature is the posterior fossette (pl. 9). The antero-labial corner of M^2 bears a strong parastyle and both the paracone and parastyle have strong labial ribs. Posterior to the paracone the wear trace is very

wide but the mesostyle appears to have been originally part of the posterior lobe joining the paracone at a late stage in wear. The metacone is very stout and a slight postero-labial swelling indicates that a weak metastyle may have been present. The protocone is crescentic with the wear trace of its anterior region joining the parastyle and closing the fossette anteriorly (pl. 9). The posterior end of the protocone joins the metaconule in the median valley. The metaconule is also crescentic and is posterior end joins the metacone or possibly the metastyle thus closing the posterior fossette. At the anterior end of the metaconule is a small crest which is produced into the median valley on the lingual side of the main region of fusion between the wear traces, this crest joins the protocone enclosing a small median enamel island in M^1 and M^2 but this is not developed on M^3 (pl. 9). Each molar has a strong entostyle in the median valley; in each case this is produced from the antero-lingual region of the metaconule but on M^3 it joins a strong lingual cingulum produced from the postero-lingual face of the protocone (pl. 9). Anterior cingula are present on each molar and posterior cingula were present on M^1 and M^2.

A single badly shattered molar showing very little wear is known (P.M.F.). The mesostyle has a strong labial rib which is joined to the metacone. The metacone has a weak labial swelling and the metastyle has a strong labial rib. The protocone and metaconule are angularly crescentic and the latter is smaller than the protocone. A strong accessory crest is present in the posterior fossette.

The molars of *Prolibytherium* are smaller than those of *Zarafa*, detailed comparison is difficult owing to the heavily worn condition of the *Prolibytherium* dentition but the details of the median valley region differ between the two genera; this difference is due to the absence of the small conule in the anterior fossette of *Prolibytherium* resulting in a more simple wear pattern at the posterior end of the protocone.

P^4 is three rooted and brachyodont, it is smaller, relative to the molars and its lingual region is smaller than in *Zarafa*. The parastyle is strong with a large labial swelling and the paracone is very stout with lingual and labial ribs; the lingual rib is weaker than in *Zarafa* but it has an anterior groove as in *Zarafa* and *Palaeomeryx*. Posterior to the paracone rib, the labial wall is almost flat as far as the metastyle. The metacone is stout and almost completely fused with the paracone, its labial swelling is weak though slightly stronger than that of *Zarafa*. The protocone is stout and joins the labial lobe at both ends thus closing the fossette. The fossette of P^4 is much deeper than that of *Zarafa*, this is also true of the fossettes of the molars indicating that the upper dentition of *Prolibytherium* is much higher than that of *Zarafa*, though still brachyodont relative to the advanced giraffids or sivatheriids. At the posterior end of the fossette of P^4 is a weak accessory crest (pl. 9). The antero-lingual cingulum of the P^4 is weak relative to that of *Zarafa*.

P^2 is stout with a heavily worn crown which is concave antero-posteriorly. There are three strong ribs on the labial face which correspond to the parastyle, paracone and metacone. Between the parastyle and paracone ribs is a very deep groove (pl. 8) and a shallower groove separates the paracone and metacone ribs. No surface features are visible except a small, transversely elongate enamel island at the posterior end of the tooth.

Lower Dentition. The lower dentition forms a closed series from P_2 to M_3. The

enamel of the molars is finely rugose.   P.M.B. has almost unworn molars and M.26681 exhibits signs of only slight wear, these molars show that the cheek teeth are higher in *Prolibytherium* than in *Zarafa*.

M_3 has an accessory column but the anterior region differs only slightly from the other molars.   The mesostylid has a strong lingual rib which runs postero-ventrally from the antero-lingual corner of the tooth (pl. 10, fig. 4).   The metaconid is high and transversely compressed (pl. 10, fig. 3), its posterior end lies lingual to the anterior end of the entoconid which is lower than the metaconid and has a more diagonal orientation on the tooth (pl. 10, fig. 3).   The protoconid is crescentic and slightly angular, its anterior end joins the mesostylid early in wear.   The posterior end of the protoconid joins the anterior end of the entoconid early in wear (pl. 10, fig. 3) and a little later the metaconid joins the entoconid thus isolating the hypoconid until very late in wear; plate 11, fig. 1 shows a heavily worn dentition in which the hypoconid of the M_3 has just joined the protoconid.   The hypoconid is lower than the protoconid, its anterior end stops in the median valley near the entoconid. The hypoconid is not crescentic in the unworn condition as the posterior region stops near the middle of the cuspid and in this region the cuspid falls away and is continued labially a few millimetres below the top of the crown; thus after moderate wear the cuspid becomes crescentic but the posterior region is always shorter and appears narrower even in the heavily worn condition.   This feature is restricted to the M_3 and is related to the presence of the accessory column.   The accessory column is more simple in *Prolibytherium* than in *Zarafa*; it consists of a stout hypoconulid which is as high as the hypoconid and is similar in shape to the anterior half of that cuspid.   The posterior half of the hypoconulid has a weak lingual twist but there is no approach to the crescentic shape found in the giraffids.   The anterior half of the hypoconulid meets the postero-labial face of the entoconid and on the lingual side of this junction is a small fold of enamel which is probably a weak ectostylid. M_3 has a feeble anterior cingulum and usually an ectostylid in the median valley.

M_1 and M_2 are similar to the anterior region of M_3.   At the postero-lingual corner of M_2 is a small entostylid which joins the postero-lingual extension of the hypoconid; in all specimens the entoconid is joined to the entostylid in this region.

P_4 is long and narrow (pl. 11, fig. 1).   The protoconid is the highest part of the tooth but the metaconid is almost as high, these two cuspids are joined by a narrow ridge which has a deep groove on its antero-lingual face (pl. 11, fig. 1).   The anterior part of the tooth curves lingually and from the lingual face the lingual and antero-lingual paraconid and parastylid are produced; these branches are separated by a shallow lingual valley which is quickly lost during wear, leaving a single anterior region (pl. 11, fig. 1).   Between the paraconid and metaconid is a deep, wide lingual valley at the lingual end of which is a strong stylid.   The posterior region of P_4 consists of a stout labial hypoconid to which a postero-lingual entostylid and a lingual entoconid are joined.   These two cuspids are separated by a shallow lingual valley which is lost early in wear but may persist for some time as a small enamel island. Between the protononid and the posterior region is a deep valley separating the metaconid and entoconid lingually and labially a deep groove separates the protoconid and hypoconid (pl. 11, fig. 1).   A single unworn P_4 is known; on this the posterior

region is entirely separated from the anterior region as the lingual and labial valleys join over the crown of the tooth. The separation of these two regions is found in the giraffids and in some palaeomerycids.

P_3 has a high protoconid with a strong postero-lingual wing—the incipient metaconid. The anterior region consists of a single wear trace derived from a paraconid and parastylid as in P_4. A lingual stylid closes the anterior valley but this is much weaker than in P_4. The posterior region is separated from the protoconid by a strong lingual valley and a weaker labial valley. The hypoconid is feeble in P_3. The entoconid is strong but the entostylid is very slender and forms the posterior face of the tooth.

The P_2 of *Prolibytherium* is a high conical tooth (pl. 11, fig. 2) of the primitive ruminant premolar form. The protoconid is high and a weak postero-lingual fold represents the metaconid. Anteriorly the paraconid consists of an unbranched crest which runs anteriorly from the face of the protoconid (pl. 11, fig. 1) and twists lingually at the distal end. The posterior region is transversely wide with a weak entoconid and entostylid. This tooth is similar that of *Palaeotragus rouenii* but in this species the anterior crest is divided into a parastylid and a paraconid which is a more advanced condition.

The Skull as a Whole. The dorsal view of the skull is dominated by the enormous ossicones which are completely fused to the frontal and parietal bones. The great thickening of the basioccipital region and the occipital condyles is directly related to the presence of the ossicones. Though the facial region is poorly known it is of great interest as a lacrymal fossa and paired lacrymal foramina are present, these are primitive features previously unrecorded in the Giraffoidea but similar to the cervoid or dremotherioid condition. The maxilla is shallow as in *Capreolus* and it is likely that the basicranial and basifacial regions were widely divergent as in *Zarafa*. The endocranial cast shows similarities to the dremotherioids. In most features the skull of *Prolibytherium* is similar to the early pecorans but this resemblance is decreased by the presence of the ossicones in *Prolibytherium*.

TABLE 8

Prolibytherium magnieri. Measurements of the skull and dentition

The Skull

	B.M.21901
Postorbital length. (From anterior edge of orbit to occipital condyle)	132 mm
Width of ossicones above the orbit	320 mm
Maximum length of the ossicones	425 mm
Width of condyles	51 mm
Height of occipital region	71 mm
Height of occipital region plus ossicones	114 mm
Maximum width of occipital region	93 mm

The Upper Dentition

	B.M.21901	
	Length	Width
P2	12·5 mm	9·0 mm

TABLE 8 (cont.)

P⁴	11·0 mm	14·0 mm
M¹	15·0 mm	17·5 mm
M²	18·0 mm	20·0 mm
M³	20·0 mm	20·0 mm

The Lower Dentition

	M.21899	M.26681	B.U.20175	P.M. A.	P.M. B.	P.M. C.	P.M. D.
P₂							
Width	5·3 mm	—	—	—	—	—	—
Length	10·0 mm	—	—	—	—	—	—
P₃							
Width	6·5 mm	—	—	7·0 mm	—	—	—
Length	11·0 mm	—	12·0 mm	12·0 mm	—	—	—
P₄							
Width	8·5 mm	—	9·0 mm	7·5 mm	—	7·5 mm	—
Length	13·0 mm	—	14·5 mm	12·8 mm	—	13·5 mm	—
M₁							
Width	12·0 mm	—	12·0 mm	12·0 mm	—	—	11·5 mm
Length	13·0 mm	—	15·0 mm	13·5 mm	14·0 mm	—	16·5 mm
M₂							
Width	12·5 mm	—	13·0 mm	13·0 mm	—	—	13·0 mm
Length	16·5 mm	—	—	18·5 mm	18·5 mm	—	17·5 mm
M₃							
Width	12·0 mm	13·0 mm	13·0 mm	12·5 mm	—	—	13·0 mm
Length	23·5 mm	26·5 mm	26·5 mm	24·5 mm	25·0 mm	—	25·0 mm

Post-cranial material. Details of the skull indicate that *Prolibytherium* was probably similar to the more primitive cervids and it is therefore likely that its post-cranial material resembled that of the cervids. On this basis the post-cranial material of *Prolibytherium* was identified by comparison with a skeleton of *Capreolus*.

MATERIAL

B.U.20153	A proximal fragment of a left scapula.
B.U.20154a	The distal end of a left humerus.
b	A complete left radius.
c	The proximal end of a left ulna.
B.U.20155	The distal end of a metacarpal.
B.U.20156	A first phalange.
B.U.20157	A first phalange.
B.U.20158	A first phalange; posterior?
B.U.20159	The proximal end of a right tibia.
B.U.20160	The proximal end of a left tibia.
B.U.20161	The distal end of a right tibia.
B.U.20162	The distal end of a left tibia.
B.U.20164	A right calcaneum.
B.U.20165	A right astragalus.
B.U.20166	A right astragalus.
B.U.20167	A left astragalus.
B.U.20168	A right astragalus.

B.U.20169   A distal, metatarsal fragment.
B.U.20170   An almost complete atlas vertebra.
B.U.20171   A slightly broken seventh cervical vertebra.
B.U.20172   A complete first thoracic vertebra.
B.U.20173   An almost complete thoracic vertebra.

Scapula. The glenoid region of the scapula has an almost circular outline with a small glenoid notch (text fig. 7a). The coracoid process is strong but the tuber scapulae is weak. The spine begins near the glenoid and rises steeply indicating the presence of a strong acromion process. The neck of the scapula is wider than in *Zarafa* or *Okapia*; it has a deep vascular groove on the medial surface and a strong tuberosity on the posterior edge which is the area of origin for the teres minor muscle. The outlines of the glenoids in four giraffoid genera (text fig. 7) demonstrate the differences which exist in the development of the coracoid process and the tuber scapulae. The tuber scapulae of *Prolibytherium* (text fig. 7a) is very feeble, in *Zarafa* it is stronger (text fig. 7c) and in the extant giraffids it is very strong (text fig. 7b and d). The coracoid process is strongly developed in *Prolibytherium* and weakly developed in the giraffids indicating that in *Prolibytherium* the coraco-brachialis muscle was more highly developed than in the giraffids. The neck of the scapula indicates that the bone was shorter and wider than that of *Okapia* and probably resembled the scapula of *Ovis*.

Humerus. The coronoid fossa is much deeper than in *Okapia* or *Giraffa*; this fossa provides origin for the extensor carpi radialis and the common digital extensor muscles, both of which were strongly developed in *Prolibytherium*. The lateral condyle is narrow with a transversely concave face, this concavity is caused by very strong lateral and intermediate ridges. The intermediate ridge separates the
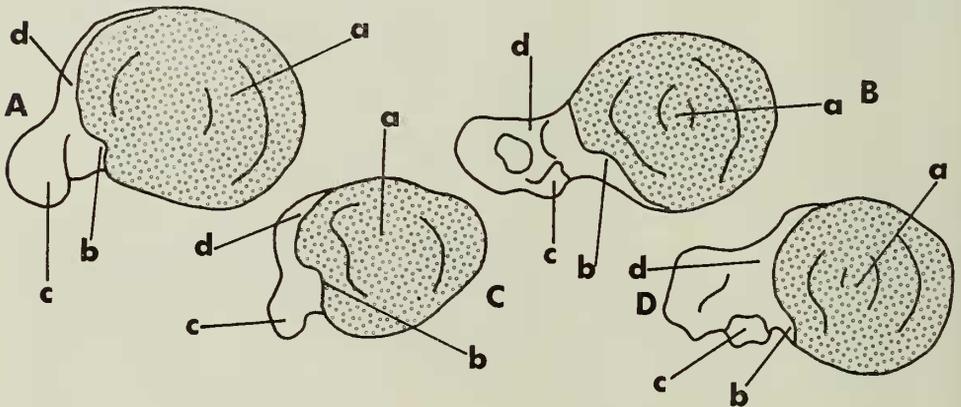

Fig. 7.   The glenoid cavity and surrounding region of the left scapula.   (A) *Prolibytherium* (B.U.20153) Natural size.   (B) *Okapia* 0·5 × Natural size.   (C) *Zarafa* (B.U.20123) 0·5 × Natural size.   (D) *Giraffa*, 0·25 × Natural size.   a: glenoid cavity.   b: glenoid notch.   c: coracoid process.   d: tuber scapulae.

condyle from the synovial fossa and all the ridges of the distal head of the humerus are much stronger than in *Okapia*. The olecranon fossa is very deep and the articular region extends further into the fossa than in *Okapia*. The medial epicondyle is very strong, it is produced distally as a large process overhanging the medial condyle (text fig. 8a). The medial condyle of *Okapia* is more weakly developed than that of *Prolibytherium* and slopes proximally from the condyle (text fig. 8b). The medial, distal and lateral faces of this epicondyle are very heavily sculptured in *Prolibytherium* and the main digital flexor muscles have areas of origin on this epicondyle. The lateral epicondyle of *Prolibytherium* is slightly stronger than that of *Okapia*, this region provides origin for the ulnaris lateralis muscle.

Radius. The central part of the proximal face of the radius is deeply excavated posteriorly for the insertion of the interosseous ligament. This excavation is about the same size in *Prolibytherium* and *Okapia* (text fig. 9). The postero-proximal region of the bone is sculptured for attachment to the ulna and this region bears two wide concave facets which are continuous with the proximal facets and articulate with the ulna. The lateral part of the proximal region forms a strong lateral tuberosity providing insertion for the lateral ligament of the elbow and also origin for the common lateral digital extensor muscles. The radial tuberosity, about the same size in *Prolibytherium* and *Okapia*, provides insertion for the biceps brachii muscle. In *Prolibytherium* it is situated at some distance distal to the articulation in contrast to *Okapia* in which the tuberosity is very near the articulation (text fig. 9).

The shaft of the radius is slender and curved anteriorly as in *Okapia* and *Capreolus*. The distal end is transversely narrower than in *Okapia*; it has the usual articulations
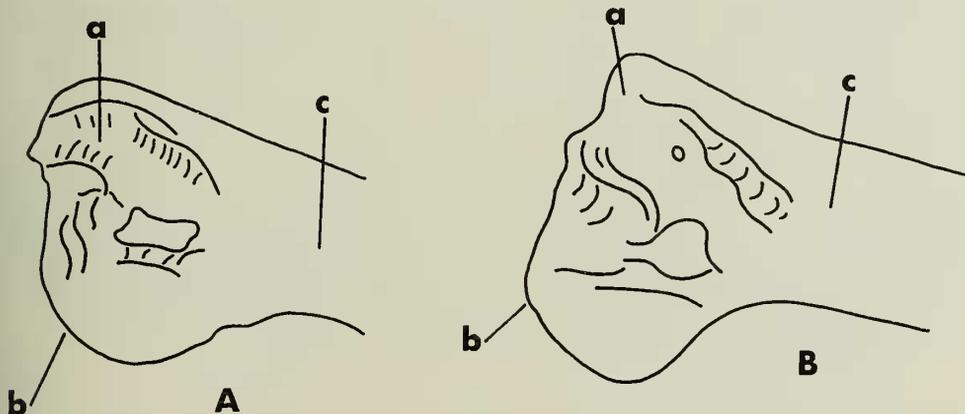

Fig. 8. Medial view of the distal end of the humerus. (A) *Prolibytherium* (B.U.20154a). Natural size. (B) *Okapia* 0·5 × Natural size. a: medial epicondyle. b: medial condyle. c: shaft of humerus.

for the carpals.   The area lateral to the cuneiform facet is sculptured indicating a very close attachment of the ulna in this region.   In *Prolibytherium* the posterior face of the radius is convex in the region immediately proximal to the distal facet; this contrasts with *Okapia* in which this face is concave.   The lateral tuberosity of the distal end is strong and the medial tuberosity is stronger in *Prolibytherium* than in *Okapia*; these tuberosities provide insertion for the ligaments of the carpal joint.

Ulna.   The olecranon process is flattened and though it is broken off distally it was probably as long as that of *Okapia*.   The shaft of the ulna is also flattened transversely and bends medially at its distal end as in *Okapia*.   The interosseous space is short and relatively narrow.   In *Prolibytherium* the articular facet is convex transversely, in contrast to *Okapia* in which the facet is flat transversely.   The greater convexity of the facet reflects the deeper synovial fossa and stronger ridges of the distal end of the humerus.   The facet of the olecranon in *Prolibytherium* extends further dorsally than in *Okapia* resulting in a more elongate facet and at full extension the olecranon fits into the deep olecranon fossa and locks the elbow.

Metacarpal.   The distal end of the metacarpal has a large nutrient foramen in the mid-line proximal to the condyles as in *Zarafa*.   The distal end of the bone is wide and indicates that the metacarpal was relatively stout.   The condyles are of the usual ruminant pattern with strong keels as in the cervids.

Tibia.   In *Prolibytherium* the proximal head of the tibia is narrower than that of *Okapia* but is otherwise similar in general anatomy.   The cnemial crest is higher in *Prolibytherium* than in *Okapia* or *Zarafa* (text fig. 10) resembling that of *Capreolus*. The medial face of the cnemial crest is plane and the anterior region of the crest is
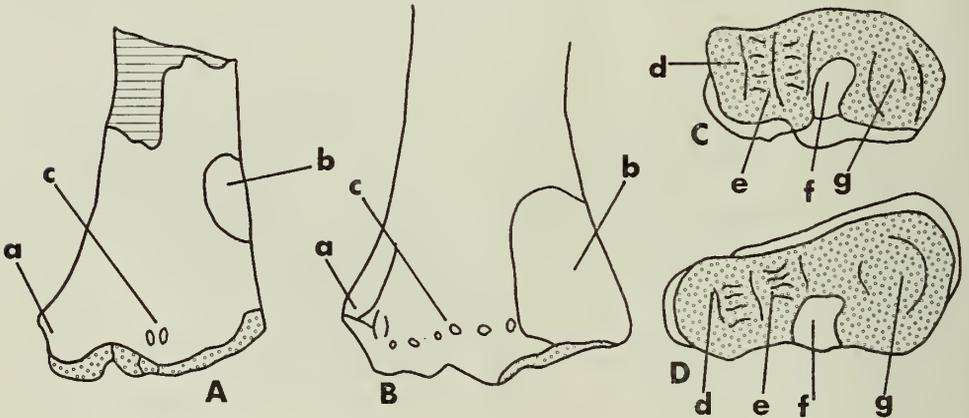
FIG. 9.   The radius of *Prolibytherium*.   (A) The anterior face of the proximal region of the radius in *Prolibytherium* (B.U.20154b).   Natural size.   (B) The anterior face of the proximal region of the radius in *Okapia*. 0·5 × Natural size.   (C) The proximal articular facet of the left radius in *Prolibytherium*.   Natural size.   (D) The proximal articular facet of the left radius in *Okapia*.   0·5 × Natural size.

heavily sculptured.   The anterior tuberosity of the crest is wide and similar to that of *Capreolus*.   The lateral face of the crest forms a deep elongate concavity which is deeper than that of *Okapia* or *Capreolus*.

The distal end of the tibia is narrow transversely.   The medial articular groove is very deep and the intermediate ridge is high resembling that of *Zarafa* or the cervids. The anterior edge of this ridge continues as a high anterior process.   The synovial fossa is large and extends laterally and medially into the articular grooves.   The articulation for the lateral malleolus consists of a wide posterior facet and a smaller anterior facet as in *Zarafa*.   The anterior and posterior facets are separated by a deep groove for the tendons of the lateral extensor muscles of the foot.   The medial malleolus is heavily sculptured and as strong as in *Okapia*.

Calcaneum.   The calcaneum differs in minor details from that of *Palaeomeryx* but in major features it is more similar to *Palaeomeryx* than to any other giraffoid.

Astragalus.   In agreement with the calcaneum the astragalus of *Prolibytherium*
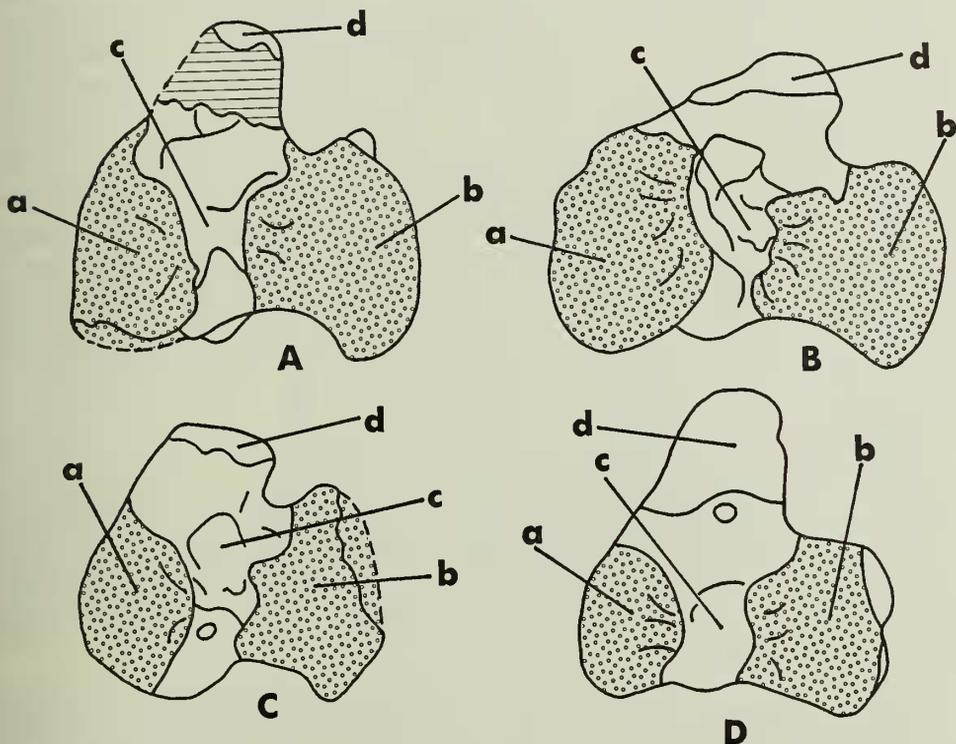

FIG. 10.   The proximal head of the right tibia.   (A) *Prolibytherium*.   (B.U.20159 and B.U.20160).   Natural size.   (B) *Okapia* 0·5 × Natural size.   (C) *Zarafa* (B.U.20146) 0·5 × Natural size.   (D) *Capreolus* Natural size.   a: medial condyle.   b: lateral condyle. c: tibial spine. d: cnemial crest.

D

resembles that of *Palaeomeryx* in all its main features. Both the astragalus and calcaneum contrast strongly with those of *Okapia* but this is mainly due to the specialized nature of the ankle in *Okapia*.

Metatarsal. This bone is larger than the metacarpal; the reverse of the condition in *Okapia* and *Giraffa* but similar to the cervid condition. The distal end is more flattened antero-ventrally than in *Okapia* or *Zarafa*. The anterior face of the bone carries a deep channel which is open and passes between the condyles, this channel is very restricted in the region just proximal to the condyles and the walls of the channel are sculptured as in *Zarafa*. The condyles are similar to the cervids or *Zarafa*.

Phalanges. The phalanges identified as *Prolibytherium* are smaller than those of *Zarafa* but are otherwise similar in all details and reference should be made to the description of *Zarafa* (p. 97).

The vertebral column

Atlas. The atlas of *Prolibytherium* (text fig. 11c and d) is identified by its size which agrees with the size of the occipital condyles. The general form of the atlas is similar to that of other ruminants. The anterior articular facets are very deep and their lateral curvature is sharper than in *Okapia*, agreeing with the condition of the occipital condyles. The wing of the atlas is broken off. The intervertebral and alar foramina are closely associated ventrally and dorsally they have a common opening (text fig. 11c) as in *Capreolus* but in contrast to *Okapia* where they are widely separated. The ventral face of the atlas is similar to that of *Okapia* and the ventral tubercle is very strong (text fig. 11d). The posterior articular facets are swollen medially and concave laterally, differing from *Okapia* in which the facets are more nearly plane. In *Prolibytherium* the posterior articular facet extends further laterally than that of *Okapia* and as in *Giraffa*, it is continued onto the postero-lateral process of the wing. Although this process is broken off it appears to have been as strong as that of *Giraffa*, indicating a strengthening of the atlanto-axis articulation in *Prolibytherium*. The bone of the atlas is very thick.

Cervical vertebrae. The centrum of the seventh cervical vertebra (text fig. 11a) is stouter than that of *Okapia* and has a strong ventral ridge. The anterior end of the centrum is displaced dorsally relative to the posterior end but less so than in *Okapia*. On the posterior face the lateral facet for the head of the rib is wider and more clearly defined than in *Okapia*. The posterior articular process is lateral only and the articular facet is more elongate in *Prolibytherium* than in *Okapia* (text fig. 11a). The anterior articular process is similar to that of *Okapia* with similarly shaped facets. The transverse processes and neural spine are broken off.

Thoracic vertebrae. The centrum of the first thoracic vertebra is very short and stout. The anterior facet of the centrum (text fig. 11g) is shallowly convex and the facets for the head of the rib (text fig. 11f) face much more anteriorly than in *Okapia*. The posterior facet of the centrum is shallowly concave with wide lateral facets for the heads of the ribs (text fig. 11e). The ventral face of the centrum is not greatly swollen. A small tubercle is produced at the anterior end of the ventral face and the paired posterior tubercles are very laterally situated. The transverse process is

strong and the saddle shaped articulation for the tubercle faces ventrally (text fig. 11f) whereas in *Okapia* it faces antero-ventrally. The anterior articular process is similar to that of *Okapia*, with wide lateral articulations extending further medially than in *Okapia*. The articulation of the posterior process is median in *Prolibytherium* and the paired facets are well defined (text fig. 11e); they are elongate, narrow and opposed at an acute angle as in *Giraffa*. The neural spine slopes more posteriorly than in *Okapia*, it is the same relative length in *Prolibytherium* and *Okapia*. The
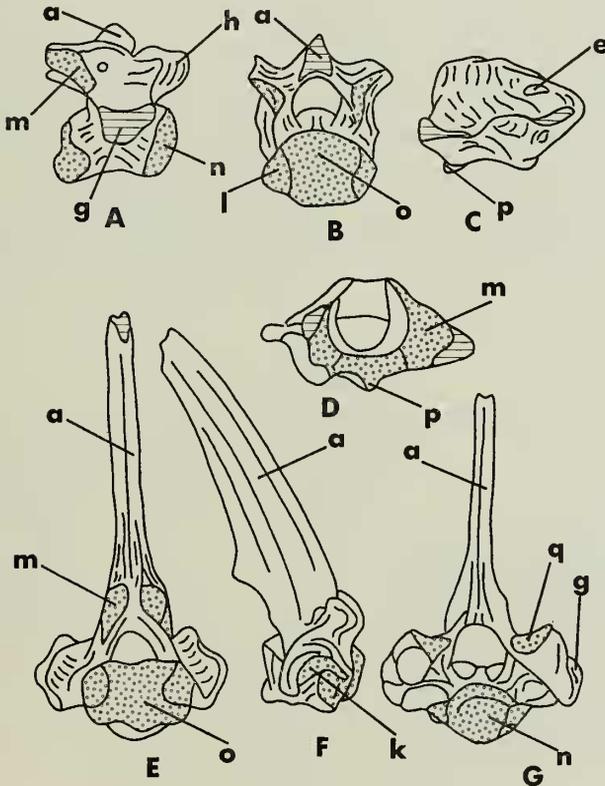
FIG. 11. The vertebrae of *Prolibytherium*. (A and B) Lateral and posterior views of the seventh cervical vertebra. (B.U.20171). (C and D) Lateral and posterior views of the atlas (B.U.20170). (E, F and G) Posterior, lateral and anterior views of the first thoracic vertebra. (B.U.20172). All 0·5 × Natural size. Fine stippling indicates articular regions. a: neural spine. e: common dorsal opening of the intervertebral and alar foramina. g: transverse process. h: anterior articular process. k: tubercular facet. l: posterior facet for the head of the rib. m: posterior articular facet. n: anterior face of centrum. o: posterior face of centrum. p: ventral tubercle.

cross-section of the neural spine is triangular with thickening of the posterior edge and heavy sculpturing in the region just dorsal to the posterior articular process.

A single vertebra is known from the posterior thoracic region of *Prolibytherium*, this is probably the tenth or eleventh thoracic vertebra. The neural spine is stronger than in *Okapia* and it slopes more steeply posteriorly. Both faces of the centrum and the anterior and posterior articular processes of *Prolibytherium* are similar to those of *Giraffa*.

Functional interpretations. Features of the fore-limb bones of *Prolibytherium* indicate that the locomotory muscles were very strong and a requirement for strength rather than speed is indicated. The animal had relatively short limbs probably not unlike those of *Ovis*. The presence of large ossicones would have necessitated great strength in the forelimbs and if the ossicones were used in intraspecific combat, as seems likely, then this requirement for strength would be exaggerated.

Details of the skull and atlas vertebra indicate that great forces were encountered by the head of *Prolibytherium*. The lower cervical region is represented by the seventh cervical and first thoracic vertebrae. If the neural spine of the seventh cervical vertebra was vertical during life, then the neck extended almost horizontally from the shoulders and it is likely that the head did not rise much above the level of the shoulders. The stoutness of the centra of the lower neck vertebrae and the shortness of the atlas indicate that the neck was short and probably very stout.

TABLE 9

Measurements of *Prolibytherium magnieri*, post-cranial material

Vertebrae

	B.U.20170	B.U.20171	B.U.20172	B.U.20173
Length of centrum	28 mm	30 mm	23 mm	27 mm
Total height of vertebra	34 mm	—	102 mm	—
Depth of centrum	—	19 mm	18 mm	16 mm
Width of anterior end of centrum	—	15 mm	19 mm	22 mm
Width of posterior end of centrum	—	27 mm	29 mm	30 mm

Scapula

	B.U.20153
Width of neck of scapula (Minimum)	25 mm
Depth of neck of scapula (Minimum)	14 mm
Width of glenoid (Anterior-Posterior)	30 mm
Depth of glenoid (Transverse)	25 mm

Humerus

	B.U.20154a
Distal end	
Width across epicondyles	35 mm
Antero-posterior depth of distal articular surface	18 mm

Radius

	B.U.20154b
Width of proximal articular surface	35 mm

TABLE 9 (cont.)

Depth of proximal articular surface:
        Minimum — 13 mm
        Maximum — 18 mm
Total length of bone — 210 mm
Width of distal articular surface — 29 mm
Depth of distal articular surface — 21 mm

Metacarpal

	B.U.20155
Width of distal end	27 mm
Depth of distal end	15 mm

Phalanges

	B.U.20156	B.U.20157	B.U.20158
Length	37 mm	37 mm	33 mm
Width of proximal end	13 mm	14 mm	13 mm
Depth of proximal end	14 mm	14 mm	14 mm
Width of distal end	11 mm	11 mm	10 mm
Depth of distal end	09 mm	09 mm	09 mm

Tibia

	B.U.20159	B.U.20160	B.U.20161	B.U.20162	B.U.20163
Width of proximal end	47 mm	46 mm	—	—	—
Depth of proximal end	46 mm	44 mm	—	—	—
Width of distal end	—	—	29 mm	27 mm	30 mm
Depth of distal end	—	—	21 mm	21 mm	23 mm

Calcaneum

	B.U.20164
Total length	70 mm
Length of tuber calcis	48 mm
Width across sustentaculum	19 mm
Depth of tuber calcis	18 mm
Maximum depth of bone	28 mm

Astragalus

	B.U.20165	B.U.20166	B.U.20167	B.U.20168
Maximum length	32 mm	36 mm	33 mm	33 mm
Minimum length	26 mm	30 mm	26 mm	25 mm
Width proximally	20 mm	20 mm	20 mm	18 mm
Width distally	18 mm	20 mm	19 mm	18 mm
Maximum depth	15 mm	16 mm	16 mm	15 mm

Family **BOVIDAE** Gray 1821.

Subfamily **BOVINAE** Gill 1872.

DIAGNOSIS: This subfamily is defined by Pilgrim (1939 p. 249).

Tribe **BOSELAPHINI** Simpson 1945.

DIAGNOSIS: This tribe is defined by Gentry (1970 p. 245).

Genus *PROTRAGOCERUS* Depéret 1887

TYPE SPECIES: *Protragocerus chantrei* Depéret 1887.

MATERIAL:

M.26687   An isolated right horn core fragment.
B.U.20113   An isolated left horn core fragment with part of the frontal attached.
B.U.20114   An isolated right horn core fragment.

DESCRIPTION: M.26687 (pl. 13, fig. 1) is the best preserved of the three specimens; part of the orbital region is preserved in the ventro-lateral region of the specimen and in the medial part of the orbital roof a small supraorbital foramen runs dorso-medially for a short distance in the bone, before turning anteriorly to emerge in the antero-medial region of the horn core, as in *Protragocerus gluten*.   The lateral region of the orbit extends slightly more laterally than the lateral face of the pedicle, which results in a weak lateral swelling in this region; however the horn core is more laterally situated than in *Protragocerus gluten* which may indicate that the Gebel Zelten species is more primitive.   The region of the frontals lying between the bases of the horn cores, is slightly higher than the edge of the orbit and in B.U.20113 the area immediately medial to the horn core base is concave as far as the median suture, which is strong and slightly raised.

The horn core is set diagonally on the skull roof and in B.U.20113 it slopes laterally at an angle of about 20° from the vertical; however in M.26687 this angle is smaller. The horn core also slopes posteriorly at an angle of 35° in all three specimens; which is very similar to the posterior slope in *Protragocerus gluten* (Pilgrim 1937).   The surface of the horn core carries many pronounced vertical ridges and grooves which terminate a short distance above the skull roof, there are no cross striations.

The anterior and posterior keels are strong but do not show any signs of the torsion exhibited by more advanced forms.   There is no medial keel but the medial face of the horn core is convex antero-posteriorly and a slight swelling may be detected near the middle of the face, this could be an incipient third keel.   The medial face is concave proximo-distally, which indicates that the horn cores, though divergent at their bases, may have become more convergent distally.   The lateral face is convex proximo-distally at the base but shows slight concavity distally.   The cross-section of the horn core agrees closely with that of *Protragocerus gluten* (Pilgrim 1937) and the agreement with *Protragocerus chantrei* (Thenius 1956) is more distant.   On the basis of this evidence the horn cores from Gebel Zelten, although more primitive than other specimens of *Protragocerus*, do exhibit features which indicate their close relationship and also incipient features which could lead to the characteristics exhibited by the more advanced species of the genus.

In B.U.20113 sufficient of the roof is preserved for an estimate of the width across the orbits to be made, this was certainly not greater than 6·5 cm and not less than 6·0 cm which is much smaller than *Protragocerus gluten* and indicates an animal in the same size range as the small mandible which has been identified as *Gazella* sp. The features of the horns and mandible which separate them into different sub-families are very conclusive and the chances that these two specimens could be from the same species are very small indeed.

Genus EOTRAGUS Pilgrim 1939

DIAGNOSIS: The genus *Eotragus* is defined by Pilgrim (1939 p. 137).

TYPE SPECIES: *Eotragus haplodon* (von Meyer) 1846.

Eotragus sp.

MATERIAL:

M.26688   A single isolated horn core.

M.26689   A single isolated horn core.

DESCRIPTION: The supraorbital foramen penetrates the roof of the orbit and the canal curves inside the bone, to open on the anterior face of the horn core base near the centre of the base.   The horns were almost vertical and perhaps slightly convergent; they were situated supraorbitally and were very near the edge of the orbit. The surface of the horn core is excavated by a large number of proximo-distal grooves but transverse grooves are totally absent (pl. 13, fig. 1).   A strong keel is present on the posterior face of the horn core; this keel is stronger in M.26689 than it is in M.26688 but as the latter is from an older individual the strength of the keel may have decreased with age.   The cross-section of the horn core agrees closely with that of *Eotragus sansaniensis* (Thenius 1952 fig. 5).   The lateral face is convex proximo-distally agreeing with *Eotragus haplodon* (Thenius 1952) and the Gebel Zelten specimens also agree in size with this species; however the horns were certainly longer in the Gebel Zelten species than in *E. haplodon* as the opposing faces converge more gradually in the former species.

TABLE 10

Horn cores

	Protragocerus		*Eotragus*	
	B.M.26687	B.U.20113	B.M.26688	B.M.26689
Maximum antero-posterior thickness of horn core	27·8 mm	—	20·6 mm	16·9 mm
Maximum antero-posterior thickness of pedicle	25·5 mm	25·7 mm	19·4 mm	16·7 mm
Maximum transverse width of horn core	18·0 mm	—	17·1 mm	14·3 mm
Maximum transverse width of pedicle	17·7 mm	—	17·0 mm	15·5 mm

Subfamily ANTILOPINAE Baird 1857

DIAGNOSIS: The subfamily was defined under the name Gazellinae by Pilgrim (1939 p. 30).

Genus *GAZELLA* De Blainville 1816

DIAGNOSIS: The genus was defined by Gentry (1970 p. 292).

Gazella sp.

REMARKS: Species of *Gazella* are identified as much on the basis of the horn cores and occipital region as by the dentition. The confused state of classification within the genus is being gradually resolved (Gentry 1964, 1966, 1970) but at the moment the material from Gebel Zelten is insufficient to identify the specimen with any existing species or to allow the establishment of a new species.

MATERIAL:

    M.26685   An isolated left mandible, dentition showing medium wear.

    M.26686   A left mandibular fragment, M_3 partially erupted.

Mandible. The mandible is clearly bovid and the dentition confirms this. For purposes of comparison mandibles of *Gazella capricornis* and *G. pilgrimi* were used: with reference to the former Gentry (1970) states:

> '*Gazella capricornis* (Wagner) is the gazelle of the famous Pikermi lower Pliocene fauna from Attica. . . . Its teeth frequently show primitive characters: basal pillars on other teeth than the upper and lower first molars, strong ribs between parastyle and mesostyle of upper molars, medial wall of lower molars not very flattened, fairly shallow mandibular horizontal rami, and probably a longer premolar row.'

The species *G. pilgrimi*; with which Gentry synonymized *G. gaudryi*; is a more advanced form from Samos in which the dentition lacks primitive characters.

In the Gebel Zelten species the mandible is deep with the deepest point lying below the anterior end of M_3. The lateral face of the mandible is convex with a strong swelling in the posterior region as in *Sylvicapra*. A small posterior mental foramen lies below the anterior end of P_2. The anterior mental foramen is very large and double as in *Sylvicapra*. The diastema is short and though the anterior region is missing its length was probably similar to that of *Gazella* or *Sylvicapra*. The medial face of the mandible (pl. 13, fig. 8) is convex dorsally but a shallow concavity runs antero-posteriorly along the ventral part of this face. The mandibular foramen is large and below it is a shallow mandibular groove as in *Gazella*.

Lower dentition. The molars of the Gebel Zelten species are more brachyodont than in *G. capricornis* or *G. pilgrimi* and cingula are lacking in all three species. On M_3 the mesostylid is as strong as that of *G. capricornis* but is weaker than in *G. pilgrimi*. The metaconid is high, transversely flattened and set diagonally on the tooth causing the metastylid to be produced lingually. In *G. capricornis* the lingual cuspids are parallel to the axis of the tooth. The metaconid has a weak lingual swelling. The metastylid is very weak and is lost after medium wear. The entoconid is as high as the metaconid and has a more feeble lingual swelling, it is set more nearly parallel to the axis of the tooth than the metaconid. The protoconid is high and crescentic with no trace of a '*Palaeomeryx* fold', its anterior region joins the mesostylid very early in wear. The posterior end of the protoconid meets the metaconid and entoconid at the lingual end of the median valley. The hypoconid is lower than the protoconid but is less isolated than in the palaeomerycids. The posterior end of the hypoconid joins the entoconid, isolating the hypoconulid which forms the accessory column; this is lower than the hypoconid and is crescentic,

resembling closely the accessory column of *G. capricornis* or *G. pilgrimi*.   Excluding the differences mentioned the M_3 of the Gebel Zelten species is very similar to the two European species.

M_2 resembles the anterior region of M_3.   The mesostylid is stronger in M_2 than in M_3 (pl. 13, fig. 2), this may be a compensatory strengthening as the metaconid is more nearly parallel to the axis of the tooth in M_2. M_1 is more worn but otherwise similar to M_2.   Each molar has a strong ectostylid and M_3 has a weak stylid in the posterior valley, these stylids are similarly developed in *G. capricornis*.

The P_4 of the Gebel Zelten species is short with a high protoconid which gives off a strong postero-lingual metaconid.   The anterior region consists of a paraconid which is stout and directed antero-lingually.   A parastyle does not appear to have been developed as the lingual face of the paraconid does not bear a groove (pl. 13, fig. 2).   The posterior region is wide and the hypoconid is stout with a strong labial swelling (pl. 13, fig. 2) which is separated from the protocone by a deep labial groove. The entoconid is strong and wide but it is heavily worn and the presence of an entostylid cannot be established; the absence of a lingual groove on the face of the entoconid(pl. 13, fig. 3) indicates that an entostylid was probably not present.

The P_4 of *G. capricornis* is similar to that of the Gebel Zelten species.   The hypoconid is strong in *G. capricornis* and has a strong labial swelling as in *Gazella* sp.. The metaconid, entoconid and entostylid are similar in the two species but the anterior regions differ as the paraconid and parastylid are widely separated in *G. capricornis* but are joined in *Gazella sp.*.   The P_4 of *G. pilgrimi* is smaller than in *Gazella sp.* and the hypoconid is more feebly developed.   The entoconid and entostylid are more widely separated in *G. pilgrimi* than in *Gazella* sp. and, as in *G. capricornis*, the paraconid and parastylid are also widely separated in *G. pilgrimi*.

The P_3 is much shorter than the P_4 (table 11); the lingual region is badly broken (pl. 13, fig. 3).   The labial wall has a strong hypoconid swelling as in P_4.   The P_3 of *G. capricornis* is highly developed and is as long as the P_4 (table 11); its paraconid and parastylid are strongly separated as on the P_4 and in contrast to the P_3 of *Gazella* sp. in which the anterior region is not divided.   The P_3 of *G. pilgrimi* is smaller than that of *Gazella* sp. but the paraconid and parastylid are separated as in *G. capricornis*.   The P_2 is missing in M.26685 but it appears to have been greatly reduced in length and was probably comparable to the P_2 of *G. pilgrimi* or *G. capricornis*.

The molars of the Gebel Zelten gazelle are therefore similar to those of the European Pliocene species and they were similar in length and width to those of *G. capricornis*; however in that species the molars are more hypsodont than in *Gazella sp.* and even after medium wear the molars of *G. capricornis* are almost as high as the unworn dentition of M.26686.   The molars of *G. capricornis* are more advanced than those of the Gebel Zelten gazelle.   The premolar row is relatively long in *G. capricornis* and short in *Gazella sp.* and *G. pilgrimi;* thus in this respect *Gazella sp.* resembles the more advanced *G. pilgrimi*.   It is not possible to place the Gebel Zelten gazelle with either of these species as it shows features which are present in both species and also exhibits some features such as degree of brachyodonty and details of the premolars, which are more primitive than in either species.

TABLE II

	Gazella sp. B.M.26685		*Gazella sp.* B.M.26686		*G. pilgrimi* B.M.4177		*G. capricornis* B.M.13014	
	Length	Width	Length	Width	Length	Width	Length	Width
P_2	5·0 mm	—	—	—	4·7 mm	2·7 mm	5·2 mm	3·7 mm
P_3	7·2 mm	4·0 mm	—	—	5·7 mm	3·7 mm	9·5 mm	5·2 mm
P_4	8·6 mm	5·5 mm	—	—	7·3 mm	4·5 mm	9·7 mm	5·4 mm
Total length of premolar row	20 mm				17·7 mm		24 mm	
M_1	9·5 mm	6·7 mm	—	—	9·1 mm	5·0 mm	10·0 mm	5·6 mm
M_2	11·0 mm	7·0 mm	—	—	10·0 mm	6·0 mm	10·6 mm	6·4 mm
M_3	14·6 mm	6·6 mm	15·0 mm	6·8 mm	14·5 mm	6·7 mm	14·7 mm	6·6 mm
Total length of molar row	34·4 mm				32·1 mm		34·0 mm	
% Premolar to Molar length (Molar length—100)	58·1%				55·1%		70·6%	
Maximum height from neck to top of crown								
P_3	5·9 mm		—		—		7·5 mm	
P_4	6·8 mm		—		—		7·7 mm	
M_1	7·0 mm				—		8·0 mm	
M_2	8·3 mm		9·1 mm		—		9·1 mm	
M_3	9·0 mm		10·5 mm		—		9·6 mm	

The presence in the Zelten fauna of three species of bovids in the early Burdigalian is surprising as, with the exception of European sites and the Hsanda Gol of Asia, bovids are of later occurrence.   The presence of three bovid genera representing the two most important subfamilies of the Bovidae indicates that the bovids were already well established in the early Miocene and therefore they must have diverged from their ancestral stock at some time during the Oligocene.   The presence of bovids at Hsanda Gol is not yet well established though Trofimov (1968) figures very bovid like lower molars of *Palaeohypsodontus* and this may indicate that the ancestry of the bovids must be sought in the Oligocene of Asia.

III. THE EVOLUTION OF PRIMITIVE GIRAFFOIDS

The Giraffoidea was established by Simpson (1931) to include the Palaeomerycidae and Giraffidae; Simpson (1945) demoted the Palaeomerycidae to subfamily level and transferred it to the Cervoidea, leaving the Giraffoidea containing the Giraffidae and the Lagomerycidae.

The Palaeomerycidae was established by Lydekker (1883) taking its name from *Palaeomeryx* von Meyer 1834.   *Lagomeryx* Roger 1904, was established to include small species of *Palaeomeryx*, bearing branching ossicones.   This situation persisted until Roman and Viret (1934) suggested that the two genera were synonymous; this suggestion was supported by Teilhard de Chardin (1939).   De Chardin also suggested that a separate family should be created to accommodate *Lagomeryx*, *Procervulus* and 'other so called cervids'.   This was left to Pilgrim (1941) who proposed the name Lagomerycidae for a family including the two genera named by de Chardin and *Climacoceras* which had been placed in the Cervidae (MacInnes 1936).

Stirton (1944) discusses the relationships of the palaeomerycids and states that *Lagomeryx* and *Palaeomeryx* are synonymous; he also proposes the retention of the family name Palaeomerycidae expanded to include:

'. . . the Old World and New World non-antlered but horned and some hornless cervoids.   The genera with forked horns from the Old World are included in the subfamily Palaeomerycinae and those from North America with pointed, bulbous or flat tipped horns are assigned to the Dromomerycinae.'   (Stirton 1944).

Whitworth (1958) discusses the affinities of the palaeomerycids at some length, supporting the synonymy of *Lagomeryx* and *Palaeomeryx* and indicating the close affinity of palaeomerycids and cervids.   This is contested by Ginsburg and Heintz (1966) who challenge the synonymy of *Lagomeryx* and *Palaeomeryx* and in their discussion of the genus *Palaeomeryx* they state:

'En dehors d'Europe, le genre a été signalé par Teilhard de Chardin (1939) dans le Miocène de Chine et par T. Whitworth (1958) dans le Miocène d'Afrique orientale.   Dans les deux cas, on peut affirmer qu'il ne s'agit pas de Palaeomeryx ne serait-ce que par la présence, chez deux formes, d'une P_1.'

The presence of a P_1 in *Palaeomeryx africanus* is questioned by Gentry (1970) but a P_1 was certainly present in the species described by de Chardin (1939); which must therefore be removed from the genus *Palaeomeryx* and should revert to its

previously applied name of *Lagomeryx simpsoni;* however the name *Lagomeryx* is not applicable as it was established (Roger 1904) to refer to European species which have been synonymized with *Palaeomeryx:* in this situation the species reverts to its original name—*Heterocemas simpsoni* Young 1937.

Pilgrim (1941) and de Chardin (1939) indicate close giraffoid affinities for the Palaeomerycidae (Lagomerycidae) and their evidence for this was summarized by Whitworth (1958):

> '(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 parts of the "antlers".'

Whitworth objected to the first on the grounds that variation occurs in the strength of the ribs in both giraffids and cervids and he states:

> 'In fact, an unequal development of the anterior and posterior external ribs are found, to a varied degree in most cervids and giraffids alike; although generally speaking, the anterior rib is more angular and better defined in the deer than in the Giraffidae.' (Whitworth 1958).

This objection is valid as is his objection to the second piece of evidence on the basis of the great variability of the enamel in the molars of the giraffids and cervids. The third piece of evidence is the strongest and Whitworth's grounds for rejecting it are correspondingly weak, he states:

> '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.' (Whitworth 1958).

This distinction is probably basic to the classification of the giraffids, cervids and palaeomerycids and Pilgrim's statement is given here:

> '. . . the skin covered "horn" was the most primitive and the nearest approximation to it is to be seen in the Lagomerycid and Giraffid "horn". From this original type it is easy to surmise that the deciduous antlered horn of the Cervidae arose, though the intermediate stage is as yet unknown.' (Pilgrim 1941).

Whitworth indicated that this could just as easily mean that the palaeomerycids were primitive cervids as giraffids but the ossicones are positive evidence in favour of the affinity of the palaeomerycids and giraffoids, whereas they can only be regarded as evidence for the affinity of palaeomerycids and cervids on purely hypothetical grounds. In this context Ginsburg and Heintz (1966) state:

> 'Les ossicones de *Palaeomeryx* offrent, avec ceux des Girafes, de si fortes similitudes que nous nous demandons s'il ne s'agit déjà d'un Girafide vrai.'

The upper dentition of *Zarafa* agrees with that of *Palaeomeryx* in many features but it also agrees with *Palaeotragus* and the skull shows close affinities with the palaeotragines. Unfortunately the skull of *Palaeomeryx* is not known but the presence of a dentition with some palaeomerycid features on a skull with giraffid affinities indicates the closeness of the palaeomerycids and the giraffids.

Much of the confusion over the affinities of the palaeomerycids can be attributed to the poorly defined limits of the family. Ginsburg and Heintz (1966) have

removed *Walangania africanus* and *Heterocemas simpsoni* from the genus *Palaeomeryx* which limits the genus mainly to the Lower and Middle Miocene of Europe. They also suggested the removal of the Oligocene genera which lack ossicones, from the Palaeomerycidae, transferring them to a position as the common stock from which the giraffids and cervids evolved; this group was named the Dremotheriidae by Ginsburg and Heintz but it is of the same status as the other main groups and should therefore have superfamily status. This regrouping of the early ruminants results in an arrangement as shown (text fig. 12).

The North American members of the Palaeomerycidae were discussed in detail by Stirton (1944) who assigned them to the subfamily Dromomerycinae and indicated an origin for this group which was close to the origin of the cervids and palaeomerycines. Simpson (1945) treated the Dromomerycinae as a subfamily of the cervidae; while Crusafont (1952) placed the tribe Blastomerycini in the Palaeomerycinae and transferred the Dromomerycinae to the Giraffoidea. Ginsburg and Heintz (1966) proposed the inclusion of the blastomerycines in the Dremotheriidae. The blastomerycines are small, hornless pecorans, at the same level of evolution as the
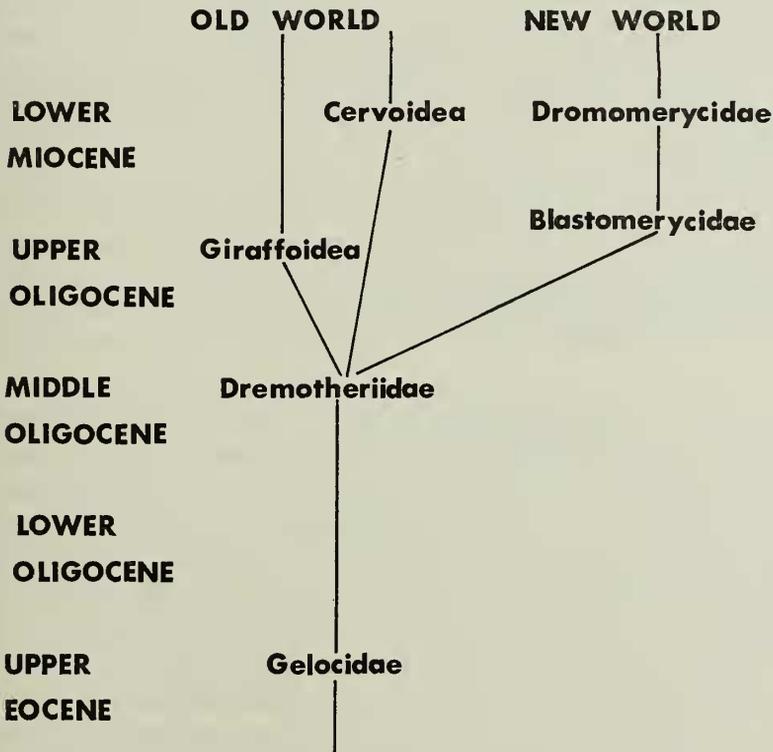
FIG. 12. The interrelationships of the early, non-bovid ruminants.

dremotheriids and, with the exception of *Eumeryx*, they are an entirely New World group.   At this level of pecoran evolution the forms are so similar that division into groups is difficult and it is proposed that the Dremotheriidae and Blastomerycidae should be treated as separate families of the Dremotherioidea.   The Dromomerycidae probably originated from the Blastomerycidae.

Eumeryx culminis from the Hsanda Gol Formation was identified (Matthew and Granger 1924) as a blastomerycine and was so classified by Simpson (1945), it is the only blastomerycine from the Old World and is of Lower Oligocene age whereas the other blastomerycines are of Lower Miocene age.   Stirton (1944) briefly discussed the position of *Eumeryx* and he states:

> 'As to whether *Eumeryx* is placed in the Cervoidea or Traguloidea is more or less arbitary but recognition of its pre-cervoid characters is quite important.'
> (Stirton 1944).

In view of the great difference of distribution in space and time and the difficulty of establishing relationships purely on the dentition, at this level of ruminant evolution; the affinity of *Eumeryx* with the other blastomerycines is doubtful.

The Pecora probably originated from the Traguloidea during the Upper Eocene or Lower Oligocene and of the two traguloid families the Gelocidae are the most likely to have given rise to the Pecora.   In the gelocids true selenodonty is developed from more bunodont forms; thus *Lophiomeryx* has very bunoid lower molars showing few signs of true selenodonty while *Bachitherium* and *Prodremotherium* have molars which are very similar to those of *Dremotherium*.   A detailed study of this group is needed and it is here that the divergence of the Bovoidea and other higher ruminants probably occurred.

The system shown (text fig. 12) appears more natural than any yet proposed for the evolution of the early, non-bovid ruminants.   The members of the Dremotherioidea appear to form a natural unit and *Palaeomeryx* with its closely allied genera are included in the Giraffoidea.   The whole pecoran classification at this level is in a state of flux as it relies upon very small differences and only the discovery of more localities and more complete material can resolve some of the outstanding problems.

IV. THE EFFECT OF THE OSSICONES ON GIRAFFOID EVOLUTION

With the exception of size, the most important differences between *Zarafa* and *Prolibytherium* are related to the frontal bones, ossicones and occipital region.   The ossicones of *Zarafa* were developed supraorbitally and probably projected dorsolaterally as in *Samotherium sinense* (Bohlin 1926 pl. VI.).   Each ossicone was probably a simple, conical projection about the same size as in *Okapia*.   The ossicones of *Prolibytherium* are well known (pl. 7).   If the origin of the giraffoids lies in the middle or late Oligocene then the divergent trends in the development of the ossicones must have been established very early to allow such great differences to evolve by the early Miocene; these trends may be revealed by the ossicones.

Frontal appendages are developed in the ruminants primarily for intraspecific combat and certain rules may be applied to their development; these were formulated by Geist (1965).   Fighting in *Giraffa* (Innis 1958) and *Okapia* (Walther 1960

and 1962) consists of lateral display and the delivery of heavy blows to the sides and neck of the opponent with the head used as a club. Lateral display is the most primitive combat method used in the ruminants and is also found in the tylopods. With this combat method strong crushing or bending forces are not experienced along the length of the neck and therefore any tendency to increase the length of the neck is not inhibited by behavioural factors; indeed increase in length of the neck may confer a small selective advantage in combat as the length of the swing and therefore the force of the blow will be increased. This slight advantage would rein-force advantages resulting from other aspects of the animals behaviour such as feeding habits. With this combat method the force of blows delivered is on the lateral region of the frontals and therefore if a protuberance is developed it will be primitively in the supraorbital position; also head to head contact will not usually occur and a skin covered appendage will be effective and will retain its skin covering at least over most of its surface as in *Giraffa* or *Okapia*. Apart from the extant giraffids many of the palaeotragines and giraffines were long necked relatively slender animals, with small ossicones and it is likely that lateral combat methods were practised by all of them.

In *Prolibytherium* the ossicones consist of a solid outer layer of bone and a cancellous interior; frontal sinuses are not present. The derivation of the ossicones in *Proliby-therium* cannot be established but certain features of the skull may indicate their mode of origin. The anterior palmation projects antero-laterally from the supraorbital region and it is possible that the anterior region was derived from a supraorbital tine similar to that of *Zarafa*. At the posterior end of the ossicones the presence of paired pillars (pl. 10, fig. 2) suggests the derivation of this region from paired supraoccipital ossicones. The occurrence of supraorbital and parietal ossicones in other sivatheriids and palaeotragines indicates that giraffoids have the ability to develop ossicones in both regions.

The ossicones of *Prolibytherium* are the earliest advanced frontal appendages known in the ruminants. Geist (1965) relates the evolution of large frontal appendages to intraspecific combat involving frontal or head to head attack with wrestling and pushing between the heads. Geist states:

'. . . cervid antlers should be regarded primarily as structures binding opponents together during pushing and wrestling matches.'

Thus the ossicones of *Prolibytherium* present a stage of evolution which is more advanced than that of *Zarafa*. The ossicones would also function in threat postures with reference to which Coope (1968) states:

'I believe that initially the "pedicels" evolved as threat display structures increasing the apparent surface area of the face and thus its deterrent value.'

Geist and Coope agree that the frontal appendages function in frontal display and attack when they are large and the effectiveness of the ossicones of *Prolibytherium* in increasing the apparent surface area of the face cannot be questioned.

Morphological and functional differences between the ossicones of *Zarafa* and *Prolibytherium* may suggest reasons for the divergence between the two main lines of giraffoid evolution. The selective advantage in intraspecific combat conferred by the large ossicones of the sivatheriids was a strong evolutionary force maintaining

the large ossicones and also the short neck and limbs necessary for their effective use. The more primitive combat methods of the palaeotragines and giraffines tended to increase the selective advantage of a long neck and, more important, made possible the elongation of the neck under other selective forces.

V. A CLASSIFICATION OF THE GIRAFFOIDEA

The discovery of *Prolibytherium* and *Zarafa* in the Burdigalian of North Africa indicates that the origin of the giraffoids must lie in the late Oligocene and that divergence within the group occurred at this time.   This was also stated by Ginsburg and Heintz (1966):

> 'On peut se demander si les soi-distant Cervides sans bois de la fin de l'Oligocene (*Amphitragulus*, *Dremotherium*, Blastomerycines) ne representant pas, non des Cervides primitifs, mais le stock commun d'ou sortiront a l'epoque suivant les Cervides, d'une part, et les Giraffoidea, d'autre part.'

Features of *Zarafa* and *Prolibytherium* indicate divergence very soon after their origin from the pregiraffoid stock and the establishment of a separate family to accommodate the sivatheres is proposed.   The evolution of the giraffines and palaeo-tragines has followed similar trends and the divergence of these two groups probably did not occur until the middle Miocene, they are therefore retained as subfamilies within the family Giraffidae.   This results in a classification of the Giraffoidea as summarized in text figure 13.

    Superfamily **GIRAFFOIDEA** Simpson 1931

    Family **PALAEOMERYCIDAE** Lydekker 1883

> *Canthumeryx* New genus.   L. Miocene; Africa.
> *Climacoceras* MacInnes 1936.   M–U. Miocene; Africa.
> *Heterocemas* Young 1937.   U. Miocene; Asia.
> *Palaeomeryx* Von Meyer 1834.   L. Miocene; Africa.
>   M–U. Miocene; Europe.
> *Procervulus* Gaudry 1878.   L–M. Miocene; Europe
> *Propalaeoryx* Stromer 1926.   L. Miocene; Africa.
> *Triceromeryx* Villalta, Crusafont and Lavocat 1946.
>   L. Miocene; Europe.

    Incertae sedis.

> *Progiraffa* Pilgrim 1908.   L. Miocene; Asia.

The Palaeomerycidae.   At present the family is best regarded as a level of ruminant evolution equivalent to the primitive representatives of the Giraffidae and Sivatherii-dae.   This system was used quite drastically by Stirton (1944) who drew straight lines across his phylogenetic diagram to indicate levels of evolution and the limits of the family.

The genus *Triceromeryx* is placed in the Palaeomerycidae as it shows close similari-ties to the members of the genus *Palaeomeryx* from Sansan.   The presence of a

supraoccipital horn sets it apart from the other palaeomerycids and, owing to its strange nature, from all the sivatheriids and giraffids; however the material of *Triceromeryx* can be interpreted differently and it is possible that the supraoccipital ossicone does not belong to *Triceromeryx*, this is also suggested by Churcher (1970). The lower dentition of *Triceromeryx* is very palaeomerycine in form and each molar bears a strong '*Palaeomeryx* fold'. The P_4 is almost indistinguishable from a P_4 of *Palaeomeryx sansaniensis* (M.5409). The presence of a '*Palaeomeryx* fold' is not evidence of palaeomerycid affinities as such a fold is also present in some specimens of *Palaeotragus* and *Honanotherium* but in these genera the occurrence of the fold is irregular. The genus *Triceromeryx* is endemic to the Iberian peninsula and certainly does not effect the evolution of the advanced giraffoids.

The main problems relating to this family cannot be resolved until an exhaustive review of the European material is made. It is unlikely that the palaeomerycids gave rise to either of the other giraffoid families or to the cervids. They represent a Miocene expansion of the ruminants into an ecological niche which was later filled by the palaeotragines and cervids. Inter-relationships within the family are not known.
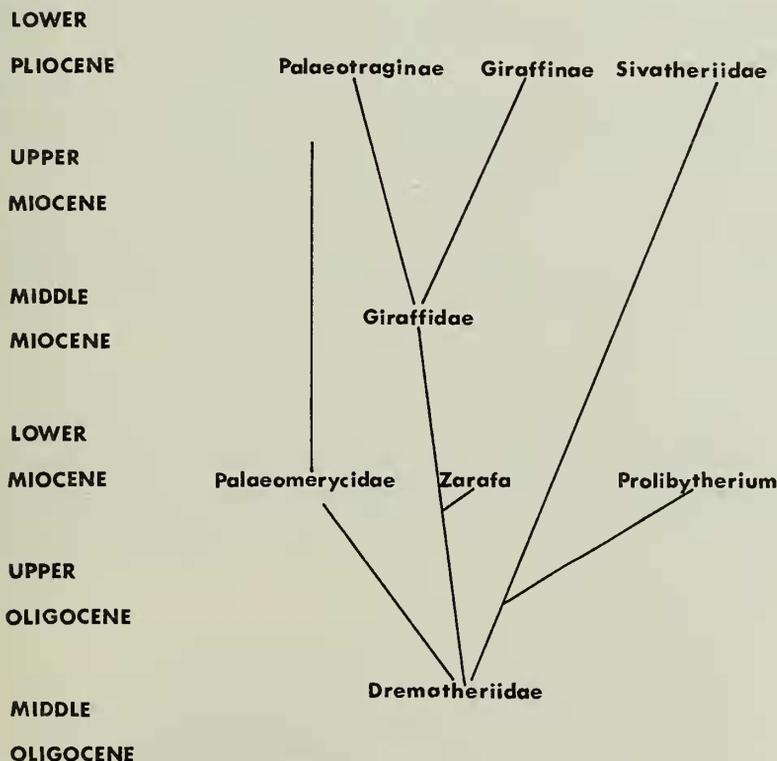
FIG. 13.   The early evolution of the Giraffoidea.

E

Family   *SIVATHERIIDAE* New family

Birgerbohlinia Crusafont 1952.   L. Pliocene; Europe
Bramatherium Falconer 1845.   M. Pliocene; Asia.
Helladotherium Gaudry 1860.   L. Pliocene; Europe, Asia,
                              and N. Africa.
Hydaspitherium Lydekker 1878.   M. Pliocene; Asia.
Libytherium Pomel 1893.   U. Pliocene and Pleistocene; Africa.
Prolibytherium Arambourg 1961.   L. Miocene; Africa.
Sivatherium Falconer and Cautley 1835.   U. Pliocene and
                                 Pleistocene; Asia.

SIVATHERIIDAE: *Prolibytherium* is the earliest representative of this family but even in this genus the ossicones are highly developed and the cheek teeth show hypsodont tendencies. The retention of a lacrymal fossa indicates the primitive nature of the genus. The family is characterized by its short neck and limbs, and also by the large ossicones; these are probably related features but they also indicate that members of the family fed near the ground and grazing forms may have developed. Meladze (1964) suggests that the family reached its climax in the late Miocene but I would place this climax in the Pliocene when the group was represented by fairly abundant, massively built forms throughout the Old World. The African genus *Libytherium* is probably the only Upper Pliocene and Pleistocene genus from Africa and with it may be synonymized such forms as *Griquatherium* Cooke and Wells 1947 and *Orangiotherium* van Hoepen 1932. The genus *Helladotherium* from Pikermi, is problematical as it lacks ossicones, indicating that it was probably the female form: with reference to this genus Matthew (1929) states:

'It appears not at all improbable that *Helladotherium* may be the female of *Bramatherium* or *Hydaspitherium*. The teeth are indistinguishable, and the skulls are by no means as diverse in degree, but differ in the same manner, as *Sivatherium* and "*Indratherium*" of the Upper Siwaliks.'

No further work has been done on this problem and *Helladotherium* is here included in the family as a valid genus, with the qualification that it is probably a female form.

Meladze (1964) also suggests that the sivatheriids were adapted to life in the savannahs but I suggest that they were probably woodland or forest forms, feeding on low vegetation or grasses of the woodland floor. The family was very successful and it may have survived in Asia to sub-recent times as suggested by Colbert (1936).

Family **GIRAFFIDAE** Gray 1821

Subfamily **PALAEOTRAGINAE** Pilgrim 1911

Giraffokeryx Pilgrim 1910.   L. Pliocene; Asia.
Okapia Lankester 1901.   Pleistocene and Recent; Africa.
Palaeotragus Gaudry 1861.   U. Miocene; Europe, Asia,
                           and Africa.   L. Pliocene; Europe
                           and Asia.

Samotherium Major 1888.   U. Miocene; Africa.   L. Pliocene
Europe and Asia.
Zarafa New genus.   L. Miocene; Africa.

Subfamily.   **GIRAFFINAE** Zittel 1893.

Bohlinia Matthew 1929.   L. Pliocene; Europe.
Decennatherium Crusafont 1949.   L. Pliocene; Europe.
Giraffa Brisson 1756.   Pliocene; Europe and Asia.
Pleistocene; Asia and Africa.
Recent; Africa.
Honanotherium Bohlin 1926.   Pliocene; Asia.

GIRAFFIDAE: A group of late Oligocene origin with *Zarafa* as the earliest known genus.   The family is characterized by a tendency to increase the length of the neck and limbs.   The giraffids reached their climax in the early Pliocene when they were well represented throughout the Old World.   It was probably during the middle Miocene or slightly earlier that the group divided into two subfamilies; the palaeotragines and giraffines.

The palaeotragines were in many ways very progressive and the development of a hypso-brachyodont dentition in later members of the genera *Palaeotragus* and *Samotherium* indicates that they probably fed upon fairly low vegetation with a high proportion of ground vegetation in their diet.   In any case they were utilizing an intermediate zone between the bovids and giraffines and in times of scarcity it is this zone which the other two groups would utilize at the expense of the palaeotragines. The subfamily has one extant member, the okapi which has survived in a tropical forest environment.

The giraffines have been relatively successful since the Pliocene.   The series *Honanotherium, Bohlinia, Giraffa* suggested by Bohlin (1935) seems to be a natural sequence and is probably the true relationship.

VI. EAST AFRICAN RUMINANTS

During this work reference has been made to the Miocene ruminants of East Africa which were described by Whitworth (1958).   A brief review of these ruminants has been made as I disagree with some of Whitworth's identifications.   These ruminants are treated as a separate section as they are nearly all previously described forms and all depend upon previously described material; also it was felt that their inclusion with the Libyan forms would confuse the description of a regionally defined ruminant group.

Superfamily **TRAGULOIDEA** Gill 1872

Family **TRAGULIDAE** Milne-Edwards 1864

Genus *DORCATHERIUM* Kaup 1833

The agreement between *Dorcatherium chappuisi* from Rusinga and Turkana (Arambourg 1933) is very close and there is no doubt that these specimens are from

the same species. The other three species described by Whitworth (1958) are *D. pigotti*, *D. parvum* and *D. songhorensis;* these are distinguished on a size basis only and with reference to these species Whitworth states:

> 'Further collecting may show that *D. songhorensis* is synonymous with *D. parvum* or *D. pigotti*, but for the present it seems preferable to treat the Songhor material separately.' (Whitworth 1958).

I agree with Whitworth on this point, there are certainly two smaller species of *Dorcatherium* and as further collections have not been made it is not possible to synonymize *D. songhorensis* with either of these.

The genus *Dorcatherium* is the only traguloid genus previously identified from the Miocene of Africa but included in the material identified as *Palaeomeryx africanus* (Whitworth 1958) are a few lower molars which differ anatomically from the type specimen. These molars exhibit traguloid features and agree closely with the lower molars of *Gelocus*.

Superfamily **TRAGULOIDEA** Gill 1872

Family **GELOCIDAE** Schlosser 1886.

DIAGNOSIS: Traguloids in which true selenodonty is developed; strong cingula developed on the labial or lingual sides of the cheek teeth. Metapodials fused to form cannon bones and side toes reduced. Lower premolars very simple. P_1 reduced and peg-like, separated from P_2 by a short diastema (After Schlosser 1886).

Genus *GELOCUS* Aymard 1855

DIAGNOSIS: A medium sized gelocid in which the selenodonty is less advanced than in most members of the family. Metaconid rounded anteriorly but less so than in *Lophiomeryx*. Premolars very simple. (Mainly after Schlosser 1886).

Gelocus whitworthi sp. nov.

DIAGNOSIS: A medium sized species of *Gelocus* possessing a rounded metaconid on the lower molars; the median valley of the lower molars is very open lingually. Length of lower molar row about 33 mm.

SYNONYMY: One specimen of this species—K.Sgr.368.49—was described by Whitworth (1958) with *Palaeomeryx africanus*.

DERIVATION OF NAME: The species is named after Dr. T. Whitworth who produced the first definitive account of African Miocene ruminants.

HOLOTYPE: K.Sgr.365.1949—a left mandibular fragment with lightly worn M_2 and M_3. From Songhor, Nyanza Province, Kenya. All specimens of this species are the property of the National Museum, Kenya.

LOCALITY AND HORIZON: Specimens are from Songhor and Rusinga Island Kenya. Both sites are referred to the Miocene.

MATERIAL:

K.Sgr.265.1949   Holotype; a left mandibular fragment with lightly worn M_2 and M_3.

K.Sgr.368.1949   An isolated M_1 showing slightly heavier wear than the holotype.

K.Sgr.581.1949   An isolated right M_3 showing light wear.

K.Sgr.159.1949   An isolated right M_2 showing medium wear.

K.R.30   An isolated right M_3, showing medium wear.

DESCRIPTION: The lower molars are almost the same size as *Walangania africanus*. On the M_2 the metaconid is conical with an anterior crest curving antero-lingually to meet the mesostylid at the antero-lingual corner of the tooth; this results in the concavity of the antero-lingual face of the metaconid similar to *Gelocus communis* but differing greatly from *Walangania* in which the metaconid is selenodont. The postero-lingual face of the metaconid is rounded with a feeble metastylid but lacking a fold such as is present in *Dorcatherium*. In *Walangania* the metastylid lies lingual to the anterior end of the entoconid whereas in *Gelocus* it is closely joined to the metaconid and lies lingual to the posterior end of the metaconid; as a result the median valley is very open lingually (pl. 13, fig. 5). The entoconid is conical with a strong anterior crest. The posterior end of the entoconid is forked and the labial branch meets the postero-lingual end of the hypoconid while the lingual branch is produced postero-lingually. This results in a strong vertical groove on the posterior face of the cuspid (pl. 13, fig. 4); a similar groove is present in *Gelocus communis* in which the lingual branch meets the postero-lingual extension of the hypoconid and the labial wing joins this part of the hypoconid. No such groove is present in *Lophiomeryx*, *Bachytherium* or *Prodremotherium*.

The protoconid is crescentic and extends antero-lingually around the anterior end of the metaconid; causing the anterior fossette to open lingually (pl. 13, fig. 4) but not to the same extent as in *Lophiomeryx*. The posterior region of the protoconid extends lingually and joins the postero-labial face of the metaconid from which a wing is produced as in *Walangania* and *Palaeomeryx*; however in *Gelocus* this wing is much more anteriorly situated resulting in a shorter anterior fossette and a longer median valley region. The anterior wing of the entoconid also meets the protoconid in this region. The hypoconid is crescentic and lower than the protoconid. M_2 has strong anterior and posterior cingula.

The metaconid of M_3 is more feeble than on M_2 and the anterior crest is weaker. In *Lophiomeryx* the anterior end of the metaconid is extremely shortened and rounded while in *Gelocus* it bears a strong crest and is truly selenodont. The entoconid is more selenodont in M_3 than M_2, this is mainly due to the presence of a strong crest in the posterior region. This crest extends posteriorly and lies lingual to the postero-lingual end of the hypoconid (pl. 13, fig. 4). The posterior end of the entoconid is not forked as in the M_2; this region is similar to *Gelocus communis* but differs from *Lophiomeryx* in which the entoconid has only a feeble posterior crest.

The protoconid is crescentic and its antero-lingual extension is stronger than in the M_2; resulting in the posterior shift of the lingual opening of the anterior fossette in the M_3 relative to the M_2 (pl. 13, fig. 4).   The hypoconid is similar to that of the M_2 but the posterior region is shorter in the M_3 as it joins the posterior extension of the hypoconid.   The accessory column consists of a strong entostylid running postero-labially from the posterior end of the entoconid and fusing with the strong hypoconu-lid.   The hypoconulid is crescentic and curves postero-labially from the face of the hypoconid (pl. 13, fig. 4).   At its posterior end the hypoconulid turns antero-lingually and almost encircles the entostylid. M_3 has a strong anterior cingulum and both M_2 and M_3 have strong entostylids in the median valleys. M_3 also has a stylid at the labial end of the posterior valley.

Features of their anatomy warrant the specific but not generic separation of these specimens from other species of *Gelocus*.   Their presence in East Africa is important as representatives of the family Gelocidae are previously unrecorded from Africa.

TABLE 12

The Lower Dentition of *Gelocus whitworthi*

	M_1		M_2		M_3	
	Length	Width	Length	Width	Length	Width
K.Sgr.365.1949	—	—	10·8 mm	6·7 mm	14·7 mm	6·9 mm
K.Sgr.368.1949	9·5 mm	5·9 mm	—	—	—	—
K.Sgr.581.1949	—	—	—	—	14·5 mm	6·8 mm
K.Sgr.159.1949	—	—	10·4 mm	6·7 mm	—	—
K.R.30	—	—	—	—	15·0 mm	6·8 mm

Family **PALAEOMERYCIDAE** Lydekker 1883

Genus *PROPALAEORYX* Stromer 1926

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 a very short diastema.   Enamel wrinkled.   Lower molars with very strong metastylid and entostylid; pronounced median rib on lingual surface of metaconid, similar rib on entoconid; accessory stylid in median, external valley developed to varying degree.' (Whitworth 1958).

TYPE SPECIES. *Propalaeoryx austroafricanus* Stromer 1926; from the Lower Miocene of South West Africa.

Propalaeoryx nyanzae Whitworth 1958

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 the median, external valley.   Teeth rather lower crowned than in type species, *P. austroafricanus*.'   (Whitworth 1958).

HOLOTYPE: M.21368 (K.324.47) Figured Whitworth 1958, fig. 12. A fragment of left mandible with M_1 and M_2 showing slight wear.

HORIZON: From the Lower Hiwegi Beds, Rusinga Island. Lower Miocene.

MATERIAL:

M.21368	Holotype.
K.1263.51	Isolated left M_2.
K.614.49	Anterior region of right M_3.
K.774.52	Right mandibular fragment with M_2 and M_3.
K.780.52	Newly erupted left M_3.
K.193.51	Heavily worn left M^2.
K.Mt.21	Lightly worn right M^1.
K.X.	Left maxillary fragment with M^1 and M^2.
K.Mt.67.51	Fragment of left maxilla with P^4 and M^1. (Listed as *Palaeomeryx africanus* by Whitworth 1958; table X.).
K.246.59	Heavily worn left M^1.

DESCRIPTION: Whitworth (1958) described the lower dentition only and upper molars here identified as *Propalaeoryx nyanzae* agree with the lower molars in details such as size, brachyodonty, degree of rugosity, depth of fossettes and strength of labial ribs and styles. The lower dentition is redescribed as it agrees closely with *Canthumeryx*.

Lower dentition. The enamel of the molars is finely rugose. M_2 has a strong anterior cingulum as in *P. austroafricanus* and *Canthumeryx*; this cingulum has a serrated occlusal edge and appears to consist of a series of small tubercles. The molars exhibit the same degree of brachyodonty as in *Canthumeryx*. On the M_2 the posterior crest of the metaconid is flexed labially in the unworn state and this flexion is indicated on the wear trace until medium wear has occurred. The lingual rib of the metaconid is as strong as that of *Canthumeryx* but does not equal the strength of this rib in *Palaeomeryx furcatus* or *Palaeomeryx magnus* in which the rib has a strong posterior fold. The metastylid is strong and projects lingually but it is weaker than the metastylid of some palaeomerycids. The entoconid is shortened in the posterior region and the posterior fossette opens lingually. The protoconid is crescentic and joins the anterior end of the metaconid; this end of the molar is very pointed as in *Canthumeryx* (pl. 14, fig. 1). The hypoconid is crescentic and its anterior end meets the protoconid in the median valley. The posterior end of the hypoconid is very long and is produced lingually.

The M_3 is similar to the M_2 in the anterior region. The posterior region of the hypoconid is produced lingually and meets the face of the strong entostylid. The hypoconulid is crescentic and joins the hypoconid labially and the entostylid lingually thus enclosing a large enamel island (pl. 14, fig. 1).

Upper dentition. The molars are four rooted with the lingual and labial pairs of roots fused. The enamel is more rugose than in *Walangania* and M^1 has a strong anterior cingulum and a weaker posterior cingulum. The parastyle of M^1 is strong with a pronounced labial rib which forms the antero-labial corner of the tooth. The paracone is stout and less transversely flattened than that of *Walangania*; this

is a primitive feature resembling the traguloid condition. The labial rib of the para-cone is stronger than that of *Walangania* (pl. 14, fig. 2) and resembles closely that of *Palaeomeryx* in which the rib flexes slightly anteriorly. The mesostyle is similarly developed in *Propalaeoryx*, *Walangania* and *Palaeomeryx*. The metacone has a feeble labial rib and the metastyle is strongly developed (pl. 14, fig. 2). The protocone is similar to that of *Palaeomeryx*; it is crescentic with a few small wings at the postero-labial end; these project into the medial valley and the anterior fossette (pl. 14, fig. 2). The anterior fossette is much shallower than in *Walangania* but resembles that of *Palaeomeryx*. The metaconule is crescentic; from its posterior region two strong accessory crests project into the fossette; these are strongly developed in all the molars and an enamel island is formed early in wear, this island is large and shallow (pl. 14, fig. 2). As wear continues the first enamel island is lost and a smaller one is developed at the posterior end of the fossette. Accessory crests are very feeble when present in *Walangania*.

The M^2 is similar to M^1 in all its main features. Each molar has a strong entostyle in the median valley and a very strong anterior cingulum which has a serrated edge as in the lower molars.

The P^4 is similar to that of *Palaeomeryx*. The labial region of the tooth is not known but the lingual region of the metacone is preserved. The protocone is crescentic and from its posterior region an extremely strong accessory crest divides the fossette into anterior and posterior regions (pl. 14, fig. 2); in the posterior region a series of small tubercles and folds are present on the face of the protocone and metacone. A strong cingulum forms a swelling at the base of the lingual face of the protocone (pl. 14, fig. 3) a similar though weaker cingulum is occasionally present in *Palaeomeryx* and *Walangania*.

The upper dentition with its shallow fossettes, stout labial cusps, strong styles and cingula and complications of the cusps by accessory crests or tubercles is more primi-tive than the dentition of *Palaeomeryx* or *Walangania* and in many features agrees closely with the tragulid dentition. The description of the upper molars of *Propalae-oryx* shows that though it is more primitive than *Palaeomeryx* it shows closer affinities with this type of dentition than with the primitive bovids.

The affinities of Propalaeoryx. Stromer (1926) indicated that *Propalaeoryx* was a member of the Bovidae but Arambourg (1933) states:

'*Propalaeoryx austro-africanus* Stomer appartient à une espèce d'assez grande taille et possède d'incontestables traits de Cervidé primitif.'

Whitworth (1958) discusses the affinities of *Propalaeoryx* and states:

'Indeed in everything except size, the lower molars of *Propalaeoryx* are precisely like those of *Micromeryx* from the Miocene of Europe.'

In spite of evidence presented by dentition, Whitworth continues his argument, citing isolated ruminant limb bones which he tentatively identifies as *Propalaeoryx*; especially a single metatarsal which:

'. . . exhibits a bovid condition in the housing of the extensor tendon while retaining a remarkably cervid-like development of the shaft.' (Whitworth 1958).

The reasons for this identification rest upon the fact that the bone agrees in size

with *Propalaeoryx nyanzae;* however true bovid dentitions of a similar size have been found in these deposits. Whitworth considered this single bone to be sufficient to cast grave doubts on the supposed cervid affinities of the genus but I do not feel that this tentative evidence can outweigh positive evidence presented by the dentition in favour of palaemerycid affinities for *Propalaeoryx*. As stated the dentition of *Propalaeoryx* is similar to that of *Palaeomeryx* and the strong metastylid, which is much stronger than that of *Walangania*, is a palaeomerycid rather than a bovid character. The lower premolars of *Propalaeoryx austroafricanus* are virtually indistinguishable from those of some palaeomerycids or from *Canthumeryx*. For these reasons *Propalaeoryx* is classified as a member of the *Palaeomerycidae*.

It is possible that *Canthumeryx* and *Propalaeoryx* are representatives of a new group of ruminants which is of African origin but in the absence of more material I prefer to group them with an existing and certainly closely related family.

TABLE 13

The Dentition of *Propalaeoryx nyanzae*

Lower Dentition

	M₁ Length	M₁ Width	M₂ Length	M₂ Width	M₃ Length	M₃ Width
B.M.21368	13·6 mm	7·2 mm	13·7 mm	7·9 mm	—	—
K.614.49	—	—	—	—	—	8·4 mm
K.1263.51	—	—	12·5 mm	7·7 mm	—	—
K.774.52	—	—	13·5 mm	7·8 mm	19·0 mm	8·3 mm
K.780.52	—	—	—	—	19·6 mm	8·2 mm

Upper Dentition

	P⁴ Length	P⁴ Width	M¹ Length	M¹ Width	M² Length	M² Width
K.193.51	—	—	—	—	12·5 mm	13·1 mm
K.Mt.21	—	—	14·2 mm	14·4 mm	—	—
K.X.	—	—	13·0 mm	14·0 mm	12·0 mm	—
K.Mt.67.51	10·0 mm	11·5 mm	12·6 mm	13·1 mm	—	—
K.246.59	—	—	12·5 mm	14·0 mm	—	—

BOVIDAE Incertae Sedis

Genus *WALANGANIA* Whitworth 1958

DIAGNOSIS: Small, lightly constructed pecoran. Frontal appendages unknown. Mandible with prominent angle and large recurved coronoid process. Cheek teeth closed from P₂ to M₃. First premolar lost. Lower molars brachyodont, selenodont and narrow. Protoconid and hypoconid angular and compressed antero-posteriorly. Upper molars square, brachyodont and selenodont. Paracone with strong labial rib, metacone lacking labial rib. Enamel of cheek teeth finely rugose. Pelvis and rear limbs of advanced pecoran type. (After Whitworth 1958).

Walangania africanus (Whitworth) 1958

Palaeomeryx africanus Whitworth 1958.
Walangania gracilis Whitworth 1958.
Kenyameryx africanus Ginsburg and Heintz 1966.

DIAGNOSIS: As for genus.

REMARKS: The species *Palaeomeryx africanus* was established on the basis of a large number of upper and lower dentitions as well as a considerable amount of post-cranial material. Ginsburg and Heintz (1966) removed the species from the genus *Palaeomeryx* on the basis of a supposed presence of a P_1 and the more primitive nature of the anterior premolars. The name *Kenyameryx* was suggested to accommodate the species. The presence of a P_1 was disputed by Gentry (1970) who identifies the P_1 as a second deciduous premolar.

The genus *Walangania* is known from the holotype only; this is an almost complete, associated skeleton in which the deciduous dentition and the first permanent molars are erupted. Except in the degree of wear the permanent molars are indistinguishable from those which Whitworth described as *Palaeomeryx africanus*. Although Whitworth states that the '*Palaeomeryx* fold' is absent in the holotype a fold is certainly present and is as strong as in many specimens of *Palaeomeryx africanus*. The dimensions of the teeth are also very similar in *Walangania* and *Palaeomeryx africanus* (table 14).

The main differences in the diagnoses of *Walangania gracilis* and *Palaeomeryx africanus* are the presence of a P_1 and a '*Palaeomeryx* fold' in *P. africanus* but neither of these differences are acceptable on closer investigation. The other differences between the species result mainly from the juvenile condition of the *Walangania* holotype and are insufficient to warrant the continued separation of the two species.

Palaeomeryx africanus was described earlier in the publication than *Walangania gracilis* but the generic name *Palaeomeryx* is not applicable to the material. The name *Kenyameryx* suggested by Ginsburg and Heintz (1966) cannot be used as the name *Walangania* has precedence. The trivial name 'africanus' is retained as it has page precedence over the trivial name 'gracilis'.

The affinities of Walangania africanus. The affinities of *Walangania gracilis* were discussed by Whitworth (1958) who concludes:

'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.'

The affinities of *Palaeomeryx africanus* were implied by its generic name and therefore with the synonymy of *P. africanus* and *W. gracilis* the affinities of the species *Walangania africanus* should lie with the Palaeomerycidae; however a study of the material indicates that even this affinity is very doubtful.

The lower molars of *Walangania* exhibit weak lingual ribs and styles these agree in strength with those of *Eotragus* and are weaker than is usual in *Palaeomeryx*. The metaconid and entoconid are aligned almost parallel to the long axis of each lower molar in *Walangania* and *Eotragus* but in *Palaeomeryx* these cuspids usually have a diagonal orientation. The metaconids and entoconids of the lower molars

Table 14

The dentition of *Walangania africanus*

(Numbers 1 to 3 are listed by Whitworth 1958, as *Palaeomeryx africanus*.)
(Number 4 is listed as *Walangania gracilis*.)

Upper Dentition

	P4		M1		M2		M3	
	Length	Width	Length	Width	Length	Width	Length	Width
(1) K.Sgr.27.49	8·0 mm	8·6 mm	9·6 mm	9·3 mm	—	—	—	—
(2) K.694·47	7·7 mm	8·6 mm	10·5 mm	10·0 mm	11·5 mm	11·5 mm	11·5 mm	11·0 mm
(3) K.547·47	6·6 mm	8·7 mm	9·7 mm	9·0 mm	10·5 mm	10·5 mm	10·0 mm	9·8 mm
(4) B.M.21389	—	—	10·7 mm	10·1 mm	—	—	—	—
(5) *Eotragus sansaniensis* (From Thenius 1952)	8·5 mm	10·0 mm	10·0 mm	13·0 mm	12·0 mm	14·0 mm	13·0 mm	14·0 mm

Lower Dentition

	M1		M2	
	Length	Width	Length	Width
(1) K.Sgr.48.47	11·0 mm	6·3 mm	12·0 mm	7·0 mm
(2) B.M.21358 (Holotype)	11·5 mm	6·6 mm	12·0 mm	7·2 mm
(3) B.M.21359	11·5 mm	6·4 mm	—	—
(4) B.M.21388	11·0 mm	6·0 mm	—	7·0 mm
(5) *Eotragus sansaniensis* (From Thenius 1952)	10·4 mm	7·0 mm	11·3 mm	8·2 mm

tend to be more selenodont in *Walangania* and *Eotragus* than in *Palaeomeryx*. The labial ribs and styles of the upper molars are far weaker in *Walangania* and *Eotragus* than in *Palaeomeryx*. In all these features *Walangania* and *Eotragus* agree and each differs from *Palaeomeryx*, the main feature in which *Palaeomeryx* and *Walangania* agree is the presence of a '*Palaeomeryx* fold' on the lower molars of both genera; such a fold is unknown in the bovids but occurs in most other primitive ruminants, its presence in *Walangania* is insufficient to debar this genus from affinity with the bovids.

Gentry (1970) has also suggested bovid affinities for *Walangania* on the basis of its mandibular ramus and he states:

'It also has a moderately deep ramus, so it is quite possible that it will one day be shown to be a bovid.'

The distinction between bovoids, giraffoids and cervoids is very difficult in species of Burdigalian age but the dentition of *Walangania* exhibits features which indicate affinity with early bovids and for this reason it is here treated as a bovid; however all the features used exhibit variation and the tentative nature of these interpretations must be emphasized.

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