FOSSIL GIRAFFES FROM THE MIOCENE OF AFRICA AND A REVISION OF THE PHYLOGENY OF THE GIRAFFOIDEA

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(*Communicated by E. I. White, F.R.S. – Received* 30 *July* 1976 –
Revised 7 *July* 1977)

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[Published 9 May 1978

Specimens of *Climacoceras africanus* are described from Maboko, Kenya. The new species *Climacoceras gentryi* is established on the basis of ossicones, mandibles, and upper and lower dentitions from Fort Ternan and Baringo, Kenya. By interpretation of its lower canines *Climacoceras* is identified as a giraffoid and is placed in the new family Climacoceridae. *Canthumeryx sirtensis* is identified from Muruarot and Rusinga, Kenya. A dentition and associated partial skeleton of this species are described. The teeth agree closely with specimens of the same species from Gebel Zelten, Libya. *Zarafa zelteni* from Gebel Zelten is synonymized with *Canthumeryx sirtensis*. Again on the basis of its lower canines *Canthumeryx* is identified as a giraffoid and is placed in the new family Canthumerycidae. Specimens of *Palaeotragus primaevus* are described from Baringo, Kenya. This material includes a cranium with the ossicones, skull roof, occipital and basicranial regions preserved. *Palaeotragus primaevus* specimens from Fort Ternan are used in this description and some of these are redescribed.

The relations of the giraffoids are assessed by methods of phylogenetic systematics. *Palaeomeryx*, *Prolibytherium* and *Propalaeoryx* are excluded from the Giraffoidea as their lower canines are not known. The Palaeotraginae is shown to be an invalid polyphyletic grouping and the genus *Palaeotragus* is also shown to be polyphyletic. *Palaeotragus microdon* is probably synonymous with *Palaeotragus rouenii* and the three species *Palaeotragus rouenii* (*P. microdon*), *Palaeotragus coelophrys* and *Palaeotragus quadricornis* are retained in the genus *Palaeotragus*. It is suggested that '*Palaeotragus*' *expectans* and '*Palaeotragus*' *decipiens* are closely related to *Samotherium*. *Palaeotragus primaevus* is probably synonymous with *Palaeotragus tungurensis* and this species is closely related to the giraffines. With slight changes the subfamilies Sivatheriinae and Giraffinae are valid monophyletic groups. *Hydaspitherium* is synonymized with *Bramatherium* and the Sivatheriinae includes the genera *Giraffokeryx*, *Birgerbohlinia*, *Bramatherium* and *Sivatherium* while the Giraffinae includes the genera *Honanotherium*, *Bohlinia* and *Giraffa* and the species '*Palaeotragus*' *tungurensis* (*P. primaevus*). *Okapia* is identified as the sister-group of the other giraffids. *Triceromeryx* is the sister-group of the Giraffidae. *Canthumeryx* is the sister-group of *Triceromeryx* plus the Giraffidae while *Climacoceras* is the sister-group of the other giraffoids.

Introduction

In 1974 I visited the Kenya National Museum, Nairobi, where I studied the collections of non-bovid ruminants. These included new specimens of *Climacoceras* from Maboko but more important was the dental and ossicone material from Fort Ternan previously noted by Gentry (1970, pp. 301–302). This included the first known mandibles of *Climacoceras* which are particularly important as the giraffoid affinities of this genus can now be established without doubt.

Canthumeryx was described (Hamilton 1973, p. 81) from the Lower Miocene of Gebel Zelten, Libya. In this description I suggested that the genus should be placed in the family Palaeomerycidae. On a recent (1973) visit to the University of California, Berkeley, I was allowed to study a mandible, upper teeth and a partial skeleton that belong with this genus. This allowed me to reassess the affinities of *Canthumeryx* and to reidentify with this genus several specimens in l'Institut de Paléontologie, Paris.

Descriptions of *Climacoceras* and *Canthumeryx* form §1 of this work. These two genera are members of the Giraffoidea but are not members of the Giraffidae. Giraffid material described in §2 was collected near Lake Baringo, Kenya. Most of these specimens are identified with *Palaeotragus primaevus* which also occurs at Fort Ternan, Kenya (Churcher 1970). This material includes a cranium and a complete adult mandible but otherwise the material is less well preserved and less complete than that from Fort Ternan.

Assessment of the relations of *Canthumeryx*, *Climacoceras* and *Palaeotragus primaevus* required analysis of the relations of the living and fossil giraffes from the rest of Africa, Europe and Asia and § 3 of this work is an attempt to assess the relations of the giraffoid genera by using a phylogenetic approach to the problem.

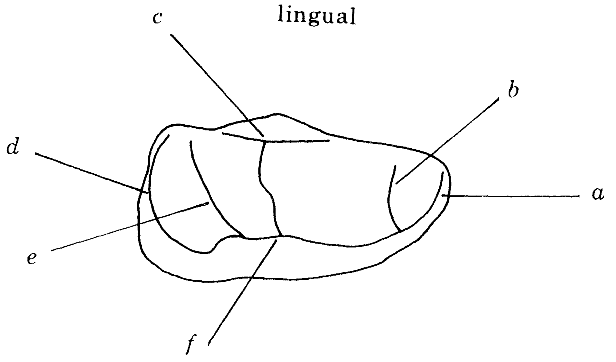

FIGURE 1. Cuspid nomenclature on the giraffoid right P_4. (*a*), (*b*) Anterior transverse crests. (*c*) Central lingual cuspid. (*d*), (*e*) Posterior transverse crests. (*f*) Central labial cuspid.

TERMINOLOGY

In descriptions of molar teeth I have used cusp names as in Hamilton (1973, p. 77). On the premolars I have avoided using cusp names, preferring names descriptive of the position on the tooth (figure 1). In descriptions of the lower canines the term 'accessory lobe' is used to describe the posterior swelling of the tooth.

Specimens in Museum collections have the following prefixes:

UCB	University of California, Berkeley.
BMM	Fossil Mammal Section, Department of Palaeontology, British Museum (Natural History).
BMO	Recent Mammal Section, Department of Zoology, British Museum (Natural History).
IPP	Institut de Paléontologie, Paris.
KNM	National Museum of Kenya, Nairobi.
UB	Department of Geology, University of Bristol.

Prefixes indicating east African localities:

FT	Fort Ternan
BN	Baringo
MB	Maboko
R	Rusinga Island
Mt, Mo	Muruarot

Field numbers are also used in the literature to refer to east African specimens. These are included in parentheses after registration numbers to allow cross reference.

1. FOSSIL GIRAFFOIDS FROM NORTH AND EAST AFRICA

A single feature of the lower canines is used to identify *Climacoceras* and *Canthumeryx* as giraffoids. Both genera have lower canines on which there is a small accessory lobe. *Okapia* and *Giraffa* have well-developed accessory lobes on their lower canines and the presence of a bifid lower canine is regarded as an apomorphic[†] feature of the group Giraffoidea (figure 3). Bifid lower canines are present in members of some other orders of mammals including the Insectivora, Primates and Chiroptera. In the Artiodactyla, however the lower canines have simple spatulate crowns in the tragulids, gelocids, cervids, bovids and antilocaprids and in the group Ruminantia the presence of a bifid lower canine may therefore be identified as apomorphic.

If the lower canine is not known, the relation of a species to the giraffoids may sometimes be established by using apomorphic features of the lower premolars (figures 4, 5 and 6). This cannot be done with species in which the lower premolars are close to the plesiomorphic pecoran pattern (p. 195) and for this reason I have excluded *Palaeomeryx*, *Propalaeoryx* and *Prolibytherium* from the Giraffoidea. In species with more apomorphic premolars such as *Triceromeryx pachecoi* and *Giraffa jumae* I have regarded the lower premolar pattern as sufficient to indicate relations with the giraffoids even though the lower canine is not known. The presence of ossicones cannot in itself be used to establish the giraffoid affinities of a genus as skin covered appendages were almost certainly present in the ancestors of the cervids and bovids (Coope 1968, pp. 215–217; Bubenik 1966, p. 29).

Description

Class **MAMMALIA**
Order ARTIODACTYLA
Superfamily GIRAFFOIDEA

Diagnosis. Artiodactyls with fully formed cannon-bones, frontal appendages present, upper incisors and canines absent, P_1 absent, lower canines bifid; stomach four chambered, ruminating and gall bladder absent in extant forms.

(*a*) *Climacoceras africanus*

Family CLIMACOCERIDAE New family

Diagnosis. Giraffoids having large ossicones carrying many tines.

Genus ***Climacoceras*** MacInnes 1936

Diagnosis. Climacocerids in which the premolar row is reduced in length relative to the molar row, cheek teeth hypsodont.

Species *Climacoceras africanus* MacInnes 1936

Diagnosis. Species of *Climacoceras* in which the ossicones carry many short irregularly spaced tines.

Remarks. MacInnes described this species from Maboko, which he called Kiboko, Kavirondo Gulf, Lake Victoria. His specimens consisted almost entirely of ossicone fragments although several cheek teeth were also (MacInnes 1936, p. 527) tentatively identified with *Climacoceras africanus*. MacInnes identified his species as a 'fossil deer' and in the introduction to his publication he states that the remains are: 'What appear to be the first examples of pre-Pleistocene fossil deer from the African continent'. Pilgrim (1941, p. 176) mentions the 'horns' of *Climacoceras* and compares them with those of *Procervulus* and *Lagomeryx*. A few lines later he compares them with those of 'one member of the true Giraffidae, *Giraffokeryx*' and mentions that

[†] The terms 'apomorphic' and 'plesiomorphic' are used here in the manner defined by Hennig (1966, p. 89).

in *Giraffokeryx* large rugose protuberances occur at the bases of the ossicones. According to Colbert (1933, p. 22) these could have been accessory knobs or branches.

Simpson (1945, pp. 155–156) following Pilgrim (1941) placed *Climacoceras* with *Lagomeryx* in the family Lagomerycidae of the Giraffoidea. *Climacoceras* was next mentioned by Whitworth (1958, p. 47) who identified bovid teeth of 'prismatic habit' from Maboko and went on to mention the presence of strangely shaped antlers of *Climacoceras*. These teeth and 'antlers' are presumably the same specimens described by MacInnes.

Holotype. BMM 15301. An almost complete left ossicone with the tine bases preserved but all the tines broken off. Figured MacInnes 1936, p. 522 fig. 1*c* and here figure 19, plate 1.

Locality. Maboko, Kavirondo Gulf, Lake Victoria, Kenya.

Material

BMM 15301. Holotype.
BMM 15302. Ossicone fragment figured MacInnes, p. 523, fig. 2*c*.
BMM 15303. Ossicone fragment figured MacInnes, p. 522, fig. 1*a*.
BMM 15304. Ossicone fragment figured MacInnes, p. 522, fig. 1*b*.
BMM 15305. Ossicone fragment figured MacInnes, p. 523, fig. 2*a*.
BMM 15306. Ossicone fragment figured MacInnes, p. 523, fig. 2*b*.
BMM 15307. Ossicone fragment figured MacInnes, p. 523, fig. 2*d*.
BMM 15308. Ossicone fragment figured MacInnes, p. 524, fig. 3*a*.
BMM 15309. Ossicone fragment figured MacInnes, p. 524, fig. 3*b*.
BMM 15310. Ossicone fragment with large piece of skull roof.
BMM 15311. Right lower molar figured MacInnes, p. 527, fig. 5*a*, *b* (figure 11, plate 1).
BMM 15312. Left lower molar figured MacInnes, p. 527, fig. 5*c*, *d* (figure 12, plate 1).
BMM 15313. Left M_3 figured MacInnes, p. 527, fig. 5*e*, *f* (figure 13, plate 1).
BMM 15314. 2 left upper molars (figures 16 and 17, plate 1).

BMM 15315: ossicone fragment. BMM 15316: thin transverse section of ossicone. BMM 30001–30120: ossicone beam and tine fragments plus attached fragments of cranium and orbits. KNM.MB.544: left P^3 (=229:49). KNM.MB.547: right lower molar (=212:49). KNM.MB.550: left P^4 (=K.B.A.). KNM.MB.487: right P^3 (=53:73). KNM.MB.554: right M^2 (=KB.1934.H). KNM.MB.545: left P^4 (=MB.239:49). KNM.MB.552: right P^{3-4} (=K.B.A.) (figures 15 and 18, plate 1). KNM.MB.490: left M_3 (=236:73). KNM.MB.549: right M_3 (=MB–). BMM 21367: left P_4 (=Kb.781.52) (figure 14, plate 1).

Description. The key points of MacInnes' description of the ossicones of *Climacoceras africanus* are: the ossicones do not show grooving of the beam; the cross section of the beam is variable but there is distinct lateral compression at the base, producing an irregular oval section; the circumference at the base varies from 70–92 mm. and the beam tapers gradually; the tines are very irregular in size and position, but all are relatively short and project almost at right angles from the beam; tines project forwards or backwards but not laterally; the beam is nearly straight and apparently ends in a distal bifurcation. The internal structure of the ossicones was described by MacInnes from longitudinal sections (BMM 30002) and cross sections (BMM 15316–7) which demonstrate that the bone structure is continuous from the frontal bone to the ossicone tip. The main objective of studying these sections was to demonstrate the differences between the ossicones and the antler structure of cervids.

Lower dentition. Lower molars described by MacInnes (1936, pp. 525–527) and new material from Maboko form the basis of this description.

The molars are high crowned and narrow and the enamel carries fine striations but is much less rugose than the enamel of *Palaeotragus primaevus*. The metaconid is narrow with well developed anterior and posterior crests and a rounded lingual swelling but no true lingual metaconid rib. The metastylid is very weak, being represented as a very small swelling of the back metaconid crest in BMM 15313 and BMM 15311 but in the more worn BMM 15312 this stylid is completely worn away. The entoconid is narrow with a long anterior crest that closes the lingual end of the median valley. The posterior entoconid crest is more strongly developed than in *Canthumeryx* (figure 25, plate 3) but on the M_2 it does not extend to the back of the tooth and as a result the back end of the posterior fossettid opens lingually. This feature was used by Gentry (1970, p. 301) to distinguish Fort Ternan specimens from bovid lower molars and it is clearly shown here in the Maboko specimens (figure 12).

The labial cuspids are crescentic and the anterior lobe is displaced lingually relative to the posterior one. The accessory column of the M_3 is simple (BMM 15313) and is not developed as a crescent. Whitworth (1958, p. 26) describes a P_4 (BMM 21367 = Kb.781:52) that he identifies as an 'indeterminate bovid'. This specimen agrees almost exactly with the P_4 of the Fort Ternan *Climacoceras* mandible (KNM.FT.2946) and is therefore identified with this genus. The specimen is almost unworn and its crest pattern consists of a labial antero-posterior crest with its highest point at the centre. Paired anterior transverse crests and paired posterior transverse crests are present. There is also a central transverse crest which is slightly swollen at its lingual end but lacks an independent lingual point (figure 14).

Upper dentition. An upper molar of *Climacoceras africanus* (BMM 15314a = Kb.783:52) is figured by Whitworth (1958, p. 25, fig. 10*d*, *e*) who cites a second similar molar (BMM 15314b = Kb.784:52). A single heavily worn upper molar (KNM.MB.554) in the Kenya National Museum completes the list of upper molars known. The upper molars are high crowned and the parastyle, paracone rib and mesostyle are strong (figure 16). The labial face of the metacone is smooth with no sign of a labial rib. The paracone and metaconule are crescentic and there is slight complication of the enamel in the median valley. An entostyle is not present.

Upper premolars of *Climacoceras africanus* from Maboko include KNM.MB.552 which is a right P^{3-4} showing medium wear. The P^4 is wide and short with a strong rib and styles on its labial face. The lingual crescent is fully developed but an accessory crest is not present in the fossette in any of the three upper fourth premolars known. The P^3 is short with a well developed lingual crescent and strong labial rib and styles (figure 18).

(*b*) *Climacoceras gentryi*

Species *Climacoceras gentryi* New species

Diagnosis. Ossicones with a slender beam bearing long tines.

Remarks. Gentry (1970, p. 301) first suggested that the Fort Ternan material might belong to a species of *Climacoceras* distinct from *Climacoceras africanus*. Features of the ossicones suggest that he was correct in this assessment.

Holotype. Left mandible – KNM.FT.2946 with I_3, C_1, P_2–M_3 (figures 20 and 22, plate 2).

Locality. Fort Ternan, Kenya.

Material. KNM.FT.2946: holotype. KNM.FT.3146: complete left ossicone (=64.463.4) (figure 21, plate 2). KNM.FT.3355: fragment of ossicone base (=62.2343.4). KNM.FT.2950: Right mandible fragment with P_2–M_3. KNM.FT.2941: Left mandible fragment with P_2–M_3. KNM.FT.2949: left mandible fragment with heavily worn P_3–M_3. KNM.FT.2944:

right mandible fragment with P_3–M_3. KNM.FT.2951: left M_{1-2}. KNM.FT.2947: D_{3-4}. KNM.FT.2940: D_{3-4}. KNM.FT.3222: D_{3-4}. KNM.FT.2943: M_1, D_{2-4}. KNM.FT.2954: M_1, D_{3-4}. KNM.FT.2942: M_1, D_{3-4}. KNM.FT.2945: M_1, D_{3-4}. KNM.FT.3238: D_4. KNM.FT.3193: M_1. KNM.FT.3221: P^2. KNM.FT.2953: P^{3-4} (figures 23, 24, plate 2). KNM.FT.2952: M^{1-2}. KNM.FT.3288: upper molar. KNM.FT.3156: atlas. KNM.FT. 3078: cervical vertebra. KNM.FT.3164: proximal head of humerus. KNM.FT.3163: proximal head of humerus. KNM.FT.3160: distal head of humerus. KNM.FT.3153: proximal part of radius. KNM.FT.3147: distal part of radius. KNM.FT.3141: lunar. KNM.FT.3150: magnum. KNM.FT.3155, 3158, 3159, 3161: anterior cannon bones (Mc.III.IV). KNM.FT. 3157: femur. KNM.FT.3096: distal end of femur. KNM.FT.3154: astragalus. KNM.BN. 927: ossicone fragment. KNM.BN.932: tip of ossicone tine. KNM.BN.254: two ossicone fragments. KNM.BN.929: ossicone fragment. KNM.BN.930: ossicone fragment. KNM.BN. 673: M^2. KNM.BN.1248: P^3. KNM.BN.934: P^3. KNM.BN.476: axis. KNM.BN.633: olecranon process. KNM.BN.716: tibia. KNM.BN.261, 719: 2 astragali. KNM.BN.852: calcaneum. KNM.BN.1201: metatarsal fragment.

Ossicones. One of the strangest specimens in the Fort Ternan collections is an almost complete ossicone that is identified with *Climacoceras* (KNM.FT.3146). The surface of this specimen was weathered before fossilization and carries heavy ridging similar to that found on the ossicone of *Samotherium africanum* (Churcher 1970, p. 74) and on many other specimens from Fort Ternan (Walker, personal communication). The original ossicone surface is, however, preserved between the first and second tines, and this shows fine ridging with grooves running along the length of the beam. The region of the skull roof medial to the ossicone shows that it was flattened and that the ossicones were in the extreme lateral position as in *Palaeotragus rouenii* (Gaudry 1867, pl. 45), *Canthumeryx* (p. 209), *Palaeotragus primaevus* (p. 186 and figures 38–40, plate 5) and *Samotherium sinense* (Bohlin 1926, pl. 6, fig. 3). The beam runs almost vertically at first having slight posterior and lateral slopes. The relative sizes and arrangement of tines are shown in figure 21. Ossicone fragments in the Baringo collections suggest the presence of this species in the Baringo fauna. The best of these specimens (KNM.BN.927) is a fragment of a right beam with the bases of two tines. It agrees closely with the upper part of the beam of KNM.FT.3146.

Mandible. The complete mandible KNM.FT.2946 (figure 22) has a shallow horizontal ramus with a long diastema (table 1). The ramus is swollen below the cheek teeth and agrees in shape and overall size with preserved parts of *Prolibytherium* mandibles (BMM 21899, 26680), however in this genus the diastema is much shorter.

Lower dentition. The lower molars (figure 20) agree closely with those of *Climacoceras africanus.* They may be distinguished from the lower molars of *Palaeotragus primaevus*, *Canthumeryx* and *Propalaeoryx* on the basis of the following features. The molars are narrow and high and the metaconid and entoconid have their axes parallel to that of the tooth whereas in the three forms named the cuspids have a diagonal orientation. The enamel of the molars is less rugose in *Climacoceras* than in the other three forms. The accessory column is simple, differing from the complex pattern found in *Canthumeryx* and *Palaeotragus* in which a full crescent and fossettid are present. An isolated and almost unworn M_3 of *Prolibytherium* (BMM 26681) from Gebel Zeltén, Libya (Hamilton 1973, pl. 10, fig. 3) agrees in general features with the M_3 of *Climacoceras africanus* and *Climacoceras gentryi*. This tooth is high crowned but less so than in KNM.FT. 2946. Its cuspids are strongly compressed transversely and its accessory column is simple. The only real similarity between these molars is therefore the greater height of these teeth relative to those of most other giraffids. With increasing height the greater transverse compression of the cuspids occurs while the simple accessory column is a plesiomorphic feature.

The P_4 has a high central point with an anterior crest that slopes downwards anteriorly and flexes lingually at the front of the tooth forking in this region to produce two transverse crests. The posterior region consists of two transverse crests that join at their labial ends and meet a posterior crest from the central labial cuspid. A central lingual crest is also produced from the central labial cuspid. This crest is slightly swollen at its lingual end but, as in *Climacoceras africanus* there is no indication of an independent central lingual cuspid. This P_4 pattern is found in the cervids, bovids, antilocaprids and many giraffes. It is apomorphic for the ruminants as a group but is plesiomorphic for the giraffoids. The development of the lingual end of the central transverse crest is far weaker than in any other giraffoid and any greater development of the lingual end of this crest can be regarded as an apomorphic character in the transformation series of the P_4 (p. 207). In *Canthumeryx*, *Palaeotragus primaevus*, *Giraffokeryx* and all advanced giraffids there is a clearly defined, vertical notch on the labial face of the P_4 near the back of the tooth. This notch is not found in *Climacoceras* and its development is the first stage in the separation of the posterior and central regions of the P_4 (p. 205).

TABLE 1. *CLIMACOCERAS*; LOWER DENTITION

Dimensions in all tables are in millimetres.

	I *W*	C *W*	*W* ant. lobe	*W* post. lobe	P_2		P_3		P_4		M_1		M_2		M_3	
					L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
C. gentryi																
KNM.FT.2946	5	5	4	1	8.5	4.5	11.5	6.25	12	6.75	14.8	8	18	9	24	9.25
KNM.FT.2941	—	—	—	—	9	5	12	7.25	13	8	15	8	19	9.5	25	10
KNM.FT.2949	—	—	—	—	—	—	11	7.5	12	7.5	16	9	18	10	26.5	10
KNM.FT.2944	—	—	—	—	—	—	10.5	7	13.8	8	15.5	9	18.5	10.5	26.5	10.5
KNM.FT.2951	—	—	—	—	—	—	—	—	—	—	15	9	17.5	10	—	—
KNM.FT.2943	—	—	—	—	—	—	—	—	—	—	16	8.5	—	—	—	—
KNM.FT.2954	—	—	—	—	—	—	—	—	—	—	15	9	—	—	—	—
KNM.FT.2942	—	—	—	—	—	—	—	—	—	—	16	8.5	—	—	—	—
KNM.FT.2945	—	—	—	—	—	—	—	—	—	—	16.5	—	—	—	—	—
KNM.FT.2950	—	—	—	—	8.5	5	10.5	7	12.5	7	15	9	19	10.5	24	10.5
KNM.FT.3193	—	—	—	—	—	—	—	—	—	—	16	8	—	—	—	—
C. africanus																
BM.M.15311	—	—	—	—	—	—	—	—	—	—	—	—	17	10.5	—	—
BM.M.15312	—	—	—	—	—	—	—	—	—	—	—	—	16.8	10	—	—
BM.M.15313	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	10
BM.M.21367	—	—	—	—	—	—	—	—	12.5	7.3	—	—	—	—	—	—
KNM.MB.547	—	—	—	—	—	—	—	—	14	8.5	—	—	—	—	—	—
KNM.MB.490	—	—	—	—	—	—	—	—	—	—	—	—	—	10	—	—
KNM.MB.549	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24	10.5

	C_1–M_3	C_1–P_2	P_2–P_4	P_2–M_3	M_1–M_3
KNM.FT.2946	150	64	32	86	55
KNM.FT.2941	—	—	34	94	61
KNM.FT.2949	—	—	*ca.* 34	*ca.* 95	62
KNM.FT.2944	—	—	*ca.* 36	*ca.* 96	62
KNM.FT.2950	160	64	35	96	61
Palaeotragus primaevus	200	89	54	133	80
Prolibytherium magnieri	*ca.* 140	*ca.* 53	34	89	55
Canthumeryx sirtensis	192	71	53	121	68

The P_3 has the same basic pattern as the P_4 but it is narrower and the transverse crests and valleys are therefore shorter. The P_2 has a high central cuspid. Its anterior crest flexes lingually at its anterior end but does not fork. The central cuspid carries a weak lingual crest while the posterior region of the tooth is similar to that of the P_3 and P_4.

The I_3 and canine have been glued back into mandible KNM.FT.2946 and they are more vertical than is natural. The roots slope antero-dorsally which suggests that the canine sloped at about the same angle as in other giraffoids. The canine is bilobed with a well developed anterior region and a small accessory lobe (figure 3). This agrees with the canine in *Canthumeryx* (p. 179) but contrasts with the canine of *Palaeotragus primaevus*, *Giraffa*, *Okapia* (Lankester 1910 pl. 11) or *Samotherium* (BMM 4215) in which the accessory lobe is much larger.

The I_3 is spatulate with a convex anterior face that carries a weak vertical groove.

TABLE 2. *CLIMACOCERAS*; DECIDUOUS LOWER DENTITION

	D_2		D_3		D_4		
	L	*W*	*L*	*W*	*L*	*W* anterior lobe	*W* posterior lobe
KNM.FT.2947	—	—	11	5.3	17.5	5.5	—
KNM.FT.2940	—	—	11	5	16.5	5.8	8
KNM.FT.3222	—	—	10	4.5	15.5	5	7
KNM.FT.2943	8.5	3.5	10.5	5	17	5.3	7
KNM.FT.2942	—	—	10.5	5	16	5.3	8
KNM.FT.2954	—	—	10	5	16	5.3	7.8
KNM.FT.2945	—	—	10.5	5.5	17	—	8
P. primaevus	10.5–13	4.5–6	15.5–17.5	7.8	20–25	—	10–12
Canthumeryx	—	—	16.3	5.7	22–23	—	11

Deciduous lower dentition. The D_4 is smaller than that of *Palaeotragus primaevus* but agrees with it in general cuspid pattern. The D_4 is more compressed transversely in *Climacoceras gentryi* and differs in details of the central labial cuspid. The front wing of this cuspid meets the back of the antero-labial crescent but does not extend lingually to meet the front of the lingual crescent. As a result the central fossettid is not usually (number = 6) closed by this cuspid, whereas in *Palaeotragus primaevus* the fossettid is closed by a lingual extension of the central cuspid in this region (number = 8). With these exceptions, the crown patterns of the D_4 are closely similar in *Climacoceras gentryi* and *Palaeotragus primaevus*.

The D_3 and P_3 have very similar patterns in *Climacoceras gentryi* and the crown pattern also agrees with the D_3 of *Palaeotragus primaevus*. Similarly the D_2 and P_2 crown patterns are very much like each other in *Climacoceras gentryi* and again this pattern agrees with that of the D_2 in *Palaeotragus primaevus*.

Upper dentition. Isolated upper molars of ruminants are more difficult to identify than lowers. This problem is important here. The molars are easily distinguished from those of *Palaeotragus primaevus* on the basis of size and crown height but confusion with *Oioceros* and *Protragocerus* is possible. As a result I have only identified two specimens with the upper dentition of *Climacoceras*. The upper molars agree closely with those of *Climacoceras africanus* and differ from the Fort Ternan bovids in details of their labial faces. The crown patterns and labial faces of the P^3 and P^4 are shown in figures 23 and 24 and further description is not necessary. These two premolars are relatively larger than those of the Fort Ternan bovids and again their labial faces carry stronger ribs and styles. The P^3 and P^4 agree in general shape with corresponding teeth of *Palaeotragus primaevus* but the P^2 (KNM.FT.3221) is relatively shorter than in *P. primaevus* but agrees in shape with the P^2 of *Prolibytherium* (Hamilton 1973, pl. 9).

Three upper cheek teeth from Baringo are identified with *Climacoceras gentryi*. KNM.BN.673 is an M^2 that is less heavily worn than FT.2952 but is the same size and shows similar cusp pattern. Two upper third premolars (KNM.BN.1248 and 934) are also identified with this species and agree closely with KNM.FT.2953.

TABLE 3. *CLIMACOCERAS*; UPPER DENTITION

	P^2		P^3		P^4		M^1		M^2		M^3	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
C. gentryi												
KNM.FT.3221	13	8	—	—	—	—	—	—	—	—	—	—
KNM.FT.2953	—	—	13	10	11	12	—	—	—	—	—	—
KNM.FT.2952	—	—	—	—	—	—	15	15	15.5	17.5	—	—
KNM.BN.673	—	—	—	—	—	—	—	—	18.3	18.6	—	—
KNM.BN.1248	—	—	11.5	10	—	—	—	—	—	—	—	—
KNM.BN.934	—	—	11.4	10.3	—	—	—	—	—	—	—	—
C. africanus												
BMM 15314*a*	—	—	—	—	—	—	—	—	16	17	—	—
BMM 15314*b*	—	—	—	—	—	—	—	—	16.5	17	—	—
KNM.MB.554	—	—	—	—	—	—	—	—	15.5	17.3	—	—
KNM.MB.552	—	—	9.8	9	9.5	11.5	—	—	—	—	—	—
KNM.MB.545	—	—	—	—	10	11.3	—	—	—	—	—	—
KNM.MB.550	—	—	—	—	10	11.3	—	—	—	—	—	—
KNM.MB.544	—	—	9.8	8.3	—	—	—	—	—	—	—	—
KNM.MB.483	—	—	10	8.8	—	—	—	—	—	—	—	—

Post cranial. Post cranial material is identified with *Climacoceras gentryi* on a size basis. This species is intermediate in size between the Fort Ternan bovids described by Gentry (1970) and the giraffids described by Churcher (1970).

Atlas. KNM.FT.3156 is much smaller than the atlases of *Palaeotragus primaevus* from Fort Ternan (KNM.FT.3077 = 61:733). This vertebra is similar to other ruminant atlases but it is relatively more elongate than that of *P. primaevus* and its ventral tubercle is more posterior.

TABLE 4. *CLIMACOCERAS*; ATLAS

	Cl. gentryi KNM.FT.3156	*P. primaevus* KNM.FT.3077	*S. africanum* KNM.FT.3124	*Can. sirtensis* UCB.V.4899/42058
anterior transverse width	72	101	112	58
posterior transverse width	73.3	108.5	118.5	*ca.* 60
maximum length	75.5	85	100	*ca.* 60
transverse width above condylar facets	59.5	78	92.5	
depth of condylar facets	22	41	34.5	23
length in mid-ventral line	34.5	42	48	35

Axis. An axis from Baringo (KNM.BN.676) is smaller than that of *Palaeotragus primaevus* (KNM.FT.3079) but is larger and more elongate than the bovid axis KNM.FT.1624 that is described by Gentry (1970) and identified with a large bovid. KNM.BN.676 agrees in size with atlas KNM.FT.3156 and probably belongs with *Climacoceras gentryi*.

Humerus. KNM.FT.3160 (= 62:2646:4) is the distal end of a right humerus that has a very high medial tuberosity and is generally similar to the humerus of *Palaeotragus primaevus* but is much smaller (table 6). This specimen is larger than the distal humerus region of *Pseudotragus potwaricus* and the lateral facet is relatively wider. Also the medial facet does not extend up the face of the shaft in KNM.FT.3160 whereas according to Gentry's (1970, p. 281, fig. 15) description the medial facet extends further in the Fort Ternan bovids.

TABLE 5. *CLIMACOCERAS*; AXIS

	KNM.BN.676	*P. primaevus* KNM.FT.3079	bovid KNM.FT.1624
length	73	92	57
width of anterior facets	52	69	41
anterior depth of centrum	*ca.* 14	22	17.5
posterior depth of centrum	*ca.* 22	40.5	20
posterior width of centrum	—	*ca.* 78	37
height of posterior end of neural spine	75	—	69

TABLE 6. *CLIMACOCERAS*; HUMERUS

	C. gentryi KNM.FT.3160	KNM.FT.3164	KNM.FT.3163	*P. primaevus* KNM.FT.3082	KNM.FT.3083
proximal articular facet					
antero-posterior diameter	—	50	—	—	—
transverse diameter	—	31	35	—	—
distal articulation					
width	55	—	—	69.5	69
antero-posterior diameter					
medial region	54.5	—	—	75.5	—
in trochlea	25	—	—	32.5	33.5
lateral region	35.5	—	—	54.5	53
maximum width of lateral facet	17	—	—	22	22
maximum width of medial facet	36.5	—	—	45	43

Radius. The juvenile left radius (KNM.FT.3153 = 61:753) has a long slender shaft. Its proximal epiphysis is preserved and indicates that the lateral articulation is relatively wide. The whole facet region is narrower than the corresponding facets of the humerus (KNM.FT. 2646) but is in the same size range and allowing for further growth of the radius it is reasonable to identify these specimens with the same species. The distal end of a left radius (KNM.FT. 3147 = 59:34) is narrower and smaller than the corresponding region of *Palaeotragus primaevus* (table 7) and is therefore identified with *Climacoceras gentryi*. The carpal facets agree with carpals described below.

TABLE 7. *CLIMACOCERAS*; RADIUS

	KNM.FT.3153 (juvenile)	KNM.FT.3147	*P. primaevus* KNM.FT.3084
proximal end			
width	46	—	73
depth	29	–	45
maximum width of shaft	27	—	45
maximum depth of shaft	17	—	27
distal end			
maximum width	—	54.5	65
maximum depth	—	34.5	47
length preserved	252	109	486
estimated length	—	336	486

Ulna. An olecranon process of a right ulna (KNM.BN.633) is similar in size to the distal facet of the humerus (KNM.FT.3160) with which it would articulate.

Lunar. Left lunar KNM.FT.3141 (=62:2151) agrees in proximal facet length (anterior-posterior) and shape with the corresponding facet of KNM.3147 and in distal facet form with magnum KNM.FT.3150.

Magnum. A left magnum KNM.FT.3150 (=61:722) agrees in distal facet size and concavo-convexity with metacarpal III.IV KNM.FT.3155 and it is probable that they belong to *Climacoceras gentryi.*

TABLE 8. *CLIMACOCERAS*; ULNA

	KNM.BN.633	*P. primaevus* KNM.FT.3084
width of proximal facet	16.5	21.5
minimum width of facet near radius	30.5	38
depth of olecranon at facet	48	69
width of olecranon at facet	13	20
length of olecranon	61	—
depth of olecranon at epiphysis	35	—

TABLE 9. *CLIMACOCERAS*; LUNAR

	KNM.FT.3141
length	31
anterior height	23
anterior width	19.5
posterior height	25.5
posterior width	15.5

TABLE 10. *CLIMACOCERAS*; MAGNUM

		P. primaevus	
	KNM.FT.3150	KNM.FT.3087	KNM.BN.1178
length	28.5	35	35
maximum anterior width	27.3	30.75	27.5
maximum posterior width	21.5	27	25
width scaphoid facet	15.5	20.8	18.5
width lunar facet	6.5	6.5	7
anterior depth scaphoid facet	10.5	14	12.5
posterior depth scaphoid facet	12.5	15	14
anterior depth lunar facet	12.5	15	—
posterior depth lunar facet	16.5	19.5	19.5

Metacarpal III.IV. The metacarpal III.IV. (KNM.FT.3155) has a pronounced antero-proximal tuberosity as in *Palaeotragus primaevus* and a groove runs distally from the junction of the magnum and unciform facets. This is the line of fusion of metacarpal III and metacarpal IV referred to by Churcher (1970, p. 53). The shaft narrows quickly from the distal articulation before becoming parallel sided. It is slender and deeper antero-posteriorly than it is wide. There is a deep posterior channel. There is no sign of metacarpal II on KNM.FT.3155 and this region is broken in the other specimens. The four specimens suggest that the cannon-bone was relatively long and slender in *Climacoceras gentryi.*

Femur. A left femur KNM.FT.3096 (=64:465) is identified with *Palaeotragus primaevus* by Churcher (1970, p. 58) but is too small for this species and would not articulate with the tibia of *P. primaevus* (KNM.FT.3100A). This tibia is large, very elongate and is almost definitely correctly grouped with the other *P. primaevus* post-cranial elements. Therefore KNM.FT.3096 probably does not belong with *P. primaevus* and is identified with *Climacoceras gentryi*. Churcher's description can still be applied. Femur shaft KNM.FT.3157 (=61:1102) belongs to a ruminant that was about the same size as KNM.FT.3096 and is also identified with *Climacoceras gentryi*. It is here used to estimate the length of the *Climacoceras* femur.

TABLE 11. *CLIMACOCERAS*; FEMUR

	KNM.FT.3157	KNM.FT.3096	*P. primaevus* KNM.FT.3094
length preserved	235	—	—
estimated length	280–300	—	—
minimum width of shaft	22.5	—	30
minimum depth of shaft	23.3	—	39
width of distal end	—	61	—
depth of medial trochlear ridge	—	85	—
depth of lateral trochlear ridge	—	68.5	—

TABLE 12. *CLIMACOCERAS*; TIBIA

	KNM.BN.716	KNM.FT.3100
width proximal end	*ca.* 70	90.5
depth including cnemial crest	57	*ca.* 75

TABLE 13. *CLIMACOCERAS*; ASTRAGALUS

	KNM.BN.719	KNM.FT.3154	KNM.BN.261	KNM.FT.3103	KNM.F
medial side	51	45.5	45	57	51
central depression	42	40	48.5	48.5	45
length of lateral side	52.5	51.5	47.5	60.5	57.5
medial depth	31	28	29	36	33
lateral depth	29.5	28	28	34.5	31.5
proximal width	32	30	30.5	40	35
distal width	30.5	30	30	41	36

TABLE 14. *CLIMACOCERAS*; CANNON-BONE (Mt. III.IV.)

	KNM.FT.3161	KNM.FT.3155	KNM.FT.3158	*P. primaevus* KNM.FT.3088
width of proximal facet	41	37.5	41	53
depth of proximal facet	28	28	28	38
minimum depth of shaft	25	23	—	30
minimum width of shaft	25	21	—	29
length preserved	155	152	96	400

Tibia. The proximal part of a right tibia (KNM.BN.716) is identified with *Climacoceras gentryi*. The head is badly eroded but its maximum width is approximately 65–70 mm, thus agreeing with the femur and other skeletal elements.

Calcaneum. A left calcaneum KNM.BN.852 is complete and agrees in general shape with the calcaneum of *Palaeotragus primaevus* (KNM.FT.3105) but is smaller.

Astragalus. KNM.FT.3154 (=61:754) is a left astragalus that is smaller and more elongate than that of *P. primaevus*. It lacks the large postero-ventral flange figured in KNM.FT.3103 (=1074c:61) by Churcher (1970, p. 63, figs 57–60) but this flange is even absent on KNM.FT.3104 which otherwise agrees in size and proportions with KNM.FT.3103 and probably also belongs with *P. primaevus.* Two other astragali (KNM.BN.261, 719) agree in size with KNM.FT.3154 and are therefore identified with *Climacoceras gentryi.*

Metatarsals III.IV. KNM.BN.1201 consists of the distal articulation and the distal 8 cm of the shaft of a metatarsal III.IV. It is much smaller than that of *Palaeotragus primaevus* but otherwise agrees with this bone in all main features. KNM.FT.3159 is the shaft of a metatarsal III.IV. which is very slender and agrees in cross section and size with KNM.BN.1201.

(*c*) *Canthumeryx sirtensis*

Family CANTHUMERYCIDAE New family

Diagnosis. Giraffoids with small accessory lobes on the lower canines; with a central lingual cuspid developed on the P_4 but not separated from the central labial cuspid; and with the posterior region of the P_4 incompletely separated from the rest of the tooth.

Genus ***Canthumeryx*** Hamilton 1973

Diagnosis. Canthumerycid in which the skull has a wide roof with ossicones in the extreme supra-orbital position.

Species *Canthumeryx sirtensis* Hamilton 1973

Diagnosis. As for genus.

Remarks. This species was established (Hamilton 1973, p. 81) on the basis of two juvenile mandibles from Gebel Zelten, Libya. In the same publication I described a skull and two upper cheek dentitions under the generic name *Zarafa.* Lower cheek teeth from Muruarot agree closely with those of *Canthumeryx* and are therefore identified with the same species. Upper cheek teeth, however, agree with those previously described as *Zarafa.* The two genera are therefore synonymized with *Canthumeryx* having precedence. Lower molars previously identified with *Zarafa* may therefore represent variants of the *Canthumeryx* lower molars. Post-cranial material from Muruarot described by Arambourg (1933, p. 22) is also identified with *Canthumeryx sirtensis.*

Holotype. BMM 26682. A right mandibular fragment with D_3–M_3; plus P_2 and P_4 dissected out. (Hamilton 1973, pl. 1, fig. 4).

Locality. Gebel Zelten, Libya; Muruarot and Rusinga Island, Kenya. Lower Miocene.

Material. BMM 26682: holotype. BMM 26683: right mandible with D_4 and M_1 plus P_{3-4} dissected out (Hamilton 1973, pl. 1, figs 2, 3 and 5). BMM 20111: isolated right M_3. BMM 26670: adult skull – holotype of *Zarafa zelteni* – (Hamilton 1973, pls 2, 3 and 4). BMM 26671: right P^4–M^3 (Hamilton 1973, pl. 6). BMM 26672: left D^{2-4}, M^{1-2} (Hamilton 1973, pl. 5, fig. 1). BMM 26673: cranial fragment. BMM 26674: cranial fragment. BMM 26675: right M_3 (Hamilton 1973, pl. 4, fig. 3; pl. 5, fig. 4). BMM 26676: right M_3 (Hamilton 1973, pl. 5, fig. 5). BMM 26677: right M_2 (Hamilton 1973, pl. 5, figs 2 and 3). UCB.V.4899/42058: partial skeleton consisting of: right mandible with P_2–M_3 (figure 25), symphysis with right DC_1 and C_1, left C_1 and roots of left and right I_{1-3} (figure 30, plate 3), left P^{2-3} (figure 29, plate 3), right M^3 (figure 27, plate 3), atlas, scapula fragments, olecranon of ulna, proximal and distal ends of radius, metacarpal fragments, phalanges, right limb with pelvis, femur, tibia, patella, calcaneum, astragalus, fragments of cubonavicular, metatarsal fragments, phalanges (figures 34 and 36, plate 4). UCB.V.4898/41873: left P^{3-4} (figure 28, plate 3). UCB.V.4898/41981: left P^4, M^1 (figure 26, plate 3). UCB.V.4898/41878: right P_3. UCB.V.4898/42020: cervical vertebra. UCB.V.4898/41914: cervical vertebra 6. UCB.V.48100/41854: ankle unit with: distal end of tibia, astragalus, calcaneum, cubonavicular. UCB.V.4898/40423: proximal end of metatarsal. KNM.MO.41A: proximal end of metatarsal. KNM.MO.41B: distal end of metatarsal. KNM.Mt.253: upper molar. IPP 1933–9: radio-ulna lacking distal epiphysis, left femur, tibia, ankle unit, metatarsals and phalanges (figures 33, 35 and 37, plate 4).

Description. The skull was described in detail in Hamilton (1973) and is therefore not redescribed here. Dental and skeletal elements (UCB.V.4899/42058) were found in association and there is little doubt that they belong to the same individual. This skeleton from Muruarot is important as it represents an almost adult individual of a medium-sized ruminant and is so far the only known example of associated dental and post-cranial elements of a medium-sized ruminant known from the African Lower Miocene.

Lower dentition. The right lower dentition of UCB.V.4899/42058 is almost complete from the P_2 to M_3. Part of the M_1 is missing and a fragment of bone in front of the P_2 is lost, but most of the diastema, the canines and the roots of the incisors are preserved. The premolars were only partly erupted but have been completely exposed for study. The lower permanent canine is preserved on the left and right sides of UCB.V.4899/42058. The canine has a serrated dorsal edge and carries a small accessory lobe (figure 30). This accessory lobe is much smaller than in advanced giraffids (figure 3) such as *Palaeotragus* but it agrees in size with that of *Climacoceras*. The M_2 and M_3 are almost complete (figure 25). The M_2 shows medium wear while the back of the M_3 is almost unworn. The M_2 and M_3 agree very closely with *Canthumeryx sirtensis* from Libya (Hamilton 1973, pl. 1, fig. 4). The lower premolars were dissected out of the mandible. They are unworn but the P_4 has lost the tip of the central labial cuspid and the front of the P_2 is missing. The P_4 has the usual crest pattern found in early pecorans, however, it shows two important features that are used to assess relations of *Canthumeryx*. The central labial cuspid carries a lingual wing which is expanded at its lingual end to form a semi-independent central lingual cuspid. The transverse crest joining the two central cuspids is depressed in its medial part. The back of the tooth carries two transverse crests. The antero-posterior crest that joins the central labial cuspid to the back of the tooth is depressed at its junction with the posterior transverse crests and in this region the labial face of the P_4 carries a very deep vertical groove. This condition represents the initial stage in the separation of the posterior part of the tooth from its central and anterior part. The P_3 has the usual pecoran crest pattern (figure 4). Its central labial cuspid carries a strong lingual crest but there is no expansion of the lingual end on the P_3. The Libyan specimen does show slight expansion of this region but the difference is inside the range of individual variation. The posterior crest of the central labial cuspid meets the back part of the tooth in a slight depression and in this region there is a shallow vertical groove on the labial face of the tooth. The front of the P_2 is missing but preserved parts of the tooth agree closely with the unerupted and incompletely formed P_2 of *Canthumeryx* from Libya (BMM 26682).

Identification of the material from Muruarot must be based on details of the lower dentition. The specimen differs widely in detail from *Climacoceras* and *Palaeotragus primaevus* lower dentitions. However its bilobed canine establishes the identification as a giraffoid. It differs from *Prolibytherium* in size, crown height and details of the lower premolars but agrees closely with specimens of *Propalaeoryx austroafricanus* (Stromer 1926, pl. 40, fig. 1) in details of its lower premolars. The Muruarot specimen is, however, much larger than *Propalaeoryx* and in all details it agrees closely with specimens of *Canthumeryx sirtensis* from Libya. On the basis of this close similarity I identify the Muruarot specimen with *C. sirtensis*. This identification is important as *C. sirtensis* thus becomes the first ruminant species to be identified from the North and East African Lower Miocene.

Upper dentition. An isolated M^3 (figure 27) and a fragment of left maxilla with P^{2-3} (figure 29) were associated with the lower dentition and post-cranial elements. The state of wear and state of preservation suggest that these specimens belong with the others grouped under the number UCB.V.4899/42058. A left maxilla fragment with P^{3-4}: UCB.V.4898/41873 (figure 28) and a fragment with P^4 and most of the M^1: UCB.V.4898/41981 (figure 26) are also identified with this species.

Table 15. *Canthumeryx*; lower dentition

	C_1 *W*	*W* ant. lobe	*W* post. lobe	P_2		P_3		P_4		M_1		M_2		M_3	
				L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
BMM 26682	—	—	—	13.5	5.3	—	—	15.8	7.5	19.5	11	20.3	13.5	29.2	13.3
BMM 26683	—	—	—	—	—	18.7	8.5	19	9.8	20	14	—	—	—	—
BMM 26675	—	—	—	—	—	—	—	—	—	—	—	—	—	33	17
BMM 26676	—	—	—	—	—	—	—	—	—	—	—	—	—	32	15
BMM 26677	—	—	—	—	—	—	—	—	—	—	—	25	17	—	—
BU 20111	—	—	—	—	—	—	—	—	—	—	—	—	—	31	13.8
UCB.V.4899/42058	6	5	1	*ca.* 13	6.5	16	8.5	18.5	9.0	—	10	17	12.5	26.5	12
UCB.V.4898/41878	—	—	—	—	—	19	9	—	—	—	—	—	—	—	—
KNM.R–A.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13.5

	C_1–M_3	C_1–P_2	P_2–P_4	P_2–M_3	M_1–M_3
UCB.V.4899/42058	192	71	53	121	68

The upper dentition of *Canthumeryx* was not identified from Libya but two upper dentitions were grouped with the skull as *Zarafa*. Discovery of the Muruarot material influences this identification. The M^3, M^1 and P^4 from Muruarot are closely similar in all details to the corresponding teeth identified as *Zarafa* from Libya. Similarities include form of the cusps, development of accessory crests and strength of the labial ribs and styles. The agreement in size (table 16) is also very close. On this basis I suggest that the upper dentitions previously identified with *Zarafa* must be placed with the genus *Canthumeryx*. The holotype of *Zarafa* is an almost complete skull that is, however, almost totally without teeth, having only the lingual face of the M^3 preserved. I can see no reason to suggest that this skull should belong to a genus distinct from the upper dentitions as the skull is giraffoid in nature and belongs to a ruminant that would carry upper teeth of the size of those identified above. I therefore suggest that the skull must also be identified with *Canthumeryx*.

Upper molars of *Palaeotragus primaevus*, *Climacoceras* and *Prolibytherium* are known. Whitworth (1958, p. 24) also mentions an isolated molar (BMM 30221 = 644:49) from Rusinga that is similar in size to the molars of *Canthumeryx sirtensis*. The molars of *Climacoceras* have higher crowns and differ from *Canthumeryx* upper molars in features of the labial face. Those of *Prolibytherium* also differ in details of the labial face and *Prolibytherium* and *Climacoceras* have smaller molars than those of *Canthumeryx*. The upper molars of *Palaeotragus primaevus* are larger and have higher crowns than *Canthumeryx*.

The P^4 of *Canthumeryx* (*Zarafa*) is described from Libya (Hamilton 1973, pl. 6) the Muruarot specimens agree closely with the Libyan specimen. The P^2 and P^3 were dissected out of a maxilla fragment and are unworn (figure 29). The back of the P^3 is broken off and is missing. The P^3

is elongate with a strong antero-labial style and a very strong paracone rib. The central lingual region is expanded and is joined by narrow crests to the anterior and posterior corners of the tooth. Several accessory crests are present. The lingual region of the P^3 is similarly developed in *Palaeomeryx* (BMM 29624) but in *Palaeotragus primaevus* the lingual region is more strongly developed. Two upper third premolars from Rusinga: BMM 30222 (= 825:50) and BMM 30223 (= 1099:51) were described by Whitworth (1958, p. 24). BMM 30222 shows medium wear and is similar to UCB.V.4899/42058. Its lingual region is similarly developed but the central lingual cusp is broken off so its development is not known. BMM 30223 is very heavily worn but is similar in size and general appearance to the other third premolars described. These premolars probably belong with the species *Canthumeryx sirtensis*.

TABLE 16. *CANTHUMERYX*; UPPER DENTITION

	P^2		P^3		P^4		M^1		M^2		M^3	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
BMM 26671	—	—	—	—	15	20	19	—	22	24	22	23
BMM 26672	—	—	—	—	—	—	21	19	23	22	—	—
KNM.MT.253	—	—	—	—	—	—	—	—	21	22	—	—
BMM 30221	—	—	—	—	—	—	—	—	—	21	—	—
BMM 30222	—	—	16.5	—	—	—	—	—	—	—	—	—
BMM 30223	—	—	17	13	—	—	—	—	—	—	—	—
UCB.V.4899/42058	15	12	*ca.* 17	13	—	—	—	—	—	—	19	19.5
UCB.V.4898/41873	—	—	18	15	—	—	—	—	—	—	—	—
UCB.V.4898/41981	—	—	—	—	15.5	17	19	18.5	—	—	—	—

The P^2 is generally similar to the P^3 but the antero-lingual and postero-lingual crests are not fully developed. The anterior crest consists of a series of small tubercles and the posterior crest is low and weak. As a result the central lingual cusp appears relatively higher and more pointed on the P^2 (figure 29). The P^2 of *Palaeotragus primaevus* (KNM.FT.2961) is more advanced than that of *Canthumeryx sirtensis* as its antero-lingual and postero-lingual regions are expanded, giving the tooth an oval to rectangular shape, rather than the elongate subtriangular shape of the P^2 in UCB.V.4899/42058.

Post-cranial skeleton. As indicated above, much of the post-cranial material is associated with the dental material. Some post-cranial material from Gebel Zelten was identified with *Zarafa* and can in most cases be treated as belonging with *Canthumeryx*. Skeletal elements of medium-sized ruminants are described from the east African Miocene by Arambourg (1933, p. 22), Churcher (1970), Gentry (1970) and Whitworth (1958, pp. 28–39).

Vertebrae. The atlas is almost complete, lacking only the postero-dorsal region. Churcher (1970, p. 38) describes an atlas (KNM.FT.3077) which he identified with *Palaeotragus primaevus*. This atlas is not elongate and has the usual ruminant form. An atlas (B.U. 20170) was identified (Hamilton 1973, p. 122) with *Prolibytherium*. This specimen is also short. Elongation of the atlas is found in *Giraffa* which has a length/width ratio of approximately 1.17 and to a lesser extent in the gerenuk *Litocranius*, and several cervids (table 17). Ratios in table 17 suggest that *Canthumeryx* showed some lengthening of its neck. Two other cervical vertebrae: UCB.V.4898/42020 and UCB.V.4898/41914 are identified with *Canthumeryx*. The former consists of two fragments: a centrum and the left dorso-lateral region. These parts cannot be fitted together but they are from the same or very similar vertebrae. The centrum is long and narrow and the left dorso-lateral region also indicates that this cervical vertebra was elongate. UCB.V.4898/41914 is a sixth cervical vertebra. It is badly broken with its left side almost completely missing. This vertebra is elongate and similar in general features to the C.VI. of *Capreolus*. An axis vertebra and a seventh cervical vertebra are known from Gebel Zelten (Hamilton 1973, pp. 98–100). These can now be identified with *Canthumeryx* and this axis shows some elongation of its centrum.

TABLE 17. LENGTH/WIDTH RATIOS OF THE ATLAS IN SOME RUMINANTS

	L/W
Canthumeryx UCB.V.4899/42058	1.03
Giraffa	1.17
Litocranius	1.11
Lama	0.71
Capreolus	0.71
Cervus elaphus	0.60
Okapia	0.62

TABLE 18. *CANTHUMERYX*; CERVICAL VERTEBRAE

		C. VI.
	UCB.V.4898/42020	UCB.V.4898/41914
centrum length	80	79
anterior width of centrum	25	25
posterior width of centrum	35	35

TABLE 19. *CANTHUMERYX*; RADIUS

	UCB.V.4899/42058	IPP 1933–9	BU 20126	BU 20127
length	—	280	—	—
proximal end				
width	41.5	42	49	—
depth	23	22.5	29	—
distal end				
width	39	—	—	44
depth	28	—	—	29

The fore-limb. The proximal region of the right scapula is preserved. The glenoid cavity is rounded and the tuber scapulae is relatively large. The coracoid process is broken off. The cavity is more rounded than that figured in Hamilton (1973, p. 118) and the Muruarot specimen is smaller than that from Libya.

The almost complete radius is preserved with IPP 1933–9 (figure 33) but only the distal and proximal regions are preserved on UCB.V.4899/42058. The radius is long and slender. It has a flattened cross section as in *Palaeotragus primaevus* and although much smaller, the radius of *Canthumeryx* is generally similar to that of *P. primaevus*. Most of the shaft and distal articulation of the fused metacarpals Mc. III and IV are preserved. The bone was long and slender with a minimum length of 290 mm (table 21) which is shorter than the cannon-bone described from Libya (Hamilton 1973, p. 102).

The hind limb. The complete hind limb of IPP 1933–9 is shown in figures 35 and 37. The distal region from the tibia to phalanges is glued together as a unit and was not separated.

Pelvis. The pelvis is almost complete, lacking only the medial part of the ischium and the distal part of the tuber coxae (figure 34). The pelvis of *Palaeotragus primaevus* is less completely known (Churcher 1970, pp. 56–58) but is larger with a more rounded obturator foramen and a tuber ischii which flares less than in UCB.V.4899/42058. The ilium of *P. primaevus* is also narrower and the flaring of the wing starts more distally than in the pelvis of *Canthumeryx*.

Femur. The femora UCB.V.4899/42058 and IPP 1933–9 are relatively short (table 22) and differences in length between these specimens and the femur from Libya (Hamilton 1973, p. 97) are probably larger than can be accounted for by the different ages of the two individuals. UCB.V.4899/42058 is more complete than IPP 1933–9 (figures 36, 35) as its articular head is preserved. The shaft is stout with the posterior face shallowly concave proximo-distally. It is more nearly circular in cross-section than the shaft of *Palaeotragus primaevus* (Churcher 1970, p. 58). The distal articulations are missing from both the Muruarot femora.

TABLE 20. *CANTHUMERYX*; ULNA

	UCB.V.4899/42058	IPP 1933–9
width of proximal facet	11	10
minimum width of facet at articulation with radius	25	23
depth of olecranon at proximal facet	40	40
width of olecranon at facet	8	8
length of olecranon	—	49

TABLE 21. *CANTHUMERYX*; METACARPAL

	UCB.V.4899/42058	BU 20128
width of proximal facet	—	46
depth of proximal facet	—	25
minimum depth of shaft	16.5	—
minimum width of shaft	17.5	—
length	*ca.* 290	317
width of distal end	35	—
depth of distal end	20.5	—

TABLE 22. *CANTHUMERYX*; FEMUR

	UCB.V.4899/42058	IPP 1933–9
length preserved	240	240
estimated length	255	—
minimum width of shaft	23.5	23.5
minimum depth of shaft	24.5	25.0
width of proximal end	66	—
depth of articular head	27	—

Patella. The patella is 39 mm long and 54 mm wide. Its proximal end is blunt while its distal end is elongate and pointed.

Tibia. The left tibia (IPP 1933–9) is almost complete (figure 37) lacking only the proximal part of the cnemial crest and part of the anterior region of the proximal facets. The right tibia (UCB.V.4899/42058) is similarly broken but most of the proximal facets are missing. The fibula (malleolus) is still articulated on the distal region of UCB.V.4899/42058. Its proximal region has a short projection, a high rounded posterior facet and a flattened anterior facet. The distal face carries a long concave posterior facet and a shorter anterior facet that curves antero-medially. Churcher (1970, p. 60) describes the tibia of *Palaeotragus primaevus* (KNM.FT.3100*a* and *b*). This bone is slender like the Muruarot specimen and in contrast to that of *Okapia.*

Churcher states that the cnemial ('tibial') crest occupies the proximal third of the anterior face as in *Okapia*. This contrasts with the Muruarot and Libyan specimens in which the cnemial crest is restricted to the proximal quarter of the anterior face. Cross sections of the middle region of the shaft indicate that it is narrower and deeper in *Canthumeryx* than in *Palaeotragus primaevus* but in both the shafts are straight.

TABLE 23. *CANTHUMERYX*; TIBIA

	UCB.V.4899/42058	IPP 1933–9	BU 20116	*P. primaevus** KNM.FT.3100
length	300	305	349	497.5
width of proximal end	—	54	68	90.4
depth of proximal end	—	53	76	82.5
minimum width of shaft	23	22.5	—	43.3
minimum depth of shaft	20	22.5	—	29.0
width of distal end	—	39	46	58.7
depth of distal end	—	39	35	43.7

* From Churcher 1970, p. 62.

TABLE 24. *CANTHUMERYX*; ASTRAGALUS

	UCB.V.4899/42058	UCB.V.48100/41854	BU 20120	BU 20121
maximum length	39	44	49	41
maximum depth	23	*ca.* 25	23	23
proximal width	25	—	29	30
distal width	25	29	29	29

TABLE 25. *CANTHUMERYX*; CANNON-BONE

	UCB.V.4899/42058	KNM.MO.41B	UCB.V.4898/40423	IPP 1933–9	BU 20117
length	260	*ca.* 280	—	260	349
width of proximal end	30	30	35	28	39
depth of proximal end	27	30	35	29	41
minimum width of shaft	17	18.5	—	18	—
minimum depth of shaft	15.5	16.5	—	16	—
width of distal end	32.5	38	—	31.8	42
depth of distal end	—	21.5	—	21.0	29

Astragalus. The astragalus is of the usual ruminant form. It is relatively long as in specimens from Libya and is more elongate than the astragali of *Okapia*, *Palaeotragus primaevus* or *Giraffa*.

Metatarsals. The complete fused metatarsals Mt. III and IV are known from left and right sides. The anterior channel is clearly visible over its full length; it becomes shallower distally but then deepens between the distal facets. There is no indication of the nearly circular bridged section near the distal facets such as is found in *Palaeotragus primaevus* (Churcher 1970, p. 68). This difference may, however, be due to the juvenile condition of the *Canthumeryx* specimens. There is of course no covering of the groove like that found characteristically in the cervids (Heintz 1963). Whitworth (1958, p. 27) shows an isolated ruminant cannon-bone (KNM. 1635. 50) which he identified with *Propalaeoryx nyanzae*. This specimen also has an open anterior groove. It is too small (Whitworth 1958, p. 39) to be identified with *Canthumeryx*. The posterior region of the Muruarot cannon-bones carries no indication of Mt. II or Mt. V. The Mt. II of *Palaeotragus primaevus* (KNM. FT. 3108) is possibly represented by a ribbon of bone fused to the face of the cannon-bone (Churcher 1970, p. 69, fig. 69) as in *Giraffa* (Fraser 1951) and *Okapia*.

A cannon-bone from Libya (BU 20117) is too long to belong with *Canthumeryx*. It is, however, very long and slender and could be giraffoid. It therefore suggests the presence in the Gebel Zelten fauna of a ruminant larger than *Canthumeryx*.

Phalanges. The first and second phalanges are more slender than those of *Palaeotragus primaevus*, *Okapia* or *Giraffa*. This probably reflects the smaller body weight of *Canthumeryx*. The third phalanges are long antero-posteriorly relative to those of *Palaeotragus primaevus* (Churcher 1970, figs 74 and 75).

Much of the post-cranial material from Gebel Zelten can now be grouped with *Canthumeryx*. However, the femur BU 20115, cannon-bone BU 20117 and tibia BU 20116 suggest the existence in the Gebel Zelten fauna of a larger ruminant for, even allowing for the juvenile nature of UCB.V.4899/42058 and IPP 1933-9 these bones from Gebel Zelten are too large to be grouped with *Canthumeryx sirtensis*.

2. Fossil giraffids from Baringo and Fort Ternan, Kenya

Introduction. Much of the giraffid material described below was collected in the Ngorora Formation which outcrops in the Ngorora administrative district about 32 km northwest of Lake Baringo, Kenya. Fossiliferous sediments in this locality are underlain and overlain by 'flows of phonolitic lava' and an age of 9-12 million years is suggested by potassium: argon dating of these phonolites (Bishop & Chapman 1970, p. 914; Bishop, Chapman, Hill & Miller 1971, p. 390; Bishop 1972, p. 230; Bishop & Pickford 1975, p. 187). Berggren & Van Couvering (1974, fig. 11) indicate an age of 11.2 million years for the Upper Ngorora Beds and almost 12 million years for the Lower Ngorora Tuffs. These deposits are thus slightly younger than the Fort Ternan deposits which are dated as 14 million years by Evernden, Savage, Curtis & James (1964, p. 165), Bishop, Miller & Fitch (1969, p. 690) and Berggren & Van Couvering (1974, fig. 11).

(*a*) *Palaeotragus primaevus*

Superfamily Giraffoidea Simpson 1931
Family Giraffidae Gray 1821

Diagnosis. Giraffoids in which the accessory lobe of the lower canine forms about one third of the crown. Posterior region of the P_4 separated from the central and anterior regions. Central lingual cuspid strongly developed on P_4 and not joined to the central labial cuspid.

Genus **Palaeotragus** Gaudry 1861

Remarks. As explained later in this work (pp. 199, 222) I do not regard the subfamily Palaeotraginae or the genus *Palaeotragus* as valid. As understood by Churcher (1970) and Colbert (1935*a* or *b*) the subfamily and genus are both diagnosed on the basis of plesiomorphic features. I regard this as invalid and therefore a diagnosis cannot be presented at this stage.

Species *Palaeotragus primaevus* Churcher 1970

Remarks. Churcher (1970, pp. 72-73) gives a diagnosis of this species. This includes plesiomorphic and apomorphic features and is in any case vague on several points and can now be shown to be inaccurate over the absence of ossicones. I have suggested below that *P. primaevus* is probably a junior synonym of *Palaeotragus tungurensis* but for the descriptive parts of this work

I have continued to use Churcher's species name. I believe that this is justified as this section deals exclusively with African material so confusion is unlikely, also other workers may choose not to accept my proposed synonymy so confusion will be avoided if this synonymy is used only in the systematic section where the proposal is defended.

Holotype. 'Simple mandible from level I/2, Fort Ternan. Right dentary with P_4, M_1–M_3, and alveoli for P_2–P_3. Left dentary with P_3–P_4, M_1–M_3, including angle.' Churcher 1970, p. 10.

Locality. Fort Ternan and Baringo, Kenya. Upper Miocene.

Material. The complete Fort Ternan collection in the Kenya National Museum (at 1974) was surveyed and relevant material was used in descriptions below. New material from Baringo is described in more detail. KNM.BN.950: left mandible with P_{3-4}, M_{1-3} and I_1 plus right I_{1-3} and C_1. KNM.BN.1446: a partial skull consisting of ossicones, cranial and basicranial regions (figures 38–40). KNM.BN.195: left mandibular fragment with M_{1-3}. KNM.BN.900: left mandible fragment with D_{2-4}. KNM.BN.1161: matrix block with P_3 and D_4; these are not necessarily the same individual as they are linked by matrix with the P_3 about 1 cm above the D_4. KNM.BN.50: back part of left P_3. KNM.BN.199: left upper molar. KNM.BN.335: right upper molar. KNM.BN.849: left upper molar. KNM.BN.198: left P^4. KNM.BN.287, right P_4 (figure 31, plate 3).

The following specimens are identified as *Palaeotragus primaevus* but have no dimension preserved that is used in the tables; they are included here to complete the record of Baringo giraffid material: KNM.BN.981: upper molar fragment. KNM.BN.535: left upper molar fragment. KNM.BN.351: right upper molar fragment. KNM.BN.372: left upper molar fragment. KNM.BN.489: right upper molar fragment. KNM.BN.897: left lower molar fragment. KNM.BN.196: right upper molar fragment.

Description. Aguirre & Leakey (1974, pp. 225–226) record the presence of *Giraffokeryx* sp.nov. from Ngorora and figure two specimens which they describe briefly. These specimens agree closely with *Palaeotragus primaevus* from Ngorora and Fort Ternan and I suggest that they are incorrectly identified with *Giraffokeryx*. Aguirre & Leakey do not refer to Churcher's (1970) description of the Fort Ternan giraffes and it is possible that they were not aware of its publication. Figures from Aguirre and Leakey are referred to where relevant in the following description.

The skull. A partial skull (KNM.BN.1446) consisting of the basicranial region, auditory region, cranial roof and frontal appendages is identified as giraffoid. This identification is based on features of the basicranial region, shape of the skull roof and the presence of ossicones. There is an apparent anomaly here. The presence of a plesiomorphic feature cannot be used to assess relations, however, when identifying specimens in a faunal collection plesiomorphic features are used. Although the presence of ossicones in *Palaeotragus primaevus* is not used to assess its relations, the presence of these ossicones can be used to identify the skull with this species as this character is not present in other species in the fauna with which confusion may be possible. Identification with *P. primaevus* is made on a size basis. Confusion here is only possible with *Samotherium* which is far larger than *P. primaevus*. Some cranial material in the Fort Ternan collections was identified with *P. primaevus* (Churcher 1970, p. 13) but the Baringo specimen is the most complete giraffid cranium from the Miocene of east Africa.

The frontal appendages are positioned in the extreme lateral supraorbital part of the frontals (figures 39 and 40) and are thus much further lateral than is usual in the bovids, but they agree with the ossicone position in *Palaeotragus rouenii* (Gaudry 1862–7, pl. 45, fig. 3), *Palaeotragus* *microdon* (Bohlin 1926, pl. 1, fig. 1), *Palaeotragus coelophrys* (Bohlin 1926, pl. 1, fig. 3), *Samotherium boissieri* (BMM 4215), *Samotherium sinense* (Bohlin 1926, pl. 6, figs 1 and 3), *Giraffokeryx punjabiensis* (Colbert 1933, fig. 2) and the assumed position for *Canthumeryx sirtensis* (Hamilton 1973, pls 2 and 3). The left and right appendages are preserved but the right one appears to be distorted and most of its surface is eroded. Much of the following description is therefore based on interpretation of the left appendage only.

The surface carries large ridges and grooves that run along the length of the ossicone and continue as far as its base. There is thus no indication of a smooth 'pedicle' region such as occurs in the bovids. The left ossicone slants slightly backwards (figure 38) but is almost vertical in the antero-posterior plane. It narrows quickly from its base to a point about 2 cm above the skull roof. In this basal part the ossicone cross section is a wide oval with its long axis running antero-laterally. On the upper part of the ossicone the medial to antero-medial face is flattened and the ossicone has a 'D-shaped' cross section. It narrows gradually over its central region and then more rapidly towards the tip which was probably sharply pointed.

Ossicones from Fort Ternan were described as a new species: *Samotherium africanum* by Churcher (1970, p. 73) who designated KNM.FT.3118 as the holotype. On these specimens heavy weathering before fossilization has resulted in the loss of most of the original surface. On the holotype, however, part of this surface is preserved over the basal 5 cm of the lateral face. This region is far smoother than the weathered surface and demonstrates the absence of a bovid type of pedicle region; it also agrees in surface texture with the ossicones of KNM.BN.1446. The *Samotherium africanum* ossicones have a rounded to broad oval cross section and lack the medial flattening described above on KNM.BN.1446. The ossicones of KNM.BN.1446 are much smaller than those of *S. africanum.*

The skull roof is preserved from about 1 cm in front of the ossicone bases almost to the nuchal crest. Sutures are not visible. There are no large cracks or fractures in the skull roof and the profile (figure 38) probably represents the original skull shape. The surface of the frontal bones is flattened between the ossicones and this flattened region extends behind the ossicones. This flattening, together with the upward slope of the parietal towards the back, result in a skull profile very similar to that of *Canthumeryx* (Hamilton 1973, pl. 2).

The basicranial, occipital and mastoid regions are difficult to interpret. During fossilization there appears to have been rotation of the left mastoid region resulting in the shifting upwards of the paroccipital process and the external auditory meatus, and the rotation of the tympanic bulla. The condyle and attached parts of the squamosal have been shifted medially so that they now lie partly above the basioccipital while the left occipital condyle has been pushed antero-medially relative to the right condyle. No junctions have been found between the bones of this region and the rest of the skull. It is probable that the whole base of the skull has also been displaced anteriorly relative to the skull roof and ossicones. The squamosal, mastoid region and tympanic bulla are preserved on the left side only. The squamosal fragment consists of the temporal condyle which was wide and convex with a well developed post-condylar process. The upper surface of this region was concave and a single sub-squamosal foramen is present. This foramen is small, having a diameter of about 2 mm and it communicates with the inside of the cranium rather than opening into the temporal canal as occurs in most bovids.

The occipital condyles are large as in *Canthumeryx* (Hamilton 1973, pl. 4, figs 1 and 2). Ventrally they join a pair of large anterior occipital swellings that are wide and form ridges across the back of the basioccipital region (figure 40). A median keel runs anteriorly from between these swellings almost to the front of the basioccipital, passing between the paired basilar tubercles which have very rugose surfaces but are low in comparison with the same tubercles in the Fort Ternan and Ngorora bovids. The paroccipital processes are both preserved. They are short and stout, and allowing for distortion they probably extended as far as the lower edges of the occipital condyles as in *Canthumeryx* and *Prolibytherium*.

A basioccipital from Fort Ternan (KNM.FT.3148) is identified with *Palaeotragus primaevus*. This specimen consists of the right occipital condyle, a fragment of the paroccipital process and the basioccipital. It agrees approximately in size with the same part of KNM.BN.1446 and with the condyle KNM.FT.3068 described by Churcher (1970, p. 16). The basioccipital region of KNM.FT.3148 is slightly wider than that of KNM.BN.1446 but the Fort Ternan specimen demonstrates the natural position of the condyles which have been displaced forwards above the anterior occipital swellings in KNM.BN.1446. The anterior occipital swellings appear weaker in the Fort Ternan specimen than in the one from Ngorora but they are the same width and have suffered some erosion of their surfaces. KNM.FT.3148 is broken behind the basilar tubercles but the preserved part indicates that they were about the same strength as on the Ngorora specimen. The flatness of the basioccipital, the strength of the median keel and the basilar tubercles indicate that these two specimens belong to the same species while the whole basioccipital region is similar to the same region in *Canthumeryx*, *Palaeotragus coelophrys* (Bohlin 1926, pl. 1) and *Samotherium sinense* (Bohlin 1926, pl. 6).

Foramina. The anterior part of the basicranium is missing on KNM.BN.1446 and the front break includes the foramen rotundum which lay vertically below the back of the ossicone. The foramen ovale is preserved but its shape cannot be established due to the displacement of the squamosal which is shifted medially above the basioccipital and has carried the sphenoid with it in this region. The eustachian canal is preserved dorso-lateral to the muscular process of the tympanic bulla. The foramen lacerum medium is large and the antero-medial face of the bulla is hollowed out as a deep vertical depression which forms the lateral border of the foramen lacerum medium. The foramen lacerum posterius is long and narrow, running alongside the basilar tubercle; however, the medial displacement of the bulla has probably affected the shape of this foramen. The bulla is large and swollen. It has undergone some crushing and is broken in the region of the stylomastoid foramen. The stylohyoid groove runs almost vertically but probably ran antero-ventrally before distortion of this region. It crosses the bulla with approximately one third of the bulla lying behind it. This is the condition found in *Giraffa*, *Okapia*, the tragulids and some bovids and deer. It is the primitive position of the groove in the ruminants (Radinsky, personal communication). The external auditory meatus lies postero-dorsal to the bulla. It is large and open posterodorsally where the border was probably formed by the squamosal. The mastoid runs vertically behind the meatus and the occipital-mastoid suture runs dorso-medially from the base of the paroccipital process as far as the break. Antero-dorsal to the external auditory meatus there appears to be a large temporal canal but the true size and shape of this cannot be established. The stylomastoid foramen lies postero-ventral to the external auditory meatus.

*Comparisons of KNM.BN.*1446 *with other giraffoid skulls.* The general skull shape of KNM.BN. 1446 agrees closely with that of other giraffoid genera with important points of agreement being the position of the ossicones and relative size of the condyles; the length of the postorbital region and the profile of the frontal: parietal: occipital region. Differences in ossicone position between KNM.BN.1446 and *Giraffokeryx* suggest that the specimen must be excluded

Table 26. *P. primaevus*; anterior lower dentition and lower cheek teeth

anterior lower dentition

	KNM.BN.950		KNM.BN.3029		KNM.FT.3030		KNM.FT.3031		KNM.FT.3032		KNM.FT.3033		KNM.FT.3035		*Climacoceras* KNM.FT.2946	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
I_1	—	8.5	—	10	—	—	—	—	—	—	—	—	—	—	—	—
I_2	—	6.5	—	—	—	9.5	—	10	—	—	—	—	—	—	—	—
I_3	—	6.0	—	—	—	—	—	—	—	11.5	—	11.5	—	—	—	4.5
C	—	10.0	—	—	—	—	—	—	—	—	—	—	—	11.0	—	5.0

lower cheek teeth

	KNM.BN.950		KNM.BN.195		KNM.BN.50		KNM.BN.287		KNM.FT.2972		KNM.FT.2899		KNM.FT.3066	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
P_3	18	10	—	—	—	11.5	—	—	—	—	19	11	—	—
P_4	19	10	—	—	—	—	21	12	—	—	21	13	20	13
M_1	20	12.5	18	—	—	—	—	—	22	14	24	14	22	15
M_2	19.5	13	20	—	—	—	—	—	23	14	24	16	23.5	16
M_3	26	13	24.5	—	—	—	—	—	—	—	33	16	33	15
P_2–M_3	112		—		—		—		—		—		*ca.* 132	
P_2–P_4	49		—		—		—		—		—		*ca.* 54	
M_1–M_3	65		64		—		—		—		80		78	
I_1–M_3	222		—		—		—		—		—		—	
diastema	84		—		—		—		65		—		—	

Table 27. *P. primaevus*; upper dentition

											Giraffidae indet.							
	KNM.BN. 335		KNM.BN. 199		KNM.BN. 849		KNM.BN. 200		KNM.FT. 851.74		KNM.BN. 883		KNM.BN. 1139		KNM.BN. 1287		*Canthumeryx* BMM 26671	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
M^u	23	24	23	25	24	25	—	—	21	23.5	22	—	28	30	28	28	—	—	22	24
P^2	—	—	—	—	—	—	20	15	18	12.5	—	—	—	—	—	—	—	—	—	—
P^3	—	—	—	—	—	—	—	—	18.5	14	17	14	—	—	—	—	23	26	—	—

from this genus while it lacks the strong posterior projection of the supraoccipital region that is found in *Samotherium*. The skull of *Okapia* is specialized in the development of supraorbital sinuses (Lankester 1902, pp. 289–290) and small sinuses are present in the extreme lateral supra-orbital region of *Canthumeryx* (Hamilton 1973, pls 2 and 3). This feature is not present in KNM.BN.1446.

The mandible. Churcher (1970, fig. 2) gives a reconstruction of the mandible of *Palaeotragus primaevus* from Fort Ternan. This is based on features of several specimens including KNM.FT. 2899, 2972 and 3075. KNM.BN.950 is similar in size to the Fort Ternan specimens but its vertical ramus appears to slope more steeply backwards from behind the M_3 and the diastema is longer than in Churcher's reconstruction. This is probably because the latter was based mainly on juvenile specimens and full allowance for growth in length may not have been made. The symphysis is long and the front of the jaw is narrow as in *Okapia*.

Lower dentition. Churcher (1970) gives a detailed description of the lower molars premolars and deciduous dentition of *Palaeotragus primaevus*. Tables 26 and 27 indicate that the Baringo specimens agree closely in size with the Fort Ternan material while figures 31 and 32, plate 3, and Churcher's descriptions mean that further description of the lower dentition is not required here.

Upper dentition. The upper dentition is usually more difficult to identify than the lower and with the Baringo material this problem is exaggerated by the absence of any associated upper teeth. However Aguirre & Leakey (1974, p. 226) figure a P^{2-4} series which confirms identifications that I had previously made in Nairobi. I identified several upper molars and premolars with *Palaeotragus primaevus*. These teeth are approximately the same size as the Fort Ternan specimens (table 28) and agree closely with upper teeth described by Churcher (1970, p. 21).

Two larger molars: KNM.BN.883 and KNM.BN.1139 (table 28) are giraffid in appearance but are intermediate in size between *Palaeotragus rouenii* and *Samotherium boissieri*. Other dental and post-cranial elements (below) also suggest the existence of a larger giraffid in the Baringo fauna and this was suggested in Bishop *et al.* (1971, p. 391) and Bishop & Pickford (1975, p. 189). These molars are unlike those of *Palaeotragus primaevus* and *Samotherium* in having lingual cusps that are less truly crescentic. This is especially true of KNM.BN.1139 which has stout cusps with a generally more rounded appearance than in *P. primaevus* and also has a strong lingual cingulum extending almost completely around the base of the protocone. This is unusual in giraffids as advanced as *P. primaevus* but occurs in a single M^1 (KNM.FT.2962) from Fort Ternan.

Aguirre & Leakey (1974, p. 222) record the presence of *Samotherium* sp. from Nakali, Upper Suguta, Kenya. This site is attributed to the 'Upper Miocene' and is correlated with the Upper Vallesian by Aguirre & Leakey (1974, p. 219). According to Berggren & Van Couvering (1974, fig. 11) this would therefore agree in age with Ngorora. None of the material figured by Aguirre & Leakey can be definitely identified with *Samotherium* but the upper molar fragment (Aguirre & Leakey 1974, fig. 5) is very like specimens of *Samotherium boissieri*.

Specimens of upper and lower teeth in the Ngorora collections indicate that two giraffids were present in the fauna. The commoner of these was *Palaeotragus primaevus* and all available specimens agree closely with specimens of this species from Fort Ternan. Identification of the larger giraffid is not possible. Churcher (1970, p. 73) named *Samotherium africanum* from Fort Ternan but the dental material from Ngorora does not agree with teeth of *Samotherium* from other parts of the world. I have therefore left the identification of this material as: *Giraffidae – large species Indet.* and more complete specimens are necessary before a more refined identification will be possible.

TABLE 28. *P. PRIMAEVUS*; LOWER DECIDUOUS CHEEK TEETH

	KNM.BN.900		KNM.FT.2972		KNM.FT.2973	
	L	*W*	*L*	*W*	*L*	*W*
D_4	—	5.75*	23	7.5	22	—
D_3	16.3	6.3	17	8	16	7.5
D_2	12.4	4.9	13	6	11.5	5

* Only the anterior lobe is preserved on the D_4 (KNM.BN.900). With this exception all tooth widths are maxima.

TABLE 29. *P. PRIMAEVUS*; CERVICAL VERTEBRAE

	KNM.FT.3125	KNM.FT.3126	KNM.FT.3078	KNM.BN.1220	KNM.BN 318
length	109	*ca.* 85	78	*ca.* 91	94
anterior centrum width	29	32	27	—	—
anterior centrum depth	31.5	31	25	—	—
posterior centrum depth	47	—	*ca.* 33	—	—
posterior centrum width across transverse processes	76	*ca.* 106	*ca.* 67	—	—
posterior centrum width	40	—	37	—	—

Post-cranial material. The two giraffid species and *Climacoceras* are represented in the Ngorora collections by post-cranial material. Identification is made on a size basis using Fort Ternan specimens for comparison. Specimens of *Climacoceras* from Fort Ternan are mentioned by Gentry (1970, pp. 301–302) and are described above.

Vertebrae. Two badly eroded and crushed centra (KNM.BN.1220, KNM.BN.318) represent cervical vertebrae of the mid-cervical (C.3–C.5) region and are identified as giraffoid as they are long and narrow. Churcher (1970) identified cervical vertebrae from Fort Ternan with *Palaeotragus primaevus* and *Samotherium africanum.* Atlas and axis vertebrae described by Churcher agree in size with occipital condyles of this species (KNM.FT.3148, KNM.BN.1446) and are probably reliably identified with *P. primaevus.* However, cervical vertebra KNM.FT.3125 (= 353:64) is identified with *S. africanum* (Churcher 1970, p. 80). This is surprising as it is almost exactly the expected relative size to fit with the atlas and axis identified with *P. primaevus* and is much too small to fit with the atlases of *S. africanum* identified and described by Churcher (1970, pp. 76–78). Churcher identifies this specimen as a C. 3 but I think that it is probably a C. 4 or C. 5. The neural spine is more centrally positioned than is usual on the C. 3, which suggests identification as a C. 4. I therefore suggest that this specimen is a C. 4 of *P. primaevus* and not a C. 3 of *S. africanum.*

KNM.FT.3078 is discussed by Churcher (1970, p. 43). This specimen agrees very closely with the C. 3 of *Kobus* in the development of a strong ventral keel and the shape of its posterior articular facet. It differs from the C. 4 in the posterior extent of the transverse processes, the length of the posterior zygapophysis facet and the position of the neural spine. It is quite unlike the C. 6.

KNM.BN.782 is a very large cervical vertebra that would be placed with an animal in the size range of P^3 (KNM.BN.1287) and is therefore assigned to the large giraffid species. The vertebra is a C.3–C.5 and is shattered with the postero-ventral region of the centrum missing. A strong ventral ridge is present on the centrum and the anterior articular facets are raised and both face dorso-medially. The posterior articular facets are low and wide.

Scapula. KNM.BN.1352, the proximal part of the right scapula, has a tuber scapulae as in *Palaeotragus primaevus* (KNM.FT.3080), *Okapia* and *Giraffa*. It also has a rolled edge on the antero-lateral margin of the glenoid as mentioned for *P. primaevus* and *Okapia* by Churcher (1970, p. 44).

Humerus. Three fragments of the distal heads of humeri: KNM.BN.1346, 952 and 1347 agree approximately in size with *Palaeotragus primaevus* humeri KNM.FT.3082 and 3083.

Radius. The proximal ends of two right radii (KNM.BN.1128 and 1157) and the distal end of a right radius (KNM.BN.1219) agree in approximate size and shape of facets with the same parts of *Palaeotragus primaevus* and are therefore identified with this species.

TABLE 30. *P. PRIMAEVUS*; RADIUS

	KNM.BN.1128	KNM.BN.1157	KNM.BN.1219	KNM.FT.3085	KNM.FT.3084
proximal end					
width	78	74	—	74	73
depth of medial facet	42	40	—	37	37
depth of lateral facet	35	35	—	35	35
width of lateral facet	40	36	—	37	35
width of medial facet	38	38	—	37	38
distal end					
width	—	—	55	65	65
depth	—	—	—	50	46

TABLE 31. *P. PRIMAEVUS*; SCAPHOID

	KNM.BN.720
antero-posterior length	35
anterior width	17
posterior width	13
anterior height	24.5
posterior height	26

TABLE 32. *P. PRIMAEVUS*; MAGNUM

	KNM.BN.1178	KNM.FT.3087
maximum antero-posterior length	*ca.* 33	34.5
lateral depth of ridge	20	21
medial depth	15	16
maximum width of central region	26	26.5

Scaphoid. A right scaphoid articulates with radius KNM.BN.1219 and is therefore the correct size for *Palaeotragus primaevus*. It has the typical ruminant form being transversely flattened with a saddle-shaped proximal facet and a distal facet that agrees in shape with KNM.FT. 3087.

Magnum. A right magnum: KNM.BN.1178, agrees in size with KNM.FT.3087 and has a proximal facet that is only slightly smaller than the corresponding distal facet of the scaphoid.

Tibia. The proximal end of a left tibia, KNM.BN.1135, agrees with KNM.FT.3100*a* (Churcher 1970, p. 61). An antero-lateral depression is present on KNM.BN.1135 but not on the Fort Ternan specimen in which there is a swelling in this region. The postero-lateral part of the lateral facet is broken and most of the cnemial crest is also missing.

Fibula. A left fibula: KNM.BN.850, has the proximal spine broken off. Its anterior region is smaller than in the Fort Ternan specimens but agrees in size with these specimens and its distal facets are similar.

Astragalus. There are five ruminant astragali from Baringo. Two of these are small and are identified with *Climacoceras* (p. 177). KNM.BN.783 is a large left astragalus that agrees closely in size with those of *Palaeotragus primaevus* from Fort Ternan. It is broken with the medial proximal region missing but available dimensions agree closely with those of the Fort Ternan species.

TABLE 33. *P. PRIMAEVUS*; TIBIA

proximal end	KNM.BN.1135	KNM.FT.3100*a*	KNM.FT.3101	*Climacoceras* KNM.BN.716
width	83	90	*ca.* 78	*ca.* 65–70
width of medial facet	38.5	38	35	—
width of lateral facet	40	46	40	—
depth	61	60	56	—

TABLE 34. *P. PRIMAEVUS*; FIBULA

	KNM.BN.850	KNM.FT.3098*b*	KNM.FT.3099*b*
antero-posterior length	30	31	34
anterior height	19.5	19.5	23
posterior height	18	19	20
length of the anterior distal facet	10	10	11
length of the posterior distal facet	16	19	16

Cubonavicular. A left (KNM.BN.894) and a right (KNM.BN.421) cubonavicular are known from Baringo. These agree in size with the Fort Ternan specimens KNM.FT.3106 described by Churcher (1970, p. 67).

Metapodials. KNM.BN.300 is a badly shattered posterior half of the proximal 30 cm of a left cannon-bone. It agrees in size with KNM.FT.3108 (Churcher 1970, figs 69–73). The posterior proximal facets are preserved and the ribbon-like Mt. II is preserved on the medial proximal face. The bone carries a deep posterior channel as on KNM.FT.3108 and its size suggests that overall the Mt. III.IV would have been the same size as the Fort Ternan specimens. Fragments of the distal ends of the cannon-bones include an almost complete distal end (KNM.BN.34), a single articular facet (KNM.BN.438) and a badly eroded distal end (KNM.BN.1167).

Phalanges. There are four fragments of first phalanges. KNM.BN.33 is slender and is identified with *Palaeotragus primaevus*. KNM.BN.670 is the proximal end of a phalange of about the same size. KNM.BN.1351 and 1348 are the proximal and distal ends respectively of phalanges that are far too large to be placed with *P. primaevus*. They are, however, certainly ruminant in form and probably belong with the same species as the larger cheek teeth (p. 190).

3. RELATIONS IN THE GIRAFFOIDEA

(*a*) *The relations of* Climacoceras *and* Canthumeryx

Climacoceras and *Canthumeryx* are identified as giraffoids using a single apomorphic character: the presence in each genus of a bilobed lower canine. The validity of establishing relations on the basis of single characters has been questioned but criticisms have usually come from workers who use both apomorphic and plesiomorphic characters in their assessments of relations, a

Table 35. *P. primaevus*; astragalus

						Climacoceras	*Climacoceras*
	KNM.BN.783	KNM.BN.35	KNM.BN.966	KNM.FT.3103	KNM.FT.3104	KNM.BN.719	KNM.BN.261
lateral length	65	56	*ca.* 62	61.5	57	52.5	47.5
medial length	—	*ca.* 51	—	57	51.5	51	45
proximal width	—	*ca.* 34	—	40	35.5	29	29
distal width	38	36	—	40	36	30	31

Table 36. *P. primaevus*; cannon-bone (Mt. III:IV)

						Climacoceras
	KNM.FT.3108	KNM.FT.3110	KNM.BN.438	KNM.BN.1167	KNM.BN.34	KNM.BN.1201
width of distal articular facets	46	43.5	—	—	43.5	33
depth of distal articular facets	32.5	31.5	33	—	31	25
depth of shaft at 50 mm from distal end	25	23	—	20	—	20.5
width of shaft at 50 mm from distal end	36.5	31	—	25	—	25

Table 37. *P. primaevus*; phalanges

							Giraffidae indet.	
	KNM.BN.33	KNM.BN.670	KNM.FT.3113	KNM.BN.192	KNM.FT.3115	KNM.FT.3114	KNM.BN.1351	KNM.BN.1348
length	71	—	*ca.* 62	41	28	—	—	—
width prox. end	21	22.5	—	26	18.5	—	25	—
depth prox. end	25	—	—	31	18	—	33	—
width dist. end	17	—	15.5	23	16	13.5	32	15.5
depth dist. end	15	—	14	29	20	18.5	—	26.5

practice that is not regarded as valid. Hennig (1966, p. 88; 1969, p. 29) discusses this problem and concludes that, especially in fossil groups, single apomorphic characters are a valid basis for establishing relations. Simpson (1961, pp. 56–57) also discusses this and seems to agree that single character classification is valid but depends on the correct selection and interpretation of 'attributes'. Indeed when investigating closely related groups the number of synapomorphies must decrease in progressively more plesiomorphic members of each group until eventually only a single synapomorphy can be used. Past investigators who also used symplesiomorphies have tended to conceal this problem under a mass of features that were irrelevant to their arguments and did not add any greater validity to their assessments of relations.

The canines are bilobed in *Giraffa*, *Okapia* (Lankester 1910, pl. 11, figs 3 and 4), *Palaeotragus* (Alexejew 1916, pl. 4; Bohlin 1926, pl. 1; Rodler & Weithofer 1890, pl. 4, fig. 4; Borissiak 1914, pl. 1), *Samotherium* (BMM 4215, Bohlin 1926, pl. 5, fig. 4), *Sivatherium* (BMM 15288*a*), *Hydaspitherium* (Colbert 1935, fig. 182) and *Giraffokeryx* (Colbert 1935, fig. 164) but in these genera the accessory lobe is large relative to the anterior lobe whereas in *Climacoceras* and *Canthumeryx* the accessory lobe is very small.

The extant ruminant group most closely related to the Giraffoidea is either the Bovidae, Antilocapridae, Cervidae or any combination of these three. In members of each of these groups the canine is simple and incisiform as it is in the Tragulidae which is the extant sister-group of the ruminants. The bilobed canine therefore represents a condition derived from a simple incisiform canine. It is possible that a canine similar to that of *Giraffa* could have arisen as a single evolutionary event with the large accessory lobe being maintained by selection as it increases the slicing and food-collecting efficiency of the anterior lower dentition. The discovery of the bilobed lower canine in *Canthumeryx* and *Climacoceras* suggests, however, that the bilobed canine arose gradually with the initial development of a small accessory lobe that gradually became larger. The small accessory lobe in *Climacoceras* and *Canthumeryx* is thus apomorphic relative to other ruminants but is plesiomorphic relative to the giraffes with large accessory lobes. The similarity between the accessory lobe in *Climacoceras* and *Canthumeryx* indicates only that they are both giraffoids, it does not indicate that they are very closely related.

On the basis of the lower canines any of the three relations in figure 2 is possible. To assess relations in more detail the lower premolars have been used. The cuspid and crest pattern on the lower premolars of bovids, cervids and antilocaprids suggests a premolar pattern as described below for the plesiomorphic giraffoid pattern. This pattern is also found in genera of the Gelocidae which may well be the fossil sister-group of the ruminants. The basic P_4 consists of a labial crest that is high in the central region and produces forked lingual crests anteriorly and posteriorly, a lingual crest is also produced from the central region. The P_3 has a similar pattern but the anterior forked crests tend to be directed more anteriorly while on the P_2 the central lingual crest is less strongly developed. Variations in any group from this basic pattern can be regarded as apomorphic and in the giraffoids a transformation series is evident and most clearly shown by the pattern of the P_4.

The P_4 of *Climacoceras* (figure 4) lacks any marked expansion of the central lingual region, its anterior crest is long and forked with relatively weak lingual flexion and there is no indication of a crescentic pattern developing in the posterior region. A vertical groove is only weakly developed in the posterior labial region. This groove is far weaker than in the giraffids and does not separate the posterior region from the rest of the tooth. The P_4 of *Climacoceras* is therefore close to the plesiomorphic ruminant pattern. The P_3 again shows no strong indication of development towards the giraffid condition while the P_2 has only a single anterior crest and the anterior region is shortened. Reduction of the anterior region of the P_2 reflects the overall shortening of the premolar row in *Climacoceras*. The presence of an unforked anterior crest also reflects the reduction of the premolar row.

Lower premolars of *Canthumeryx* (figure 4) have apomorphic features indicating closer relation to the giraffids. The posterior part of the P_4 is delimited by a strong vertical groove on the labial face. This groove does not clearly separate the wear traces of the central and posterior regions but with wear, it tends to exaggerate the already strongly crescentic nature of the posterior labial region. This is an advance over the pattern in *Climacoceras* and is more similar to the pattern of *Palaeotragus primaevus* and *Giraffokeryx* (BMM 13615*a*). The central lingual crest shows marked expansion of its lingual end (figure 4; Hamilton 1973, pl. 1, fig. 5). These two features suggest that *Canthumeryx* is more closely related to *P. primaevus* and *Giraffokeryx* than is *Climacoceras*, and relations as indicated in figure 2*a* are suggested.

The lower premolars of *Palaeomeryx* and *Propalaeoryx* are similar to those of *Canthumeryx* and close relation could be suggested between these genera (Hamilton 1973). Unfortunately the lower canine is not known for these genera and therefore I do not include them in further discussion of giraffoid relations. The lower premolars of *Prolibytherium* resemble those of *Climacoceras*. This obviously does not indicate relations as both exhibit plesiomorphic features. However both *Prolibytherium* and *Climacoceras* are apomorphic in having high-crowned cheek teeth and reduction in length of the premolar row. Both also exhibit complication of the ossicones. The mere presence of ossicones is here identified as a plesiomorphic feature as skin covered frontal appendages must have been present in the ancestors of the higher ruminants (Coope 1968, p. 216). If this is so then the conclusion that *Palaeomeryx* must be a giraffid as it possesses ossicones (Ginsburg & Heintz 1966) is invalid. The presence of complex ossicones must, however, be regarded as an apomorphic feature and on this basis close relation between *Climacoceras* and *Prolibytherium* might be suggested. But the term 'complex' is itself very vague for if ossicones are present and not 'simple' then by definition they must be complex. Detailed similarity in the form of this complexity would in my opinion be necessary before one could establish relations on this basis. For example, detailed comparison of tine presence and position in many cervids has proved a useful tool with which to assess relations. In the present case a detailed comparison does not produce points of similarity as the ossicones of *Prolibytherium* (Hamilton 1973, pl. 7) are large and plate-like, whereas those of *Climacoceras* (figure 21) have a beam and tines with almost circular cross sections. Wiley (1975, p. 238) argues a similar case with reference to a group of fishes when he states:

> As a last example, we might reject a hypothesis of homology between the anal fin modifications of osmerid and poeciliid fishes because of a lack of similarity in anything except their being anal fins (that is, although both are modified anal fins, they are modified in different ways).

The lower canine of *Prolibytherium* is not known and therefore the giraffoid nature of this genus cannot be established. Where the lower canine is not known, this leads to some difficulty with any species that might be identified as a giraffoid. This problem is however less acute in those species that show other derived features. For example, the lower canine of *Giraffa jumae* is not known; it can however be identified as a giraffid by using features of its dentition, the development of clubbed tips on its ossicones and the presence of a nasal ossicone. The lower canine is

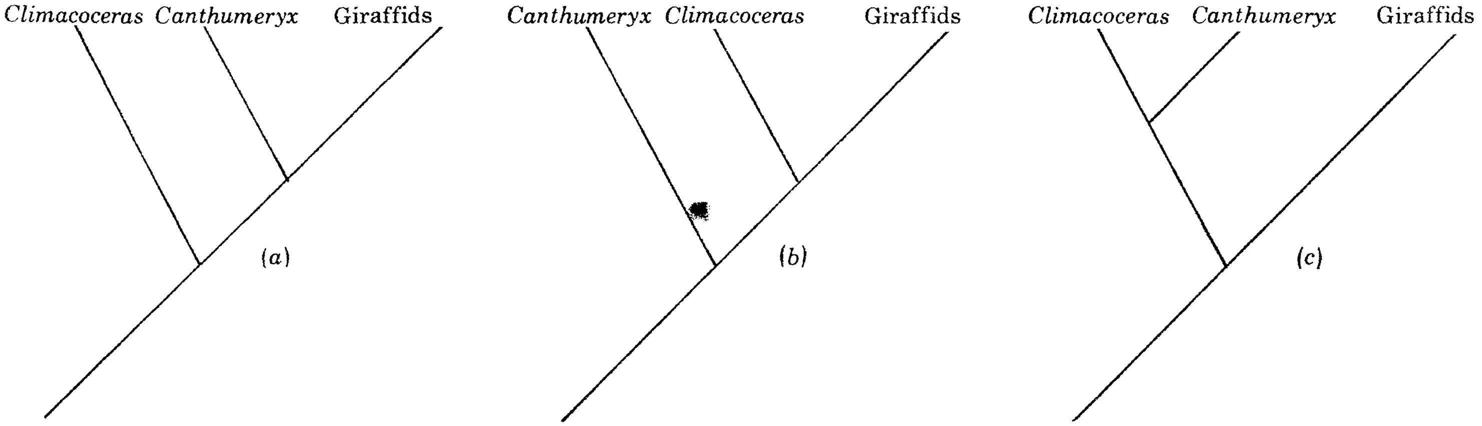

FIGURE 2. Possible relations of giraffoids based upon interpretation of the accessory lobe of the lower canine.

also unknown for *Triceromeryx pachecoi*; here there is more uncertainty but details of the lower premolars suggest that this species is probably a giraffoid and it is treated as such here. With *Prolibytherium*, *Palaeomeryx* and *Propalaeoryx*, however, there are no other derived features that can be used and therefore the giraffoid nature of these genera cannot be established. These genera may eventually be shown to belong with the giraffoids but for the present they must be treated as: *Pecora incertae sedis*. The relations of *Climacoceras* and *Canthumeryx* are as in figure 2*a*.

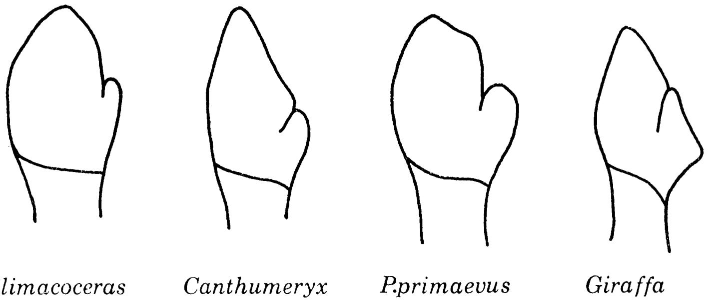

FIGURE 3. Left lower canines of giraffoids showing relative development of the accessory lobe. *Climacoceras*: natural size × 3. *Canthumeryx*: × 2. *Palaeotragus primaevus*: × 1.7. *Giraffa*: × 0.8.

(*b*) *Relations in the Giraffidae*

In the following section, I attempt to establish relations in the group 'giraffids' and a cladogram is presented (figure 9). In places, the position of branches on this cladogram is uncertain while others are based on relatively little evidence. However I feel that the diagram offers a better basis for criticism than any so far suggested as it is precise in the relations indicated and is an attempt to assess relations by using only synapomorphies, whereas earlier suggestions of relations (see for example, Colbert 1935*a*, p. 375; Churcher 1970, p. 100; Crusafont-Pairó 1952, pp. 215 and 219), rely on a mixture of synapomorphies and symplesiomorphies. Much of my assessment of relations depends on features of the lower premolars. These teeth are often highly variable in the ruminants. They are, however, important as a basis for identification. Stewart (1941) used the lower premolars to assess relations in the cervids, hypertragulids and leptomerycids, while in the giraffoids, several earlier workers have used the lower premolars, including Colbert (1936, p. 12) and Churcher (1970, pp. 89–90).

In this section I have retained existing accepted generic identities and I also refer freely to the Giraffoidea, Giraffinae, Palaeotraginae and Sivatheriinae. Use of these names is not intended to indicate that I accept the generic names, groupings or rankings as valid and text figures in this section make my understanding of relations clear.

I accept the Giraffidae as a valid monophyletic group. Giraffids all have bilobed lower canines on which the accessory lobe forms approximately one third of the crown length. The P_4 is clearly divided into anterior and posterior regions and carries an independent transversely compressed central lingual cuspid. These features are apomorphic in comparison with those of *Canthumeryx* and are indicated in figure 4.

The giraffine (p. 209) and sivatheriine (p. 216) groups exhibit synapomorphies which suggest that the groups may be monophyletic; however members of the Palaeotraginae are not distinguished by any obvious apomorphic features. Colbert (1935*b*, p. 8) gives the following diagnosis of the Palaeotraginae:

> Primitive, medium-sized giraffids, having as a rule one pair of supraorbital frontal horn-cores. There may be a second pair of horn-cores at the anterior extremities of the frontals, horn-cores in the form of simple tines, well developed in the males, feebly developed or absent in the females. Skull usually elongated. Cheek teeth brachyodont, with moderately coarse sculpture of the enamel. Limbs and neck slightly elongated.

While Churcher (1970, p. 83) quoting Colbert (1938, p. 48) defines the group as:

> The generally primitive, medium-sized giraffes, characterized by limbs and necks of approximately normal length, and in most cases by a single pair of supraorbital, frontal, spike-like horns.

The presence of more than one pair of ossicones is apomorphic but refers to autapomorphies of the genus *Giraffokeryx* and the species *Palaeotragus quadricornis*. This feature is therefore not synapomorphic for the group Palaeotraginae and should never have been included in the diagnosis. With this exception none of the features is established as being apomorphic although later I suggest that the elongation of the neck and limbs may be used in assessing relations. There is therefore the strong possibility that the group Palaeotraginae is either paraphyletic or polyphyletic in the sense of Nelson (1971, p. 471) or paraphyletic in the sense of Hennig (1975, p. 248). In this context Nelson (1970, p. 381) states: 'any definition composed only of primitive characters, when used to group organisms, can consistently result at best in paraphyletic and polyphyletic groups . . .'. I suggest that it is very unlikely that the group Palaeotraginae as currently constituted can be a valid monophyletic grouping of the giraffes.

Churcher (1970, p. 85-86) lists species in the Palaeotraginae and suggests that some of these species may be invalid, even indicating the possibility of synonymizing some species, apparently on the basis of their stratigraphic occurrence:

> . . . the paucity of measurements and recorded material together with the illustrations available suggest that when population variation is taken into consideration the Palaeotraginae may possess fewer species. These appear to be a primitive African Middle and Upper Miocene species (*P. primaevus*), a more advanced Eurasian Upper Miocene species (*P. expectans*) and one or two more advanced Eurasian Lower Pliocene species (*P. rouenii* and possibly *P. microdon*) [Churcher 1970, p. 90].

Except for the omission of *Palaeotragus germani* (Arambourg 1959, pp. 97-116), Churcher (1970, pp. 85-86) gives a complete list. Species included are listed below while Churcher should be consulted for details of geographical and geological occurrence.

(*c*) *Palaeotraginae*

Triceromeryx pachecoi Villalta, Crusafont & Lavocat 1946
Giraffokeryx punjabiensis Pilgrim 1910
Palaeotragus primaevus Churcher 1970
P. tungurensis Colbert 1936
P. coelophrys (Rodler & Weithofer) 1890
P. microdon (Koken) 1885
P. rouenii Gaudry 1861
P. quadricornis Bohlin 1926
P. expectans (Borissiak) 1914
P. decipiens Bohlin 1926
P. germani Arambourg 1959

Samotherium boissieri (Forsyth Major) 1888
S. neumayri (Rodler & Weithofer) 1890
S. sinense (Schlosser) 1903
S. eminens (Alexejew) 1916
*S. tafeli** (Killgus) 1922
S. africanum Churcher 1970
Okapia johnstoni Lankester 1901

Before investigating relations in the Palaeotraginae it is necessary to establish the validity of the above species; to in effect define the units between which relationships can be suggested.

Attempts to distinguish species of *Palaeotragus* on a size basis are largely unsuccessful as the degree of overlap and wide size variations in species make confusion possible (table 38). *Palaeotragus germani* and *Palaeotragus decipiens* are exceptions as they are both very large, but larger *Palaeotragus* species could be confused with *Samotherium.*

Faced with this a brief review of relevant anatomical features is presented. This relies on a survey of literature backed by study of specimens in the British Museum (Natural History).

Triceromeryx pachecoi was described in detail by Crusafont-Pairó (1952, pp. 49–70). He suggested that the skull of *Triceromeryx* carried a pair of supraorbital ossicones and a strange forked ossicone in the supraoccipital region. Association of the forked 'ossicone' with the dental material has been questioned (Churcher 1970, p. 84; Hamilton 1973, p. 137) and I believe that a valid assessment of *Triceromeryx* can only be made on the basis of the dentition. Churcher (1970, p. 86) placed *Triceromeryx* with *Palaeotragus* while I (Hamilton 1973, p. 136) placed it in the Palaeomerycidae and I regard *Triceromeryx pachecoi* as a valid species.

The lower canine of *Triceromeryx* is not known so it cannot definitely be assigned to the Giraffoidea. However the lower premolars show apomorphies that strongly indicate giraffoid affinities. I have accepted *Triceromeryx* as a giraffoid but discovery of lower canines could confirm or refute this identification. Details of the premolars are described and discussed below (p. 206).

Palaeotragus primaevus has a molariform P_4 showing several features that are apomorphic relative to those of *Canthumeryx* (figure 4). However, when the P_4 of *Palaeotragus primaevus* is compared with that of *Palaeotragus rouenii* (figure 6), it presents many features that are relatively plesiomorphic. In comparison with its small dental dimensions the post-cranial elements of *P. primaevus* are surprisingly elongate (table 38). This species is clearly distinct from members of *Palaeotragus* such as *P. rouenii* and *Palaeotragus coelophrys* but confusion is possible with *Giraffokeryx.* The skull of *P. primaevus* (figure 38) carries only a single pair of ossicones in the supraorbital position. The front of the skull is broken but the bone continues far enough anteriorly to have shown indications of the presence of other ossicones had they been present. Therefore on this basis *P. primaevus* is distinguished from *Giraffokeryx.*

Distinction between *Palaeotragus primaevus* and *Palaeotragus tungurensis* is much more difficult. *P. tungurensis* is known from cranial and dental elements only. The upper premolars (Colbert 1936, figs 3 and 4) appear relatively uncompressed (table 38) and the lower premolars are also long without any marked shortening of the anterior region of the P_2. The P_3 and P_4 agree closely in pattern with those of *P. primaevus.* There is also close agreement in size between the two species (table 38) so that synonymy between *P. primaevus* and *P. tungurensis* seems very likely. For the rest of this section I refer to these species as *P. tungurensis* (*P. primaevus*) although most of my comments regarding this group are based on my study of the *P. primaevus* material.

As mentioned above the premolars of *Giraffokeryx punjabiensis* (figure 4) agree closely with those of *Palaeotragus tungurensis* (*P. primaevus*) and distinction on the basis of the dentition may

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* Not *Samotherium tateli* as in Churcher 1970.

TABLE 38

	P^2–M^3	P^2–P^4	M^1–M^3	P_2–M_3	P_2–P_4	M_1–M_3	humerus	Radio/ulna	Mc.III:IV	femur	tibia	Mt.III:IV
Canthumeryx	—	—	63	121	53	68	—	280	290	240	305	260
Triceromeryx	108	50	58	116.5	—	—	—	162	—	—	—	—
P. tungurensis	133–137	56–57	65–81	139–141	49–51	73–91	—	—	—	—	—	—
P. primaevus	125–160	53.5	65–74	112–133	49–54	65–80	—	488–489	440–446	—	497	404–460
G. punjabiensis	131.5	60	71.5	148.5	62.5	86	—	—	—	—	—	—
P. rouenii	118	52	68	127	55	76	—	—	403	—	—	401
P. microdon	121–129	53–57	67–75	130–136	47–50	80–93	314	396–480	368–430	348	398–430	401–420
P. coelophrys[c, d]	131–141	57–66	74–90	141–170	55–65	87–100	—	460	334–371	—	430	340–397
P. expectans	149	60	89	157.5	63	94.5	—	—	—	—	—	—
P. quadricornis	130–155	61–67	74–91	155–170	55–60[e]	—	—	—	—	—	—	—
P. decipiens	178	78–80[f]	108–120[f]	187–198	69–78	115–120	—	—	—	—	—	—
P. germani	176	74–77	103–110	—	—	—	—	595–630	457–522	427–490	525–552	525–583
Samotherium boissieri	195–205	84–86	118–128	200–250	74–84	130–133	455[a]	530–535[a]	410[a]	515[a]	525–530[a]	450–455[a]
var. *minor*	168–180	70–75	104–118	183–195	67–74	117–124	397[a]	461[a]	354[a]	449[a]	443[a]	380[a]
S. neumayri[a]	180–200[d]	74–78	110–128[c]	195–209	74–77[d]	125[d]–134[c]	—	490[c]	—	—	—	410–430[c]
S. sinense[a]	187–190	79	116	198	76	122	410–427	530–571	425–466	520–524	502–508	495–526
S. eminens[b]	189–207	74–78	116–128	192	76	120	—	570	415–430	550	510–550	522–460
S. tafeli	190[g]	—	—	—	—	—	—	—	—	—	—	—
Samotherium sp.	—	83	—	—	—	—	—	—	70	—	—	—
Okapia	118	52	66.5	125–136	50–55	78–85	280–300	310–380	270–310	290–330	310–350	300–330

Measurements from: (*a*) Bohlin (1926), (*b*) Alexejew (1916), (*c*) Rodler & Weithofer (1890), (*d*) Mecquenem (1924), (*e*) Schlosser (1921), (*f*) Schlosser (1903) (*g*) Killgus (1922).

not be possible. However the presence of an additional pair of ossicones in *Giraffokeryx* is autapomorphic and *Giraffokeryx punjabiensis* is therefore regarded as a valid species.

Palaeotragus quadricornis also has two pairs of ossicones; but the anterior ossicones are small (Bohlin 1926, p. 43). This contrasts with *Giraffokeryx* in which the ossicones of each pair are large (Colbert 1933). *Giraffokeryx* and *Palaeotragus quadricornis* are about the same size (table 38) but the upper premolars of *P. quadricornis* (Bohlin 1926, p. 44) are more compressed than those of *Giraffokeryx* (Colbert 1933, p. 333) with the anterior regions of the P^2 and P^3 showing marked shortening. The lower premolars also exhibit shortening with the anterior region of the P_2 very reduced in *P. quadricornis*. The P_4 of *P. quadricornis* shows apomorphic features (figure 6) resembling those of *Palaeotragus rouenii* while the P_3 is plesiomorphic relative to that of *P. rouenii*. *P. quadricornis* is accepted as a species distinct from *Giraffokeryx punjabiensis* and is distinguished from other species of *Palaeotragus* by the presence of two pairs of ossicones. It is, however, possible that this is merely a variation within another species of the genus and a similar situation occurs in the species *Samotherium tafeli* (p. 204).

The dentition of *Palaeotragus coelophrys* is consistently larger than that of *Palaeotragus microdon* (table 38) but its post-cranial elements are either smaller or about the same size. Measurements of post-cranial material are all taken from Rodler & Weithofer (1890) whereas dental measurements are from Bohlin (1926). This may invalidate comparisons by using dental and post-cranial material together. There may also be an element of circular argument in distinguishing *P. coelophrys* dental elements from those of *P. microdon* using size differences, as Bohlin (1926) probably used size differences to distinguish material of the two species in his descriptions and identifications. Bohlin, however, certainly used other distinctions, for example he states:

> Die permanente Bezahnung . . . Bei *P. microdon* sind die Marken der Prämolaren mehr zusammengedrückt. [Bohlin 1926, p. 27.]

In this feature *Palaeotragus microdon* is more apomorphic than *Palaeotragus coelophrys*. The molars of *P. microdon* have a more simple form than those of *P. coelophrys* with the crescents lacking accessory crests and projections of enamel. This feature is again commented on by Bohlin (1926, p. 27) and is also more apomorphic than the condition in *P. coelophrys*.

A surprising feature is the incidence of a P_1 in the specimen of *Palaeotragus coelophrys* figured by Bohlin (1926, pl. 3, fig. 5). This may possibly be a retained D_2 or it may truly be a P_1. It does not occur regularly, however, and I have not considered it in assessing relations. Features of the upper premolars, molars and lower premolars (p. 208) all allow *P. coelophrys* to be distinguished from *Palaeotragus microdon* and it is probably a valid species.

I was unable to find any records of post-cranial measurements for *Palaeotragus expectans*. Its upper premolars are more antero-posteriorly compressed than those of *Palaeotragus coelophrys* (table 38) and this compression is particularly evident if the anterior regions of the P^2 and P^3 (Borissiak 1915, pl. 1, fig. 1*c*) are compared with those of *P. coelophrys* (Bohlin 1926, pl. 2, fig. 2). The skull of *P. expectans* (Borissiak 1915, pl. 1, fig. 1) is similar to that of *Palaeotragus microdon* and the ossicones slope at the same angle. *P. expectans* is large but still in the size range of *P. coelophrys* (table 38). It may, however, be distinguished from *P. coelophrys*, *Palaeotragus rouenii* and *Palaeotragus microdon* by the plesiomorphic condition of its P_3 and P_2 while it can be distinguished from *Palaeotragus tungurensis* (*P. primaevus*) and *Giraffokeryx* by apomorphies of the P_4 and the greater compression of the premolars. Distinction between *P. expectans* and *Palaeotragus* *quadricornis* relies on details of the premolars (p. 209) and the presence of only a single pair of ossicones in *P. expectans*.

There does not appear to be any clear distinction between *Palaeotragus rouenii* and *Palaeotragus microdon*. Bohlin (1926, p. 36) indicates close similarity between the two species with the only marked distinction being features of the ossicones which are straight in *P. microdon* (Bohlin 1926, pl. 1, fig. 1) and curved in *P. rouenii* (Gaudry 1861, fig. 2). Bohlin (1926, p. 36) states:

> *Palaeotragus rouenii* ist dem *P. microdon* aus China sehr ähnlich und es ist nicht ausgeschlossen, das die Arten indentisch sind, doch ist das Material der beiden Arten noch zu unzureichend, um diese Frage mit Sicherheit zu entscheiden.

In all features of the dentition, particularly details of the lower premolars, these two species are indistinguishable. *Palaeotragus rouenii* has many apomorphic features. Its upper molars consist of labial and lingual crescents that are fully formed in contrast to those of, for example, *Canthumeryx* and there is some reduction of the antero-lingual region on the P^2 and P^3. The lower premolars (p. 208) may be used to distinguish *P. rouenii* and *Palaeotragus microdon* from all other giraffids. For the rest of this work these two species will be referred to as *P. rouenii* (*P. microdon*) to indicate their probable synonymy.

As mentioned above *Palaeotragus decipiens* is a very large species (table 38). Its size range overlaps those of *Palaeotragus germani* and species of *Samotherium*. Large size may be an apomorphic feature of *P. decipiens* and certainly distinguishes it from other species of *Palaeotragus* except *Palaeotragus germani*. This distinction is only of use, however, if the species is correctly identified with the genus *Palaeotragus*. The generic assignment of '*decipiens*' is discussed below.

Samotherium boissieri was the species on which the genus *Samotherium* was established by Forsyth Major (1888). It has well-developed ossicones and the lower premolars show features that are interpreted as characteristic of the genus and are used (p. 208) for establishing synapomorphies in the *Samotherium* group. Bohlin (1926, p. 87) established large and small varieties in the species *Samotherium boissieri* and these varieties appear to have coexisted in the Samos fauna. The P_4 and P_2 of *S. boissieri* show apomorphic features (p. 206, figure 5) while the P_3 appears plesiomorphic. Bohlin (1926, p. 92) discusses the variability of the P_3 in this species and indicates that the greatest variability with a small, poorly developed central lingual cuspid occurs most frequently in the smaller variety. In the British Museum (Natural History) specimens BMM 4224, 4234, 4235, 4236 and 4242 have the plesiomorphic P_3 pattern while there are no specimens with marked development of a central lingual cuspid. There is no doubt that *S. boissieri* is a valid species distinct from any of those described above. Some features of its dentition occur in other *Samotherium* species and may be used to distinguish between the two genera *Palaeotragus* and *Samotherium*.

The lower molars of *Samotherium boissieri* are much higher than those of *Palaeotragus rouenii* (*P. microdon*) and the cuspids are elongate. The P_4 shows marked reduction of the posterior region which forms only 22.2 % of the length of the tooth (table 39). This reduction is an apomorphic feature that is found in other species of *Samotherium*. The P_4 has a strongly developed central lingual cuspid that forms the face of the tooth (figure 5). The presence of this cuspid indicates close relation to the *Palaeotragus* group and is apomorphic relative to the P_4 of *Canthumeryx*. The central labial cuspid of the P_4 forms a large crescent that is continued as far as the postero-lingual corner of the tooth by the small postero-lingual cuspid of the posterior lobe. This strong crescent is an apomorphic feature that is developed on all three lower premolars of

S. boissieri. In the ruminants the lower premolars may become functionally molariform in one of two ways. The premolar can develop anterior and posterior lobes that are approximately equal in size with each consisting of a labial and lingual crescent. This gives an almost exact copy of a molar and this is found in the P_4 of *P. rouenii* (*P. microdon*) and several other species of *Palaeotragus*. Alternatively the premolar can develop a single lobe consisting of a labial and lingual cuspid. This method of molarization is found in *Samotherium boissieri* with the central region dominant but a reduced posterior region retained. *Samotherium sinense* is described in detail by Bohlin (1926, pp. 51–73). Its dentition and post-cranial skeleton agree closely in size with *S. boissieri*. Diagrams of the skull (Bohlin 1926, p. 84) suggest differences in the ossicones but Bohlin states that there is great variability in the ossicones so that these differences may have little significance. Wide variation is also found in the ossicones of other giraffids, e.g. *Sivatherium* (Harris 1974), and the taxonomic significance of this variation is probably relatively small.

The upper dentitions of *Samotherium boissieri* and *Samotherium sinense* are very similar. This similarity extends to details such as shortening of the premolar row (table 38), compression of the anterior ends of the P^2 and P^3 and development of accessory crests. Crown views of the lower dentition are not figured by Bohlin but an M_3 is figured by Schlosser (1903, pl. 9, fig. 7) and this resembles the same tooth in *S. boissieri*. Lower premolars are also figured by Schlosser (1903, pl. 9, fig. 10) but these teeth are difficult to interpret as they lack many of the features characteristic of other members of the genus *Samotherium*. The back part of the P_4 is very large; the central labial cuspid is not strongly crescentic even on the P_4 and a fork is present at the front but not the back of the central lingual cuspid. The P_3 also resembles *Palaeotragus* or *Giraffa* much more closely than *S. boissieri*. I think that these teeth are probably incorrectly identified with *S. sinense* and although there are real differences I suggest that closer agreement exists with the premolars of *Giraffa sivalensis* figured on the same plate (Schlosser 1903, pl. 9, fig. 17). Bohlin (1926, pp. 79–80) discusses the teeth of '*Alcicephalus sinensis*' figured by Schlosser and allocates them to several other species, he does not, however, mention the lower premolars or the M_3.

I suggest that *Samotherium boissieri* and *Samotherium sinense* are probably synonymous. From now on these two 'species' will be referred to as *S. boissieri* (*S. sinense*).

Samotherium tafeli was described by Killgus (1922, p. 251) on the basis of a skull that is not figured by either Killgus or Bohlin. Killgus identified this skull as a distinct genus: *Schansitherium tafeli* (Killgus 1922, p. 251). In his description he states that the skull roof is flat and the frontals carry two ossicones that are thick and slope outwards. These ossicones had roughened surfaces with spaces for blood vessels. Also at the front of the frontals there was another pair of ossicones consisting of two conical knobs of bone with smooth surfaces. There were also knobs of bone on the parietals. Killgus also states that the nasals were broad, a feature that contrasts with the usual (Bohlin 1926, p. 81) condition in *Samotherium*. Bohlin (1926, p. 81) suggests that *S. tafeli* is very closely related to *Samotherium sinense*. He suggests that the skull represents an aberrant individual and quotes a personal communication from De Chardin that a similar development of additional ossicones had been found on a skull of *S. sinense*. It is obviously not possible to synonymize these two species without study of the material but they are probably the same or at least very closely related. In the absence of descriptions of other elements of the skeleton, the relations of *Samotherium tafeli* cannot be assessed.

The skull and upper molars of *Samotherium neumayri* are similar to those of *Samotherium boissieri* (*S. sinense*). Its post-cranial skeleton (table 38) is not well known but the elements are small for a species of *Samotherium*. In general features *Samotherium neumayri* resembles *Samotherium boissieri*

(*S. sinense*); there are, however, differences of the premolars (p. 207) which suggest that *S. neumayri* may be a valid species.

Bohlin (1926, p. 94) thought that *Samotherium eminens* was distinct from *Samotherium sinense*. This conclusion was based on comparison of skeletal features; however Bohlin suggested close relation with the large variety of *Samotherium boissieri* and with *Samotherium neumayri*. The lower premolars do not help in assessing the relations of *Samotherium eminens*. They are figured under the name *Khersonotherium* (*Chersonotherium*) *eminens* by Alexejew (1916, pl. 5, fig. 6) but these are heavily worn and the crescentic form of the central labial cuspid is not clear. The P_3 has a well-developed central lingual cuspid but the apparent strength of this cuspid is always increased by heavy wear. *S. eminens* cannot be satisfactorily distinguished from other *Samotherium* species on a size basis and there is not enough known to establish its relations beyond Bohlin's suggestion that it is closely related to *S. boissieri*.

Samotherium africanum was described from Fort Ternan by Churcher (1970, p. 73). There is not enough known to establish the validity of this species. Indeed there is insufficient knowledge to establish its identity with the genus *Samotherium*. *Samotherium* is also recorded from north Africa (Stromer 1907, p. 118) but again insufficient is known for the validity of the identification to be established.

Table 39. Expansion or reduction of the posterior region of the P_4

$$P_4 : \frac{\text{length of posterior region}}{\text{length of whole tooth}} \times 100$$

Climacoceras gentryi	29.8 %
Canthumeryx sirtensis	29.7 %
Triceromeryx pachecoi	25.6 % (*a*)
Palaeotragus tungurensis	31.0 % (*b*)
P. primaevus	31.4 %
Giraffokeryx punjabiensis	34.8 %
Palaeotragus coelophrys	35.9 % (*c*)
P. microdon	34.1 % (*d*)
P. rouenii	35.0 %
P. quadricornis	34.4 % (*e*)
P. expectans	22.0 % (*f*)
P. decipiens	21.4 % (*g*)
Samotherium boissieri	22.2 %
S. neumayri	20.9 % (*h*)
S. eminens	21.2 % (*i*)
Sivatherium giganteum	31.4 %

Measurements were taken from figures of specimens as indicated.

(*a*) Crusafont (1952), (*b*) Colbert (1936), (*c*) Mecquenem (1924), (*d*) Schlosser (1903), Bohlin (1926), (*e*) Bohlin (1926), (*f*) Borissiak (1914), (*g*) Bohlin (1926), (*h*) Bohlin (1926), Rodler & Weithofer (1890), Mecquenem (1924), (*i*) Alexejew (1916).

(*d*) *Indications of relations based on features of the lower premolars*

A lower premolar pattern like that found in *Canthumeryx* (figures 4 and 25; Hamilton 1973, pl. 1, fig. 5) is regarded as plesiomorphic for the giraffids. It shows apomorphies in the presence of a weak central lingual cuspid on the P_4, the beginning of separation of the back and central regions and a well developed postero-lingual wing on the central cuspid of the P_3. These features indicate close relationship to the giraffids and suggest that *Canthumeryx* is more closely related to the giraffids than *Climacoceras* (figure 2*a*) which lacks these apomorphies. This supports relations as indicated in figure 2*a* with *Climacoceras* as the sister-group of *Canthumeryx* plus the giraffids, and *Canthumeryx* as the sister-group of the giraffids.

The P_4 of *Triceromeryx* (Crusafont-Pairó 1952, pl. 13) is more apomorphic than that of *Canthumeryx* because its central lingual cuspid is separated from the central labial cuspid and the posterior region of the tooth is fully separated from the central region (figure 4). The specimen figured by Crusafont is lightly worn and the central lingual cuspid has a rounded wear trace. Even with further wear this would not reach the transversely compressed form found in *Palaeotragus tungurensis* (*P. primaevus*) or *Giraffokeryx*. The back of the central labial cuspid is forked in *Triceromeryx* as in *P. tungurensis* (*P. primaevus*) and *Giraffokeryx*, a feature that is apomorphic relative to that found in *Canthumeryx* but is plesiomorphic relative to the condition of *Palaeotragus rouenii* (*P. microdon*).

The P_3 of *Triceromeryx* agrees closely with that of *Palaeotragus tungurensis* (*P. primaevus*) and *Giraffokeryx* and the P_2 provides no evidence that can be used to assess relations. Assessment must therefore be based entirely on features of the P_4 (figure 4). The development of the lingual central cuspid, the posterior region and the antero-lingual region shows that *Triceromeryx* is more closely related to *P. tungurensis* (*P. primaevus*) and *Giraffokeryx* than it is to *Canthumeryx*. This means that it has sister-group relation to the giraffids as indicated in figure 9.

The P_4 of *Palaeotragus tungurensis* (*P. primaevus*) shows major apomorphies relative to the P_4 condition found in both *Canthumeryx* and *Triceromeryx*. The central lingual cuspid is compressed and forms the complete lingual wall of the anterior and central parts of the tooth. This cuspid is separated from the labial cuspid by a deep antero-posterior fossettid but forking of the anterior and posterior ends of the central labial cuspid indicates reduced cross-crests. The posterior region of the P_4 is separated from the central region (figures 4, 31, 32) and consists of a labial crescent and a lingual crest. The labial crescent is not clearly shown in Colbert's drawings of the P_4 of *P. tungurensis* (reproduced here in figure 4) but this may be a wear factor. The P_3 shows no apomorphic features that can be used to assess relations in *P. tungurensis* (*P. primaevus*). The P_4 of *Giraffokeryx* (figure 4) is very similar to that of *P. tungurensis* (*P. primaevus*) and neither. possesses apomorphies of the premolars that allow closer relations to be suggested with other groups of giraffids. Other features of the skeleton are therefore used to assess the relations of these two giraffids.

(*e*) *The* Samotherium *group*

In the *Samotherium* group, the P_4 shows two clearly defined apomorphies. The central region of the tooth is greatly expanded, the posterior region is reduced (table 39) and the central labial cuspid has a strong crescentic form which is continued by the reduced postero-lingual cuspid so that these two cuspids together make a broad curve from the antero-lingual to the postero-lingual corners of the tooth. This crescentic cuspid form is clearly shown in *Samotherium boissieri* (figure 5) and *Samotherium neumayri* (figure 5) but becomes less evident after the P_4 becomes heavily worn (see, for example, figure 5). The reduction of the posterior region of the tooth (table 39) remains relatively well marked even in heavily worn dentitions. Some refinement of relations is possible by using features of the P_3 and even the P_2.

Samotherium boissieri and *Samotherium neumayri* show development of the crescentic cuspid on the P_4. This feature is also found on the P_3 (figure 5) except after heavy wear, and on the P_2 (figure 5, BMM 4224). The central lingual cuspid is always well developed and transversely compressed on the *Samotherium* P_4 but the central lingual cuspid of the P_3 usually retains a circular wear trace until very late in wear (figure 5). The central lingual cuspid is transversely

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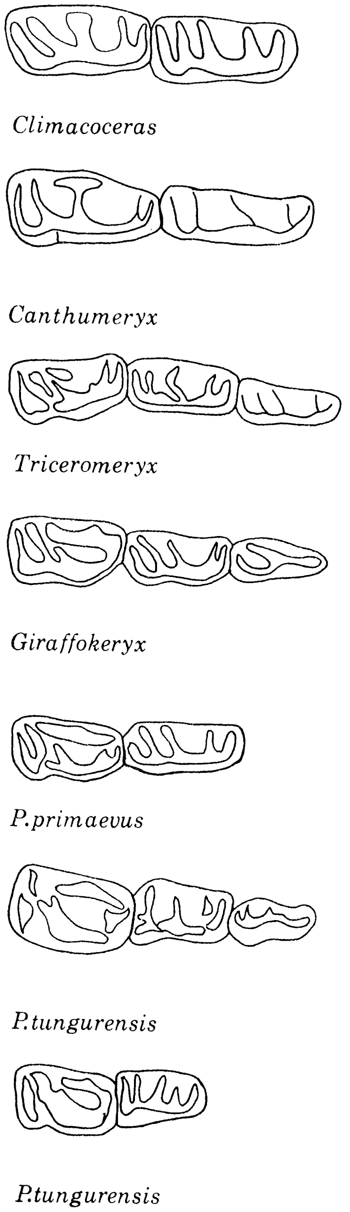

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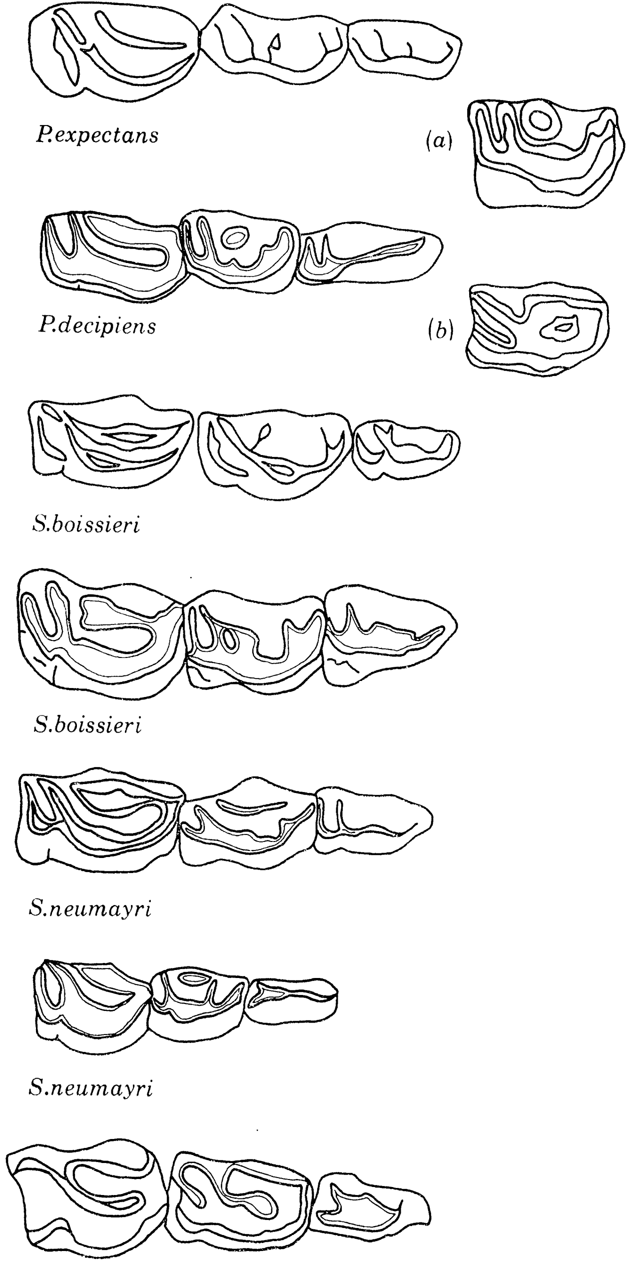

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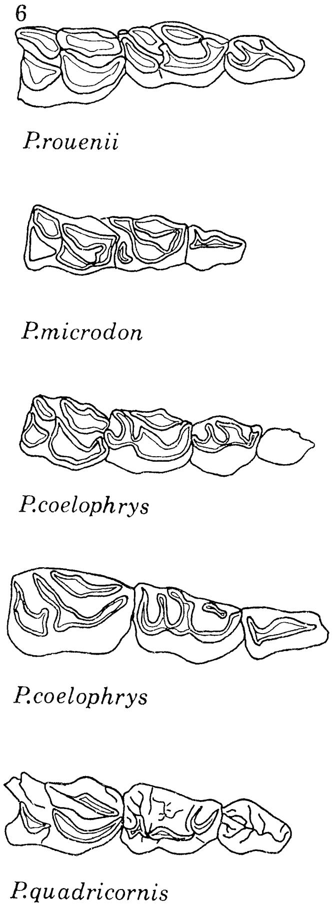

FIGURE 4. Crest and cuspid patterns on the lower premolars of giraffoids. *Climacoceras:* right P_{3-4}, × 1.6. *Canthumeryx:* right P_{3-4}, × 1.0. *Triceromeryx:* right P_{2-4}, × 0.9 (from Crusafont 1952). *Giraffokeryx:* right P_{2-4}, × 0.7 (from Colbert 1933). *Palaeotragus primaevus:* right P_{3-4}, × 0.8. *Palaeotragus tungurensis:* right $P_{2-\bar{4}}$, × 0.8 (from Colbert 1936). *Palaeotragus tungurensis:* right P_{3-4}, × 0.8 (from Colbert 1936).

FIGURE 5. Cuspid patterns of the lower premolars of giraffoids II. *Palaeotragus expectans:* right P_{2-4}, × 0.9 (from Borissiak 1914). *P. decipiens:* right P_{2-4}, × 0.7 (from Bohlin 1926); (*a*) right P_3 (from Bohlin 1926, fig. 47); (*b*) right P_3 (from Bohlin 1926, fig. 46). *Samotherium boissieri:* right P_{2-4}, × 0.8. *S. neumayri:* right P_{2-4}, × 0.7 (from Rodler & Weithofer 1980). *S. neumayri:* right P_{2-4}, × 0.5 (from Mecquenem 1924). *S. eminens:* right P_{2-4}, × 0.74 (from Alexejew 1916).

FIGURE 6. Cuspid patterns of the lower premolars of giraffoids III. *Palaeotragus rouenii:* right P_{2-4}, × 0.7. *P. microdon:* right P_{2-4}, × 0.6 (from Bohlin 1926). *P. coelophrys:* right P_{1-4}, × 0.5 (from Bohlin 1926). *P. coelophrys:* right P_{2-4}, × 0.7 (from Mecquenem 1924). *P. quadricornis:* right P_{2-4}, × 0.66 (from Bohlin 1926).

compressed on the P_3 of *Samotherium neumayri* figured by Rodler & Weithofer (1890, pl. 3, fig. 4). This is a lightly worn specimen but the tooth figured by Mecquenem (1924, pl. 2, fig. 2) has a more rounded central lingual cuspid even though this specimen is more heavily worn. As mentioned above (p. 203), the central lingual cuspid of the P_3 has a circular wear trace in the more lightly worn specimens in the collections of the British Museum (Natural History). The strongly developed crescentic cuspid pattern that extends to the anterior premolars suggests that *Samotherium boissieri* and *S. neumayri* are closely related and they are here identified as sister-species.

The P_4 of *Palaeotragus expectans* (Borissiak 1914, pl. 1, fig. 7) resembles that of *Samotherium boissieri* which suggests relation to the *Samotherium* group. This suggestion is, however, based on interpretation of a single figured specimen and therefore cannot be regarded as conclusive. The P_3 of *P. expectans* lacks any development of a crescentic form on the central-lingual cuspid and shows no marked reduction of the posterior region.

The P_4 of *Palaeotragus decipiens* (Bohlin 1926, pl. 4, fig. 8) shows the crescentic central labial cuspid and reduction of the posterior region; while the P_3 (Bohlin 1926, p. 33, fig. 47; Schlosser 1903, pl. 9, fig. 22) shows reduction of its posterior region and development of an independent central lingual cuspid. The crescentic cuspid pattern of the P_4 and P_3 in *P. decipiens* suggest that this species is closely related to the *Samotherium* group and the reduction of the posterior region of the P_3 with an independent central lingual cuspid indicates that *P. decipiens* is more closely related than *Palaeotragus expectans* to *Samotherium boissieri* (*S. sinense*) and *Samotherium neumayri*. The posterior regions of the premolars are more reduced in *Samotherium boissieri* and *Samotherium neumayri* than in *P. decipiens* and the posterior region of the P_2 is reduced in the two *Samotherium* species but not in *P. decipiens;* therefore relations as in figure 9 are suggested.

(*f*) *The* Palaeotragus *group*

In the *Palaeotragus* group the P_4 has a large posterior region that is usually about one third the length of the tooth (table 39) and is thus expanded over the plesiomorphic condition of *Canthumeryx* and *Climacoceras*. The apomorphic P_4 condition is found in *Palaeotragus rouenii* (*P. microdon*) in which the posterior region of the P_4 is clearly separated from the anterior region (figure 6) and is relatively large. The postero-labial cuspid is crescentic and the postero-lingual cuspid has a diagonal orientation and is similar in appearance to the entoconid of a molar. The central labial cuspid is crescentic and does not fork at either end. The central lingual cuspid runs antero-posteriorly and resembles the metaconid of a molar. The cuspids lack accessory crests and the P_4 is almost fully molariform. This pattern is found in *P. rouenii* (*P. microdon*) and *Palaeotragus coelophrys* (Bohlin 1926, pl. 3, fig. 5). The P_3 of *P. rouenii* (*P. microdon*) (figure 6) has a pattern that is similar to that of the P_4 of *Palaeotragus tungurensis* (*P. primaevus*) and *Giraffokeryx punjabiensis*, a fact that was commented on by Colbert (1936, p. 13). Apomorphies of the P_3 are the separation of the anterior and posterior regions with the posterior region approaching a molariform condition (figure 6) and the strong development of an independent central lingual cuspid. The central labial cuspid curves from the front of the tooth but forks at its posterior end and does not develop the smooth curve from the antero-lingual to the postero-lingual corners that is found in members of the *Samotherium* group. An apomorphic feature of the P_2 is the development of a strong postero-lingual crest from the face of the central labial cuspid.

On the basis of the lower premolars it is suggested that *Palaeotragus coelophrys* is the sister-species of *Palaeotragus rouenii* (*P. microdon*) as they show synapomorphies of the third and fourth premolars. *Palaeotragus quadricornis* shows apomorphies of the P_4 that are similar to those exhibited by *P. rouenii* (*P. microdon*) and *P. coelophrys*. The P_3, however, shows the plesiomorphic crest arrangement with no marked development of the central lingual cuspid. *P. quadricornis* is therefore related to the other two species on a sister-group basis (figure 9).

(*g*) *Relations in the Giraffinae*

Beyond indicating its inclusion in the Giraffidae, the lower premolars of *Giraffa* cannot be used to establish its relations. The most obvious features of *Giraffa* are the long limbs and neck. It has usually been assumed that these are 'advanced' features without any attempt being made to quantify them. Graphs in McMahon (1975, figs 2, 4–7) show that *Giraffa* differs markedly from other ruminants in features of its limbs. In an attempt to quantify some features of *Giraffa* limbs I used the metapodials. These bones are easily handled so that a large number of measurements can be taken quickly. They are also frequently preserved as fossils. Graphs (figures 7 and 8) indicate that the cannon-bones of *Giraffa* are very elongate and slender but that relatively they are no longer or more slender than those of many smaller ruminants. The apomorphic feature appears to be the presence of such slender cannon-bones in such a large animal. Figure 8 shows that all giraffes are large and that most have long slender cannon-bones: however *Palaeotragus rouenii* (*P. microdon*) and *Palaeotragus coelophrys* agree more closely with *Giraffa* than any of the sivatheres or the *Samotherium* group and relations are tentatively suggested on this basis (figure 9). The limbs of *Palaeotragus tungurensis* (*P. primaevus*) are very long and slender and relations with *Giraffa* rather than *P. rouenii* (*P. microdon*) may be suggested on this basis.

In the ruminants frontal appendages: horns, antlers or ossicones, are primitively in the extreme lateral supraorbital position, as demonstrated by *Canthumeryx* (Hamilton 1973, pl. 3), *Antilocapra* and many bovids and cervids. In the giraffid group this ossicone position is found in *Palaeotragus tungurensis* (*P. primaevus*), *Samotherium boissieri* (*S. sinense*) (Bohlin 1926, pl. 6, fig. 3), *Palaeotragus coelophrys* (Bohlin 1926, pl. 1, fig. 3), *Palaeotragus rouenii* (*P. microdon*) (Gaudry 1861, p. 388; Bohlin 1926, pl. 1, fig. 1). Therefore any different position of the ossicones will be apomorphic. In *Giraffa* the ossicones are positioned posteriorly so that they are supported by the parietals instead of the frontals and they lie near the mid-line of the skull. Other apomorphic features of *Giraffa* are its large size and features of the skull roof. Frontal and parietal sinuses are extremely well developed, the ossicones have clubbed rather than pointed tips, a feature not found in other giraffids but indicated in *Triceromeryx* (Crusafont-Pairó 1952, pl. 10). In the males of *Giraffa camelopardalis* a nasal ossicone is developed. These apomorphies of *G. camelopardalis* distinguish it from any giraffids mentioned so far. The long slender limbs are an important feature that indicates close relation to the *Palaeotragus* group. I have interpreted the presence of elongate limbs and neck as indicating that the giraffines are the sister-group of the *Palaeotragus* group. Other features may suggest different interpretations of relations. The posterior position of the ossicones, well developed frontal sinuses and brachycephaly of *Giraffa* are features also found in *Sivatherium*. I interpret these similarities as due to convergence and similar features often occur in other ruminants. Edinger (1950) gives numerous examples of the independent evolution of large frontal sinuses; the frontal appendages are shifted posteriorly in many bovids, e.g. *Taurotragus*, *Oryx* and *Alcelaphus*. Brachycephaly occurs in many large ruminants and its development may be associated with large body size. Long

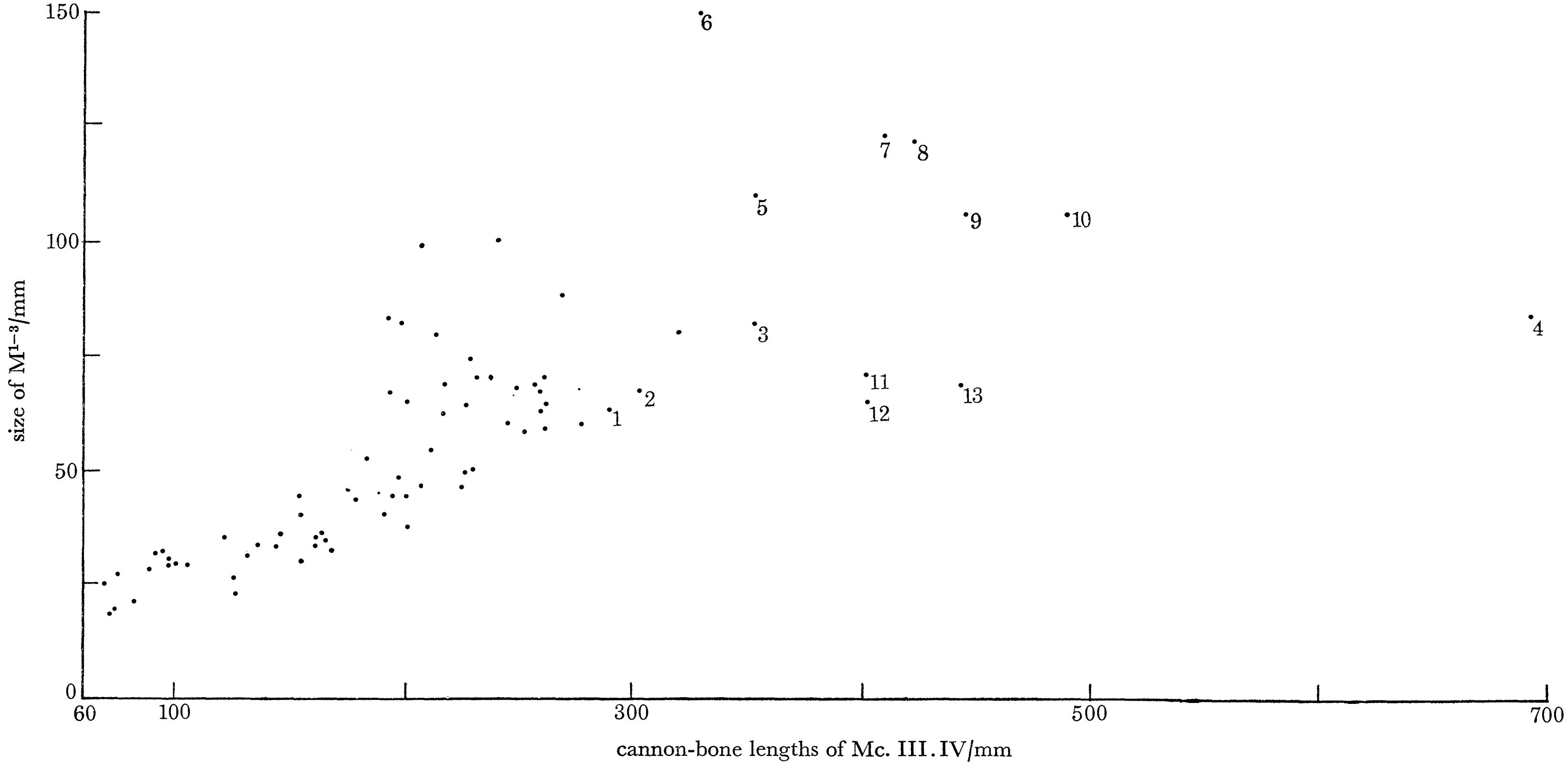

FIGURE 7. Cannon-bone lengths (Mc. III.IV) in relation to size (M^{1-3}) in the ruminants. Giraffids are consistently large with long cannon-bones but *Canthumeryx sirtensis* and *Okapia johnstoni* agree approximately with the other ruminants. (1) *Canthumeryx sirtensis*, (2) *Okapia johnstoni*, (3) *Palaeotragus coelophrys*, (4) *Giraffa camelopardalis*, (5) *Samotherium boissieri* var. *minor*, (6) *Sivatherium giganteum*, (7) *Samotherium boissieri* var. *major*, (8) *S. eminens*, (9) *S. sinense*, (10) *Palaeotragus germani*, (11) *P. microdon*, (12) *P. rouenii*, (13) *P. primaevus*.

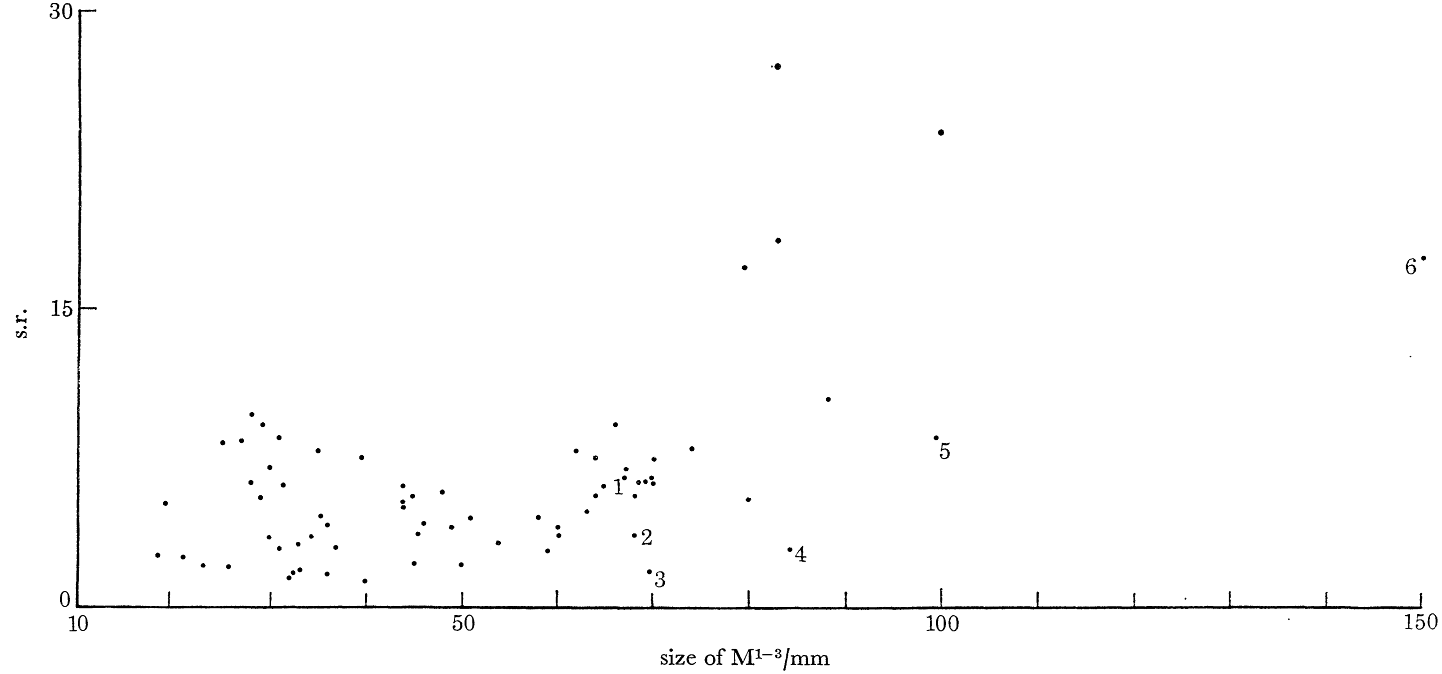

FIGURE 8. Slenderness of the cannon-bones (Mc. III.IV) in ruminants. The slenderness ratio (s.r.) is derived from the expression s.r. = [(minimum width of shaft)/(length of cannon-bone)] × 100. M^{1-3} is assumed to be approximately proportional to body size. (1) *Okapia johnstoni*, (2) *Palaeotragus rouenii*, (3) *Palaeotragus primaevus*, (4) *Giraffa camelopardalis*, (5) *Samotherium boissieri*, (6) *Sivatherium giganteum*.

limbs also occur in other ruminant groups and the cannon-bones of the elk *Alces alces* agree closely in slenderness with those of *Giraffa*. However lengthening of the limbs and neck only occurs in the gerenuk *Litocranius* and closely related genera, and in the camels.

Giraffa gracilis was described by Arambourg (1947, p. 208), from Omo, and later discoveries at Olduvai are mentioned and figured by Leakey (1965, p. 35). This species is smaller and more slender than *Giraffa camelopardalis* and shows a more apomorphic feature in the presence of a well-developed central lingual cuspid on the P_3 (Arambourg 1947, p. 364). This is, however, a very heavily worn tooth (Arambourg 1947, pl. 21) and the apparent strength of the cuspid is partly a wear factor. The limbs and P_4 suggest that *G. gracilis* is more closely related to *G. camelopardalis* than any of the *Palaeotragus* group.

Giraffa jumae was described briefly by Leakey (1965, pp. 35–36) and the type skull of this species is BMM 14957. This species agrees closely with *Giraffa camelopardalis*. In the absence of a skull of *Giraffa gracilis*, *G. jumae* is the only fossil giraffe with a nasal ossicone. Differences of the posterior ossicones (Leakey 1965, p. 36, footnote 1) and slight size differences distinguish this species from *G. camelopardalis* but it agrees very closely with the living species. Relations as in figure 9 are suggested for these three giraffes.

Colbert (1935*a*, *b*), Matthew (1929, p. 546) and Bohlin (1926) grouped *Orasius* and *Honanotherium* as giraffines. This was followed by Simpson (1945) except that following Matthew's (1929, p. 546) suggestion he used the name *Bohlinia* instead of '*Orasius*'. Crusafont-Pairó (1952, p. 188) groups *Giraffa*, *Honanotherium* and his new genus *Decennatherium* in the Giraffinae but places *Bohlinia* with *Okapia* in the Okapiinae.

Schlosser (1903, p. 103) states that skeletal elements of *Honanotherium schlosseri* agree closely with *Giraffa camelopardalis*. Bohlin (1926, p. 102, fig. 148; pl. 10, figs 1, 2) shows that the ossicones of *Honanotherium* were supraorbitally positioned and therefore the genus is plesiomorphic when compared with *G. camelopardalis*. However Bohlin (1926, p. 102, fig. 148) indicates that the ossicones were relatively massive which suggests relation with either the sivatheres or giraffines. Relation with the giraffines is more likely because the post-cranial skeletons of *Honanotherium* and *Giraffa* are very similar. Bohlin (1926, p. 102) mentions the development of sinuses in the frontal and parietal regions.

Honanotherium sivalense (syn. *Camelopardalis sivalensis* Falconer and Cautley 1843) is a large long-limbed giraffid (Lydekker 1883; Pilgrim 1911) but its skull is not known and detailed relations cannot be established. Matthew (1929, p. 549) disagrees with Bohlin's transfer of this species to *Honanotherium* and suggests closer affinities with *Bohlinia* or *Giraffa*. In this situation, the species is best retained as '*Giraffinae indet.*' under its usually accepted name of *G. sivalensis*. Reasons for using the generic name *Bohlinia* as a synonym of *Orasius* are discussed by Matthew (1929, p. 546). A synonym list for *Bohlinia attica* is given by Bohlin (1926, p. 123), who describes an almost complete skull (Bohlin 1926, p. 123, fig. 195) from Pikermi. Bohlin (1926, p. 125) suggests that the ossicones of this species are shifted posteriorly and towards the mid-line of the skull. Post-cranial material of *B. attica* is figured by Gaudry (1862–7) and the synonymy between Gaudry's species *Camelopardalis attica* and *B. attica* is indicated by Bohlin (1926, p. 123). This species has limb bones that are as long and slender as those of *Giraffa*. This coupled with features of the skull suggests close relation between this species and *Giraffa*. *Bohlinia* is more advanced than *Honanotherium* in features of the ossicones and is therefore identified as the sister-genus of *Giraffa*.

Decennatherium was established by Crusafont-Pairó (1952, p. 76) on the basis of dental and post-cranial elements. He placed this genus in the Giraffinae, mainly on the basis of his interpretation of the dental material. Reasons for allocation of *Decannatherium* to the Giraffinae are possibly correct but there is no basis on which to assess relations beyond this.

Relations in the Giraffinae are as indicated in figure 9 with *Decennatherium pachecoi* and '*Giraffa*' *sivalensis* placed as *Giraffinae indet.* with the qualification that the naming of the latter species as '*Giraffa*' does not indicate congeneric relation to the other three species that are assigned to this genus.

The sister-group relation of the Giraffinae and the *Palaeotragus* group was indicated above but this suggestion raises the problem of the correct relation of *Palaeotragus quadricornis*. The post-cranial skeleton of *P. quadricornis* is not known and the suggestion of sister-group relation with *Palaeotragus coelophrys* plus *Palaeotragus rouenii* (*P. microdon*) depended (p. 209) on features of the P_4. The posterior region of the P_4 appears (table 39) to be enlarged in *P. quadricornis* and this character suggests close relation to *P. coelophrys* and *P. rouenii* (*P. microdon*) even though its P_3 is as plesiomorphic as that of *Giraffa camelopardalis*. I am fully aware that this is slender evidence on which to suggest this relation. However, it should be clear that here it is the exact relation of *P. quadricornis* that is in question and the sister-group relation of the Giraffinae and the *Palaeotragus* group is not questioned here.

(*h*) *The relations of* Okapia

Assessments of relations of the okapi have been presented regularly ever since it ceased to be a zebra (Sclater 1901). Perhaps the two most divergent opinions have been those of Bohlin (1926) on the one hand and Matthew (1929) and Colbert (1935, 1938) on the other. Bohlin suggested that *Okapia* should be placed in the Okapiinae and he suggested close relationship to *Giraffa*. Colbert (1938) grouped *Okapia* with *Palaeotragus* and he stated that *Okapia* is 'in many ways more primitive than the earliest of the fossil giraffes' (Colbert 1938, p. 63). This assessment was based on an impressive list of characters and I believe that Colbert's case is convincing. If this assessment is correct then *Okapia* may be identified as the sister-group of the rest of the giraffids. An assessment of features used by Colbert should, therefore, show that the rest of the giraffids are more closely related to each other than any is to *Okapia*.

The skull of *Okapia* carries an assortment of characters that allowed Bohlin and Colbert to make their conflicting assessments. Frontal sinuses are well developed in *Okapia*, *Giraffa* and *Sivatherium* but they are not well developed in *Palaeotragus rouenii* (*P. microdon*), *Samotherium boissieri* (*S. sinense*) or *Honanotherium*. The ossicones are positioned slightly posteriorly in *Okapia*. This could suggest relations with the giraffines and sivatheres but Bohlin (1926) and Colbert (1938) both mention the correlation between the posterior shifting of the ossicones and the development of large frontal sinuses. If these really are correlated features then it is the development of frontal sinuses that is important with, at least, the initial posterior shifting of the ossicones occurring as a direct consequence. Edinger (1950) has demonstrated the frequent and sporadic occurrence of large frontal sinuses in almost every major group of larger mammals which indicates that these sinuses have developed in parallel many times. They could therefore have occurred in parallel in the sivatheres, giraffines and *Okapia*. In this situation the slight posterior shift of the ossicones may not be significant but I still interpret the greater posterior shift in, for example, *Sivatherium*, *Bramatherium* and *Giraffa* as being of use in assessing relations.

Colbert (1938) states that the orbit of *Okapia* lies over the front of the M^1 but its position is somewhat variable. An anteriorly situated orbit is found in *Canthumeryx* and in several cervids and bovids that are regarded as plesiomorphic on the basis of other independent features. Of course the fact that a species exhibits some plesiomorphic features is no assurance that it will show a plesiomorphic condition in other features. Indeed Nelson (1970, p. 381) states that it is not even evidence supporting the suggestion that it will be plesiomorphic in these features. Fortunately in this instance the assumed plesiomorphic condition is also present in the tragulids which are the extant sister-group of the ruminants. The orbit is more posteriorly situated in members of the *Palaeotragus* and *Samotherium* groups and in the sivatheres and giraffines. This feature suggests that these giraffes are more closely related than any is to *Okapia*.

The presence of a long postorbital region on the skull is related to the position to the orbit, so an anteriorly positioned orbit and long postorbital region are complimentary features. If the distance from the back of the skull to the back of the M^3 is used more accurate comparisons of the length of the posterior region of the skull are possible. *Okapia* has a long posterior region on the skull, a feature in which it agrees with *Canthumeryx*, *Hyemoschus* and some of the more plesiomorphic cervids and bovids. Members of the giraffines, sivatheres, *Samotherium* and *Palaeotragus* groups all have shorter posterior regions on their skulls which is a synapomorphy distinguishing them from *Okapia*. However, in contrast to Colbert's interpretation, *Giraffokeryx* is shown to be more plesiomorphic, having a longer posterior region on its skull even though its 'postorbital' region is shorter.

The angle between the basicranial and basipalatal axes of the skull increases as the skull becomes more flexed and as may be expected the brachycephalic giraffines and sivatheres have a high angle. This angle is also high in *Samotherium* but is lower in *Palaeotragus* though still somewhat higher than in the skull of *Okapia*. This angle is small in *Canthumeryx* and *Hyemoschus* and a higher angle may be regarded as an apomorphic feature indicating close relation between *Samotherium*, *Palaeotragus*, *Giraffa* and *Sivatherium*.

Several other features of the skull are also used by Colbert. The narrowness of the frontals in *Okapia* appears to be a secondary specialization as *Canthumeryx*, *Giraffa*, members of the *Palaeotragus* and *Samotherium* groups and males of *Sivatherium* all have wide frontals while *Okapia*, females of *Sivatherium**, tragulids and many cervids have narrow frontals.

The tympanic bullae are large in *Okapia*, *Giraffokeryx*, *Canthumeryx*, *Palaeotragus tungurensis* (*P. primaevus*) and *Bramatherium* but they are small in *Giraffa* and members of the *Palaeotragus* group. The large bullae is the plesiomorphic condition but small bullae may have developed independently in the *Giraffa* and *Palaeotragus* groups. The distribution of large bullae in the giraffids suggests that this feature cannot be used to assess relations.

The D^3 of *Okapia* and *Giraffa* lacks a labial cingulum but a labial cingulum is present on the D^3 of *Palaeotragus* and *Sivatherium*. This feature was regarded as important by Bohlin but was rejected by Colbert. The presence of a labial cingulum on the D^3 of *Okapia stillei* (Dietrich 1941) suggests that this character was lost independently in *Okapia johnstoni* and *Giraffa camelopardalis*. Small ossicones are present in *Triceromeryx* (Crusafont-Pairó 1952, pl. 11) probably *Canthumeryx* (Hamilton 1973, p. 3) and *Okapia* but in all the males of the advanced giraffes the ossicones are much larger. Small ossicones may be regarded as the plesiomorphic condition and the larger ossicones of *Giraffa*, the *Palaeotragus* and *Samotherium* groups and male sivatheres may be regarded as indicating closer relation while the large ossicones of *Climacoceras* must on this interpretation have arisen in parallel.

The development of the frontal sinuses and the correlated posterior shift of the ossicones

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* *Indratherium:* identified as *Sivatherium* female by Murie 1871.

can be regarded as features that have developed in parallel in *Okapia*, the sivatheres and the giraffines while the loss of the labial cingulum of the D^3 has occurred in parallel in *Okapia* and *Giraffa*. Alternatively the posterior position of the orbit, reduction in length of the posterior region of the skull, development of flexion of the skull and increased size of the ossicones can be regarded as parallel developments in *Giraffa* and the *Palaeotragus* and *Samotherium* groups while most of these features would also have developed in parallel in the sivatheres. There is again no shortage of examples of other ruminants in which these features have clearly developed in parallel.

Colbert also concluded that the post-cranial skeleton of *Okapia* was primitive. The proportions of the cannon-bones (figures 7 and 8) show that *Okapia* is little different from other ruminants of the same size while its general limb proportions agree closely with those of the cervids and bovids. Specializations of the ankle (Fraipont 1907, pp. 78–79) are autapomorphic in *Okapia*. The okapi has a short neck and specializations of the lower cervical region (Fraipont 1907; Lankester 1908) are also autapomorphic in *Okapia*. In contrast the cannon-bones in the *Palaeotragus* and *Samotherium* groups and the giraffines show lengthening and the limbs are long in these groups. Even the sivathere cannon-bones show more elongation than those of *Okapia*. In the *Palaeotragus* and *Samotherium* groups and in the giraffines there is also lengthening of the neck.

The limbs of some cervids, particularly *Alces alces* and some bovids particularly *Litocranius* and *Ammodorcas*, are elongate and in these two bovids there is also marked lengthening of the neck. This demonstrates the potential for convergent evolution of these features in the ruminants. The vertebrae of *Canthumeryx* also suggest some elongation of the neck (p. 181) but the cannon-bones and other limb bones suggest a ruminant with limb proportions like those of *Okapia*.

The post-cranial features therefore suggest that the sivatheres, giraffines, *Palaeotragus* and *Samotherium* groups are closely related while *Okapia* cannot be placed in this grouping. Therefore my interpretation of the post-cranial region does not conflict with the interpretation of the cranial features presented above. If this interpretation of the post-cranial features is correct then it places restrictions on how the cranial features can be interpreted. If following Bohlin *Okapia* is regarded as closely related to *Giraffa* then during the evolution of *Okapia* the long limbs must have been secondarily lost. Alternatively we must suggest that the frontal sinuses are convergently developed features in *Okapia* and *Giraffa*.

On the basis of my interpretation of the cranial and post-cranial features of *Okapia* I therefore suggest that the sivatheres, giraffines and the *Samotherium* and *Palaeotragus* groups are more closely related to each other than any is to *Okapia* which is in turn more closely related to this group than *Canthumeryx* or *Triceromeryx*. Therefore *Okapia* is the sister-group of the advanced giraffids (figure 9).

Okapia stillei is recorded from Olduvai (Dietrich 1941). This species may be correctly identified with *Okapia* and is distinguished from *Okapia johnstoni* partly on the basis of the deciduous dentition: 'An okapi-like creature with palaeotragine milk molars' (Leakey 1965, pp. 34–35). The presence of a labial cingulum on the D^3 of *Okapia stillei* suggests that the loss of the cingulum in *O. johnstoni* and *Giraffa camelopardalis* occurred in parallel and does not indicate close relationship between these two species.

(*i*) *The Sivatheriinae*

Sivatheres are large, short-limbed giraffids characterized by the presence of large complicated ossicones in the males. Restorations of the skull of *Sivatherium giganteum* are figured by many authors including Colbert (1935, p. 347) and Murie (1871). There are two pairs of ossicones: the anterior pair are small, conical supraorbital spikes while the posterior pair is on the parietals and the back of the frontals and are flattened with the anterior edge thick and rounded. I do not think that the mere existence of complex ossicones can be used for assessing relationships (p. 196) but close similarity can of course be used. *Sivatherium* is extremely brachycephalic and this may be an advanced feature.

Sivatherium giganteum is known from Asia and most of the African members of the Sivatheriinae are in the species *Sivatherium olduvaiense* (Singer & Bone 1960, p. 491) which is also referred to as *Libytherium olduvaiensis* by Leakey (1965). Arambourg (1960) synonymized *Libytherium* and *Sivatherium* after reinterpreting Pomel's (1892) specimen of *Libytherium maurusium* (not *Libytherium maurusicum:* Bohlin 1926, p. 162). Arambourg also suggested that *Sivatherium olduvaiense* and *L. maurusium* were synonymous, therefore the African species is *Sivatherium maurusium.* Singer & Bone retain *Sivatherium* (= *Griquatherium*) *cingulatum* as a valid species and this is used by Harris (1974, p. 189). Some doubts about the validity of this species were expressed by Singer & Bone (1960, p. 523) who stated that retention of *Sivatherium cingulatum* may be warranted but the name could be a *nomen vanum.* For this discussion I retain *S. cingulatum* as the sister-species of *S. maurusium.*

The P_4 of *Sivatherium giganteum* is clearly shown on BMM 40667 (Colvin 1837, pl. 9; Murchison 1868, pl. 21) which is cited as a paratype of the species by Colbert (1935*a*, p. 340). Comparative specimens used are BMM 16258, 16387 and 28106. These specimens are described by Lydekker (1883, pp. 60–61) and BMM 28106 also carries the P_3. The P_4 carries a well-developed central lingual cuspid: its posterior region is divided off and carries crescentic labial and lingual cuspids. The back of the P_4 shows some reduction of both its antero-posterior and transverse dimensions but this reduction is less extreme than that shown by *Samotherium boissieri.* On lightly worn specimens the back of the labial cuspid is forked. This condition is found on the P_3 of *Palaeotragus rouenii* (*P. microdon*) but its presence on the P_4 is more plesiomorphic than in *Palaeotragus.* The P_3 lacks a strongly developed central lingual cuspid and is therefore no more advanced than the P_3 in *Okapia*, *Giraffa* or *Samotherium.*

The P_4 of *Sivatherium maurusium* (BMM 14200 = Holotype *Helladotherium olduvaiensis:* Hopwood 1934, p. 14) and Olduvai F. 2991 (Singer & Bone 1960, pl. 20) appears more advanced than that of *Sivatherium giganteum* as the forking of the posterior end of the central labial cuspid is less pronounced. The *S. maurusium* P_3 is figured, in the P_4 position, by Pomel (1892) and Singer & Bone (1960, pl. 53). This tooth lacks a well-developed central lingual cuspid and is similar to the P_3 of *Honanotherium* and *Giraffa* figured by Bohlin (1926, pp. 110, 202). I do not think that the premolars can be used to assess relationships of *Sivatherium.* Useful information on sivathere relations is probably best provided by interpretation of the ossicones.

Bramatherium (Colbert 1935*a*, p. 355; Lewis 1939, pl. 2) has two pairs of conical simple ossicones with the anterior pair fused at their bases and posteriorly situated relative to those of *Sivatherium giganteum.* Lewis (1939, p. 276) suggested that *Bramatherium* and *Hydaspitherium* are synonymous but this has been ignored by other workers (e.g. Singer & Bone 1960; Harris 1974). Lewis suggested synonymy after reinterpretation of the holotype skull of *Hydaspitherium* *megacephalum* (Lydekker 1878, pls 26–27). A cast (BMM 3723) of this skull was available for comparison with casts (BMM 20009, Bettington 1845) of the skull of *Bramatherium perimense*. Lydekker based *Hydaspitherium* on the presence of only a single pair of ossicones, suggesting that this was homologous with the anterior pair of *Bramatherium*. Inspection of the skull and Lewis's interpretation shows that a pair of posterior ossicones was present. Therefore the ossicones of *Hydaspitherium* were probably similar to those of *Bramatherium*. Other differences between the two genera are very minor. Lewis (1939, pp. 276–7) found differences in the teeth to be within the range of variation in living giraffes. I therefore support the synonymy of these two genera with *Bramatherium* having precedence. Lewis retained *Bramatherium megacephalum* as a valid species but he had obvious reservations over this and he stated:

> They seem to be two different species with distinctly differentiated skull morphology. However since the differences are of degree rather than of kind, we must consider the possibility of their being only sexual differences. If this could be demonstrated, we should be able to reduce the species of this genus to a single one, the genotype. [Lewis 1939, p. 279.]

It is difficult to see how this could ever be 'demonstrated' but descriptions of wide variation in the ossicones of the African *Sivatherium* (Harris 1974) indicate that variation of the ossicones can be very great in sivatheres which would support the suggested synonymy of the species *Bramatherium perimense* and *Bramatherium megacephalum*. I have retained them as sister-species (figure 9) but they are very closely related.

Harris (1974, figs 2–4) shows that two pairs of ossicones are present in *Sivatherium maurusium* with the larger pair posterior and in his types 'A and B' the posterior ossicones are palmate as in *Sivatherium giganteum*. Harris's skull type 'C' does not carry well-developed anterior ossicones but in his other three figures small conical ossicones are indicated in the supraorbital region. I suggest that the anterior and posterior pairs of ossicones are homologous in *S. giganteum* and *S. maurusium* and this indicates that *S. giganteum* is the sister-species of *S. maurusium* plus the possibly synonymous *Sivatherium cingulatum*. Harris (1974, p. 197) states that: 'the anterior ossicones, if interpreted as such are sited more posteriorly and are less prominently developed' than those of *Sivatherium giganteum*. The more posterior position of these ossicones may be correlated with the differences in orientation of the dominant posterior ossicones. Harris (1974, p. 197) also states:

> There is some doubt whether the 'anterior ossicones' of the East African sivatheriines can be interpreted as discrete structures or merely represent an anterior extension, or the beginning of the posterior ossicones.

Even if Harris's doubts are valid the presence of palmate 'posterior' ossicones indicates that the African and Asian species of *Sivatherium* are more closely related to each other than to *Bramatherium*.

Birgerbohlinia schaubi was described by Crusafont-Pairó (1952, p. 100) who placed it in the Sivatheriinae. The limbs and particularly the cannon-bones of this species agree in slenderness with those of *Samotherium boissieri* (*S. sinense*) but features of the deciduous dentition agree more closely with the sivatheres. Although I have accepted Crusafont's allocation of *Birgerbohlinia* to the sivatheres I do not believe that it rests on any very solid basis except that the ossicones are large for a member of any other giraffid group, although small and therefore plesiomorphic for a sivathere. A closer investigation of this genus is warranted and only the discovery of a skull roof and permanent dentition will clearly establish relations.

Helladotherium duvernoyi was described by Gaudry (1862) from Pikermi. Gaudry's specimen consisted of a skull and post-cranial material. Unfortunately the skull lacked ossicones and for this reason it has been a continual source of difficulty. Matthew (1929, p. 550) states:

> It appears not at all improbable that *Helladotherium* may be a 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*' from the Upper Siwaliks.

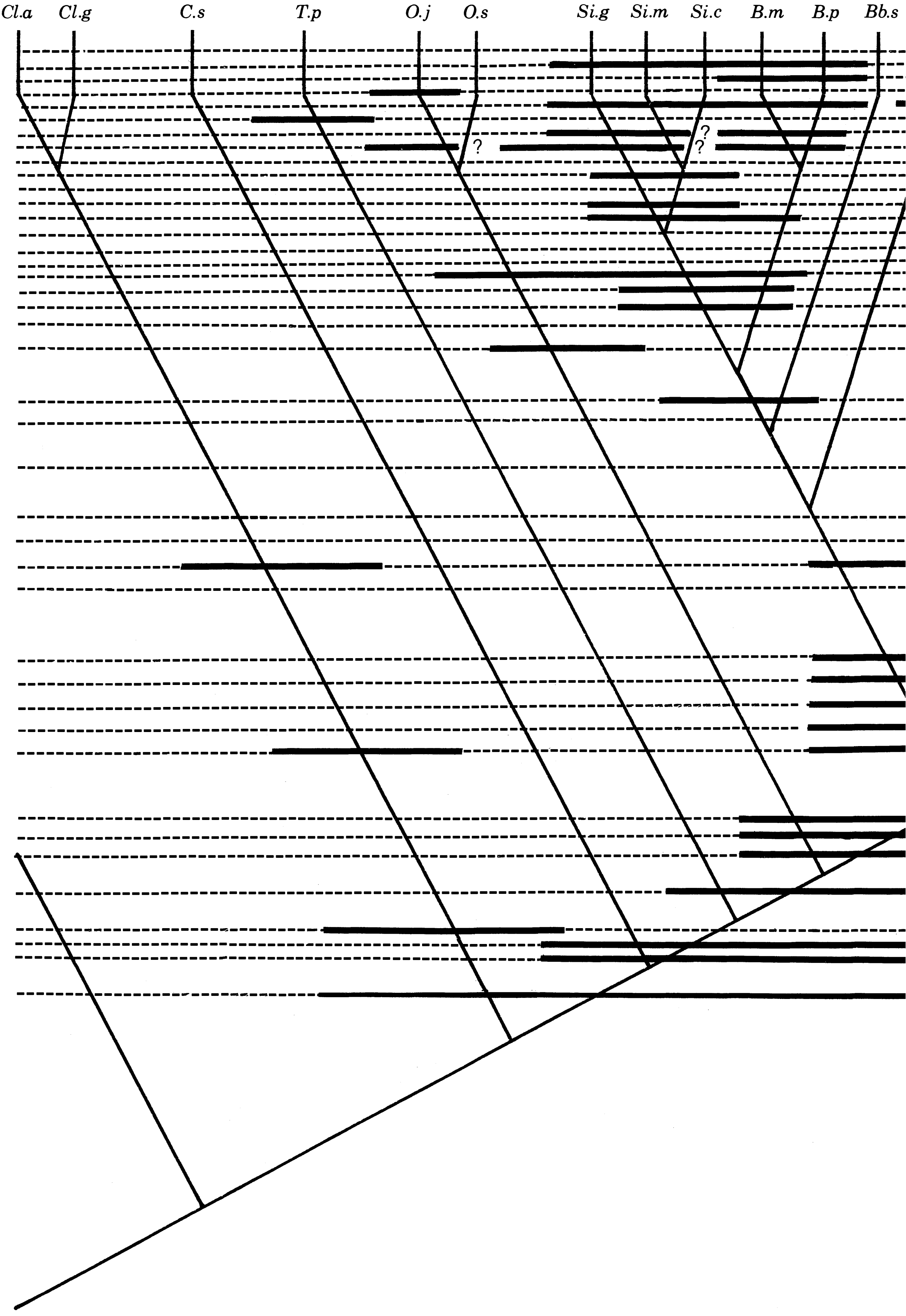
Matthew (1929, p. 547) placed *Helladotherium* as 'ancestral' to *Bramatherium/Hydaspitherium* separating them on a stratigraphical basis. The only problem over synonymizing *Helladotherium* with *Bramatherium* is one based on negative evidence. In the Siwaliks and in East and South Africa the remains of sivathere ossicones are relatively common but in the very large collections from Pikermi there are no published specimens, and no specimens in the collections of the British Museum (Natural History) that could be identified as ossicone fragments of the 'male *Helladotherium*'. I therefore suggest that the formal synonymy of *Helladotherium* with any sivathere will have to await the discovery of such specimens. I have therefore retained *Helladotherium* as: Sivatheriinae *incertae sedis*.

Helladotherium grande was described by Pilgrim (1911, p. 11) on the basis of an immature skull. Matthew (1929, p. 550) identified this specimen as a juvenile of *Hydaspitherium megacephalum* and the synonymy of this latter species is discussed on page 217.

FIGURE 9. Relations in the Giraffoidea. Synapomorphies and apomorphies found in more than one group are indicated by thick lines. Absence of information or plesiomorphies are indicated by dotted lines except in situations where absence of information may be critical; a question mark is then used. Autapomorphies are generally omitted.

Cl.a	*Climacoceras africanus*	*B.p*	*Bramatherium perimense*	*G.j*	*Giraffa jumae*
Cl.g	*C. gentryi*	*Bb.s*	*Birgerbohlinia schaubi*	*G.g*	*G. gracilis*
T.p	*Triceromeryx pachecoi*	*Gx.p*	*Giraffokeryx punjabiensis*	*Bo.a*	*Bohlinia attica*
O.j	*Okapia johnstoni*	*S.b*	*Samotherium boissieri*	*H.s*	*Honanotherium schlosseri*
O.s	*O. stillei*	*S.n*	*S. neumayri*	*P.t*	'*Palaeotragus*' *tungurensis*
Si.g	*Sivatherium giganteum*	*P.d*	'*Palaeotragus*' *decipiens*	*P.q*	*P. quadricornis*
Si.m	*S. maurusium*	*P.e*	'*P.*' *eminens*	*P.c*	*P. coelophrys*
Si.c	*S. cingulatum*	*G.c*	*Giraffa camelopardalis*	*P.r*	*P. rouenii*
B.m	*Bramatherium megacephalum*				

Apomorphic features. (*a*) Bilobed canine. (*a* 1) Accessory lobe of canine forming about one third of crown. (*b*) Vertical groove on postero-lingual region of P_4. (*b* 1) Back of P_4 separated from central part. (*c*) Central lingual cuspid developed on P_4. (*c* 1) Central lingual cuspid of P_4 independent. (*c* 2) Central lingual cuspid of P_4 transversely compressed. (*d*) Ossicones with tines. (*e*) Ossicones large. (*e* 1) Ossicones very large. (*f*) Back of skull shortened. (*g*) Orbits positioned posteriorly. (*h*) Skull flexed. (*h* 1) Skull brachycephalic. (*i*) Some lengthening of metapodials/limbs. (*i* 1) Further lengthening of limbs. (*i* 2) Limbs long and slender. (*i* 3) Limbs very long and slender. (*j*) Auditory bullae small. (*k*) Cheek teeth with high crowns. (*l*) Lengthening of neck. (1 1) Marked lengthening of neck. (*m*) Ossicones slightly posterior in position. (*m* 1) Ossicones more posterior. (*n*) Body massive. (*o*) Frontal sinuses well developed. (*o* 1) Frontal sinuses very large. (*p*) Posterior region of P_4 reduced. (*p* 1) Posterior regions of P_3 and P_2 reduced. (*q*) Central-labial cuspid of P_4 crescentic. (*q* 1) Central labial cuspid of P_3 crescentic. (*r*) Posterior region of P_4 expanded. (*s*) Ossicones shifted medially. (*t*) Posterior pair of ossicones palmate. (*u*) Posterior ossicones large. (*v*) P_3 with well developed central lingual cuspid. (*w*) Ossicones with clubbed tips. (*x*) Two pairs of ossicones. (*y*) D^3 lacking labial cingulum. (*z*) Anterior ossicones large.


Cl.a
Cl.g
C.s
T.p
O.j
O.s
Si.g
Si.m
Si.c
B.m
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Bb.s
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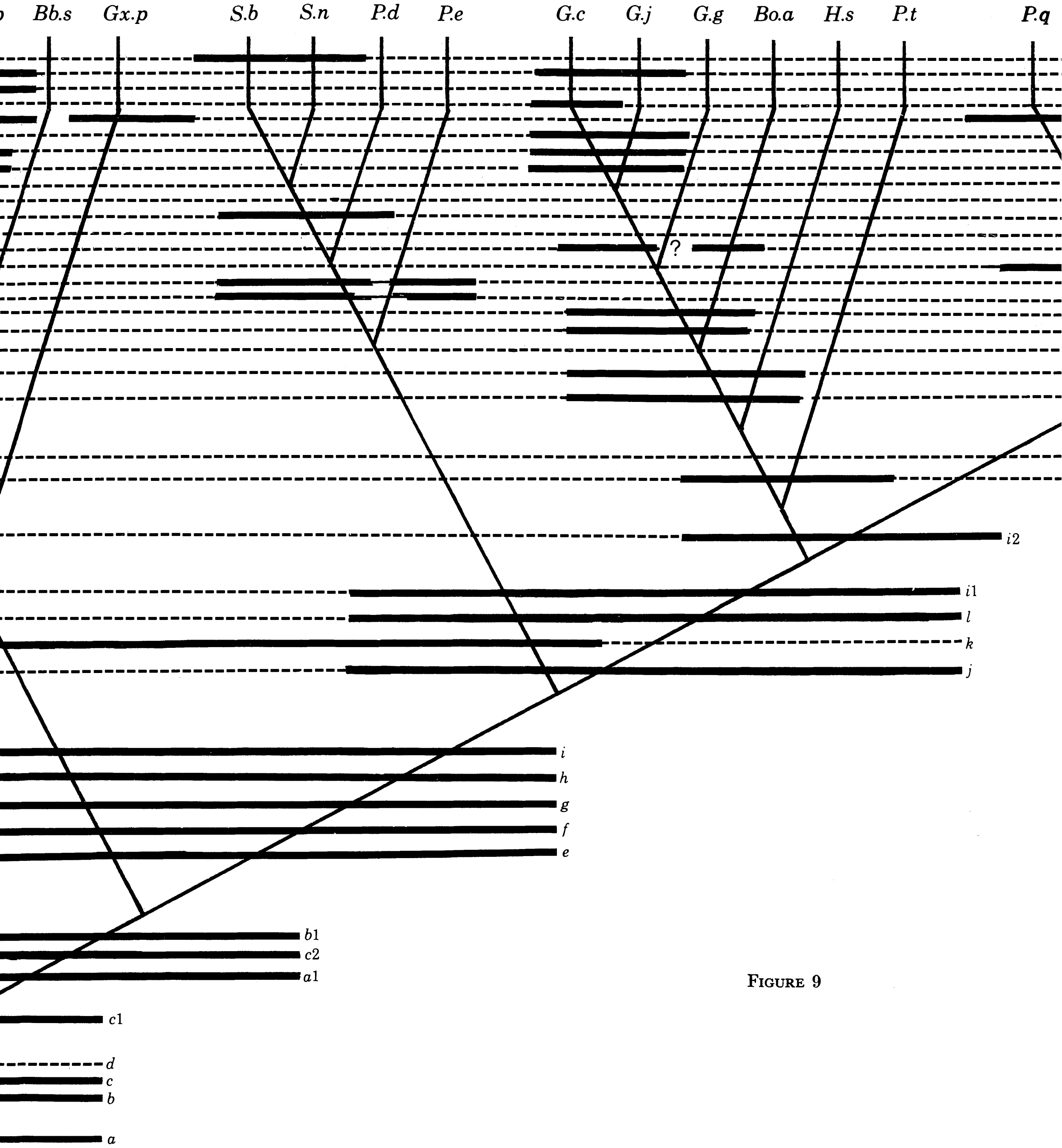
Bb.s
Gx.p
S.b
S.n
P.d
P.e
G.c
G.j
G.g
Bo.a
H.s
P.t
P.q
?
i2
i1
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b1
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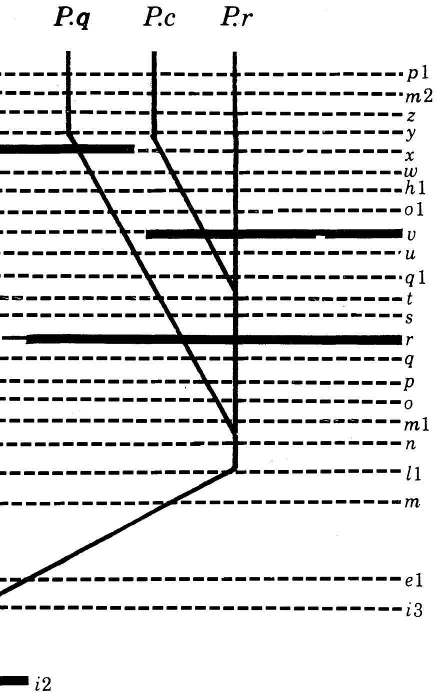
FIGURE 9



(Facing p. 218)

Relations in the Sivatheriinae are shown in figure 9. This group is characterized by the large ossicones which are unlike those found in any other giraffid. Features of the metapodials, neck and possibly the P_4 suggest that the *Samotherium* and *Palaeotragus* groups and the giraffines are closely related and the sivatheres are identified as the sister-group of these giraffids. *Giraffokeryx* is the only other giraffid which may be identified with the sivatheres. The synapomorphy linking this genus with the sivatheres is the presence of two pairs of well developed ossicones. The *Bramatherium* species were shown to have an apomorphy of the ossicones in which the anterior pair were large and the posterior pair small. The *Sivatherium* species have the apomorphy of large posterior ossicones and smaller anterior ones. The condition in *Giraffokeryx* with both pairs of ossicones approximately the same size may be identified as plesiomorphic for the sivathere group. Pilgrim (1941, p. 147) indicated the development of some complication of the ossicones in *Giraffokeryx*. Identification of *Giraffokeryx* as a sivathere would not conflict with any of the evidence presented by the dentition: indeed the P_3 and P_4 of BMM 30224 are surprisingly similar to those of *Giraffokeryx*. This interpretation would, however, require that *Okapia* had developed its slightly more apomorphic P_4 condition in parallel but this assumption is already indicated in my identification of *Palaeotragus tungurensis* (*P. primaevus*) as the sister-group of the giraffines. Therefore on the basis of ossicones *Giraffokeryx* is included in the sivathere group of giraffids.

Conclusions

Relations in the Giraffoidea are summarized on the cladogram (figure 9). *Climacoceras* and *Canthumeryx* are identified as giraffoids because each has an accessory lobe on its lower canine. This feature is an autapomorphy of the giraffoids and is not found in the bovids, which are probably the sister-group of the giraffoids (Hamilton 1978), or in the cervoids, antilocaprids, tragulids or gelocids. The P_4 of *Canthumeryx* carries a central lingual cuspid that is weakly developed relative to that of the giraffids but is more strongly developed than that of *Climacoceras*. Separation of the back and central regions of the P_4 in *Canthumeryx* is also used to indicate close relation to the giraffids. By using these two features of the P_4 *Canthumeryx* is identified as the sister-group of the giraffids and *Climacoceras* is the sister-group of *Canthumeryx* plus the giraffids. The presence of large ossicones with well developed tines is an autapomorphy of *Climacoceras*.

Triceromeryx is identified as a giraffoid because its P_4 carries a strongly developed central lingual cuspid. However the lower canine of *Triceromeryx* is not known and discovery of this tooth would either confirm the identification with the giraffoids or require the removal of *Triceromeryx* from the giraffoids. The central lingual cuspid of the P_4 is more strongly developed in *Triceromeryx* than in *Canthumeryx* and this suggests that *Triceromeryx* is more closely related to the giraffids than *Canthumeryx*.

In *Okapia*, the sivatheres, the giraffines and members of the *Samotherium* and *Palaeotragus* groups the lower canine carries a large accessory lobe which forms up to one third of the crown. This feature is apomorphic and indicates the close relation of these five groups. Features of the P_4 are used to support this relation. Colbert (1938) assessed features of *Okapia* and suggested that the genus was more 'primitive' than any of the, then known, fossil giraffes. Features of the ossicones, back of the skull, position of the orbits, flexion of the skull and limb proportions suggest that *Okapia* is the sister-group of the sivatheres, *Samotherium* group, giraffines and *Palaeotragus* group. I suggest that three apomorphic features developed in parallel in *Okapia* and other giraffids. These are: the posterior position of the ossicones, this feature is also found in the giraffines; the development of the frontal sinuses, a feature also found in the sivatheres and giraffines; and the absence of a cingulum on the D^3, an apomorphy also found in *Giraffa camelopardalis*.

The lower premolars and lengthening of the limbs and neck are used to give the left to right sequence of major groups in figure 9. It is possible that the limbs were secondarily reduced in length in the sivatheres as members of this group tended to more massive body size. If this were demonstrated a reassessment of relationships would be required. *Giraffokeryx* is identified as a sivathere because it has two pairs of well-developed ossicones. Complication of these ossicones (Pilgrim 1941) may support the suggestion that it is a sivathere. The presence of large anterior ossicones and smaller posterior ones is autapomorphic for *Bramatherium* while the presence of small anterior ossicones and large posterior ones is autapomorphic for *Sivatherium*.

Samotherium boissieri and *Samotherium neumayri* are identified as sister-species. In each the anterior region of the P_4 is expanded and the posterior region is reduced; also the crescentic form of the central labial cuspid is very strongly developed. By using these features it is suggested that '*Palaeotragus*' *decipiens* and '*Palaeotragus*' *eminens* should be placed in the *Samotherium* group.

The giraffines are identified as the sister-group of the *Palaeotragus* group using lengthening of the limbs and neck as a synapomorphy. Lengthening of the limbs and neck is most pronounced in the giraffines with species of *Giraffa* showing its greatest development. The strongly marked posterior shifting of the ossicones is also used to interpret relations in the giraffines. I suggest that the development of large frontal sinuses, posterior and medial shifting of the ossicones and brachycephaly are features developed in parallel in the sivatheres and giraffines. The three *Palaeotragus* species are grouped together by using features of the P_4, particularly the expansion of the posterior region which suggests that in the *Palaeotragus* group, the P_4 was evolving towards a molariform condition in which the anterior and posterior lobes are almost equal in size.

The cladogram (figure 9) reflects my assessment of relations in the Giraffoidea. It is based on information currently available and further discoveries will certainly require reassessment of relations within or between groups. I have expressed reservations about the suggested relations of several genera or species and I shall now summarize these. *Triceromeryx* is possibly incorrectly identified as a giraffoid. In known features it is relatively plesiomorphic and its lower canine is not known. *Okapia stillei* is known mainly from its dentition and discovery of skeletal elements may require reassessment of its relations. *Sivatherium cingulatum* is poorly known and may be synonymous with *Sivatherium maurusium*. *Birgerbohlinia schaubi* is poorly known and may be incorrectly grouped with the sivatheres. The relations of the *Samotherium* group are based mainly on limb proportions. In the ruminants these often change in parallel and further discoveries in the sivatheres, *Samotherium* or *Palaeotragus* groups could require a reassessment of relations of this group. The skull of *Giraffa gracilis* is not known but cranial features are used to suggest the close relation between *Giraffa jumae* and *Giraffa camelopardalis*. The discovery of a skull of *Giraffa gracilis* would necessitate a reassessment of relations between these three species. *Palaeotragus tungurensis* is identified as a giraffine on the basis of its long slender limbs. This feature is often developed in parallel in the ruminants. The relations of *Palaeotragus quadricornis* are based only on the back of the P_4. This species may be the sister-group of the giraffines plus the *Palaeotragus* group.

(*a*) *Stratigraphic occurrence of the giraffoids*

Hennig (1966, pp. 141–142), Brundin (1966, pp. 27–28; 1968, pp. 482), Nelson (1972*a*, *b*, p. 367) and Schaeffer, Hecht & Eldredge (1972) have argued that the use of stratigraphy and biostratigraphical data has very little relevance to assessment of relations. This point of view is strongly contested by Simpson (1961, p. 83). In this work I have largely ignored the stratigraphic occurrence of the species or specimens and my assessment of relations (figure 9) was made without reference to the stratigraphic level from which the species came. This follows Schaeffer *et al.* (1972, p. 39) who state:

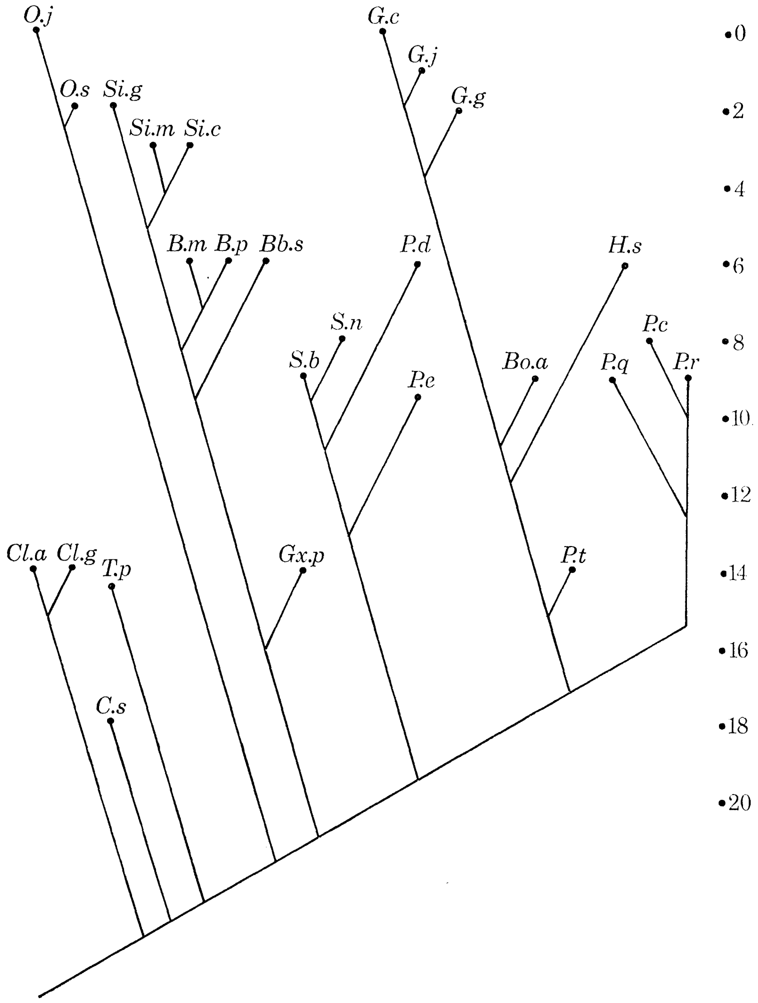


Figure 10. Stratigraphic occurrence and relations of the giraffoids. Abbreviations as in figure 9. Vertical scale in millions of years.

> By maintaining that biostratigraphic data should be ignored when evaluating relationships, we are simply arguing that phylogenies must be based on comparative morphology. Data concerning relative stratigraphic position necessarily bias the results by narrowing the range of possible relationships held by the taxa in question.

This does not suggest that biostratigraphic data must be completely ignored and Schaeffer *et al.* later suggest that stratigraphic evidence may be used to check cladograms that have been developed by comparative methods and they state:

> There is no way of formally testing a phylogenetic tree, but the congruence of morphocline and chronocline increases our confidence in the hypothesized phylogeny.

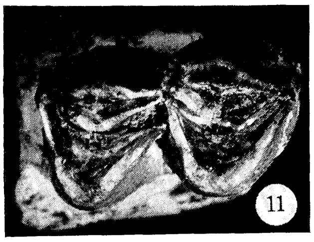
If this opinion is correct then the stratigraphic data on fossil giraffes should agree with, or at least should not contradict, suggestions of relations indicated on the cladogram (figure 9). Figure 10 can be interpreted to indicate that in the Sivatheriinae and Giraffinae the stratigraphic evidence provides support for the cladogram. The evidence is neutral for the *Palaeotragus* group and is slightly unfavourable for the *Samotherium* group. If the diagram is viewed as a whole then there is good agreement with *Climacoceras*, *Canthumeryx* and *Triceromeryx* occurring early and the more apomorphic giraffids occurring later.

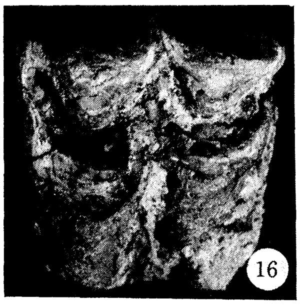
(*b*) *A classification of the giraffoids*

The cladogram (figure 9) can be used to make a classification of the Giraffoidea. This classification should reflect relationships indicated on the cladogram and here I have followed methods of classification outlined by Nelson (1972*a*, 1973) using his 'type 2' (1972*a*) system for classifying a group in which there are Recent and fossil species and not all the relations are known.

For this classification I have assumed that the ranking of the Giraffidae as a family is valid and I have also retained the subfamilies Giraffinae, Sivatheriinae and Palaeotraginae. Where species are moved into new groups a change of generic name may be necessary. I have not done this but have indicated the use of a generic name that is probably invalid by the use of inverted commas.

Superfamily GIRAFFOIDEA	
Family CLIMACOCERIDAE	*Climacoceras africanus*
	C. gentryi
Family CANTHUMERYCIDAE	*Canthumeryx sirtensis*
Family TRICEROMERYCIDAE	*Triceromeryx pachecoi*
Family GIRAFFIDAE	
Subfamily OKAPIINAE	*Okapia johnstoni*
	O. stillei
Subfamily SIVATHERIINAE	
	Giraffokeryx punjabiensis
	Birgerbohlinia schaubi
	Bramatherium perimense
	B. megacephalum
	Sivatherium giganteum
	S. maurusium
	S. cingulatum
Incertae sedis	*Helladotherium duvernoyi*





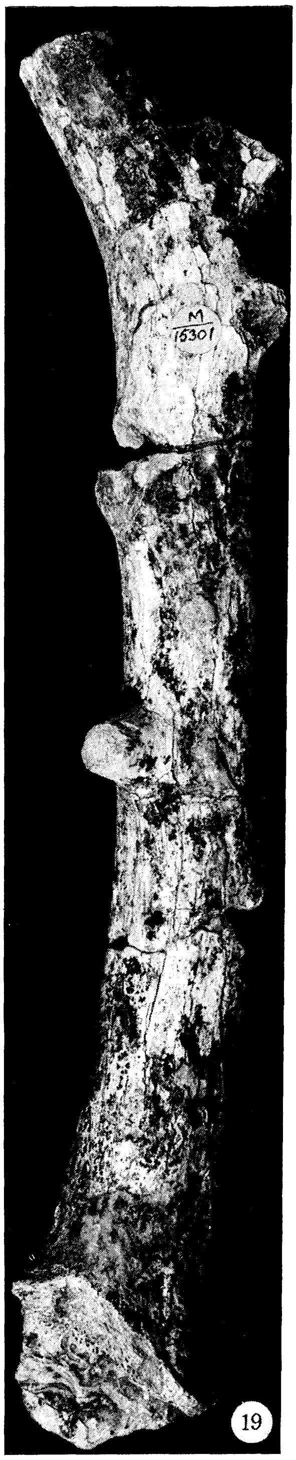


FIGURE 11. *Climacoceras africanus*. Right M$_2$; Maboko, Kenya, BMM 15311: × 2.06.

FIGURE 12. *C. africanus*. Left M$_2$; Maboko, Kenya, BMM 15312: × 2.26.

FIGURE 13. *C. africanus*. Left M$_3$; Maboko, Kenya, BMM 15313: × 1.60.

FIGURE 14. *C. africanus*. Left P$_4$; Maboko, Kenya, BMM 21367: × 3.12.

FIGURE 15. *C. africanus*. Right P$^{3-4}$; Maboko, Kenya, KNM.Mb.552: × 2.59. Occlusal view.

FIGURE 16. *C. africanus*. Left M^2; Maboko, Kenya, BMM 15314b: × 2.24.

FIGURE 17. *C. africanus*. Left M^2; Maboko, Kenya, BMM 15314a: × 2.31.

FIGURE 18. *C. africanus*. Right P$^{3-4}$; Maboko, Kenya, KNM.Mb.552: × 2.59. Labial view.

FIGURE 19. *C. africanus*. Left ossicone; Maboko, Kenya, BMM 15301, (holotype): × 0.83.

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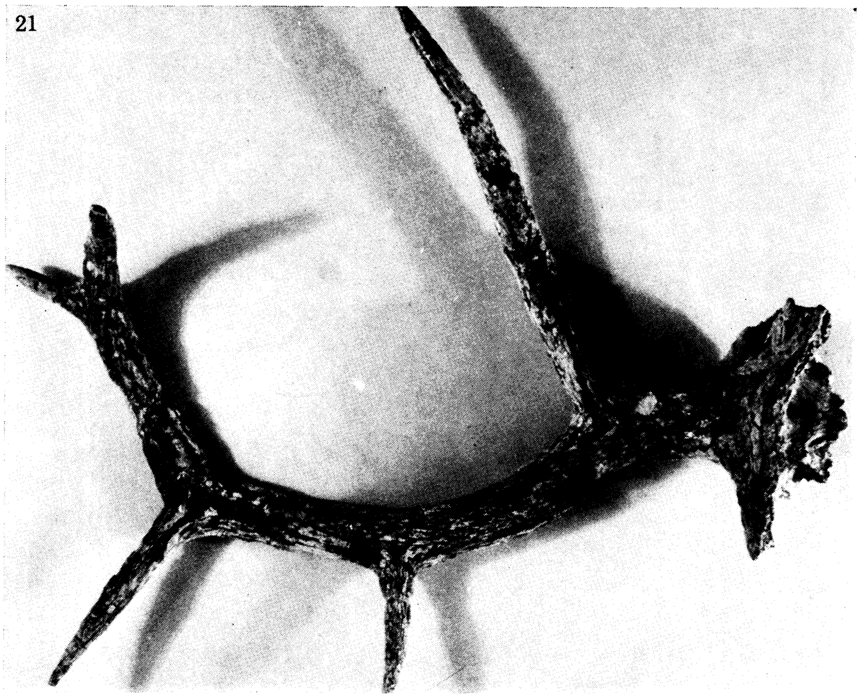

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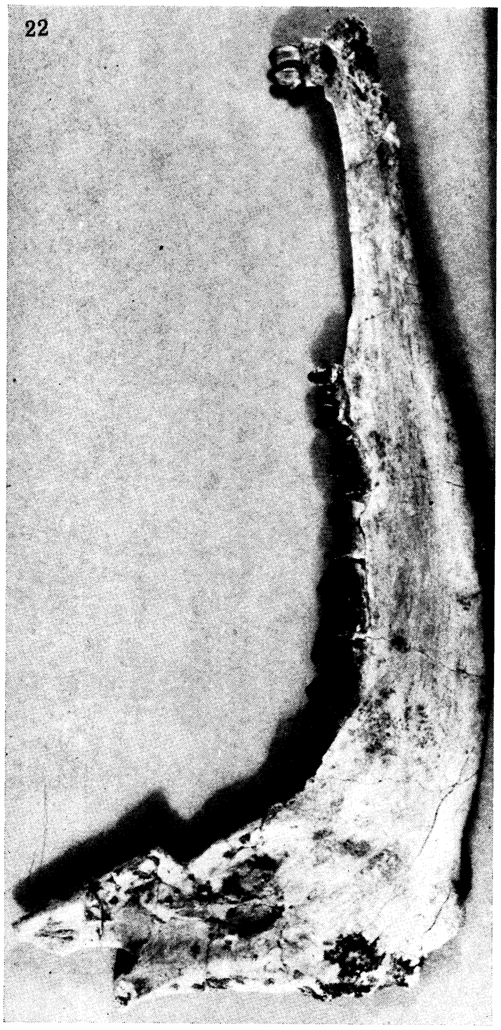

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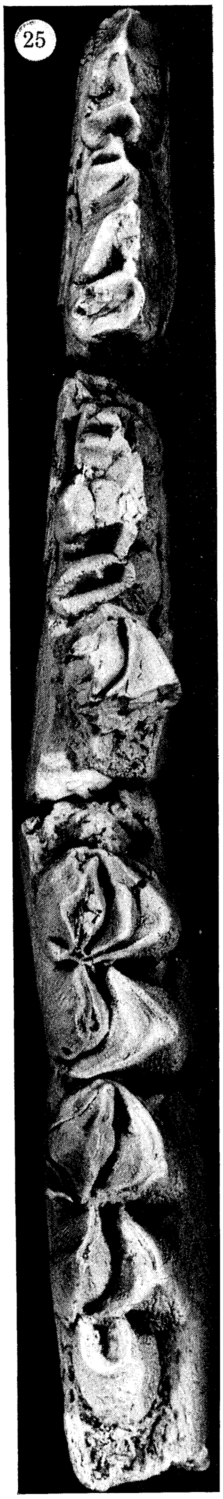
FIGURE 20. *Climacoceras gentryi.* Left lower dentition; Fort Ternan, Kenya, KNM.FT.2946: × 1.16. Occlusal view.

FIGURE 21. *C. gentryi.* Left ossicone; Fort Ternan, Kenya, KNM.FT.3146: × 0.38. Medial view.

FIGURE 22. *C. gentryi.* Left mandible; Fort Ternan, Kenya, KNM.FT.2946: × 0.60. Medial view.

FIGURE 23. *C. gentryi.* Right P^{3-4}; Fort Ternan, Kenya, KNM.FT.2953: × 2.56. Occlusal view.

FIGURE 24. *C. gentryi.* Right P^{3-4}; Fort Ternan, Kenya, KNM.FT.2953: × 2.56. Labial view.



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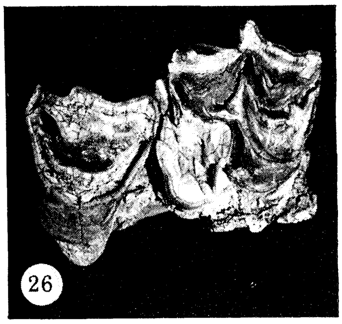

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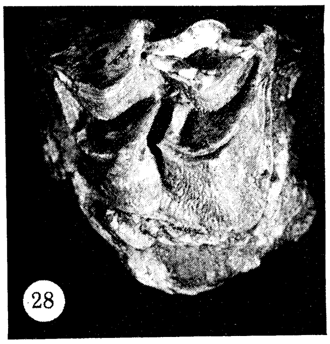

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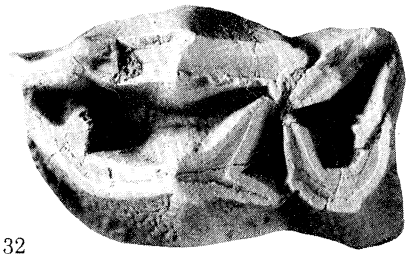

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FIGURE 25. *Canthumeryx sirtensis.* Right mandible with P_2–M_3; Muruarot, Kenya, UCB.V.4899/42058: × 1.61. Occlusal view.

FIGURE 26. *C. sirtensis.* Left P^4 and M^1; Muruarot, Kenya, UCB.V.4898/41981: × 1.15. Occlusal view.

FIGURE 27. *C. sirtensis.* Left P^{3-4}; Muruarot, Kenya, UCB.V.4898/41873: × 1.16. Occlusal view.

FIGURE 28. *C. sirtensis.* Right M^3; Muruarot, Kenya, UCB.V.4899/42058: × 1.63. Occlusal view.

FIGURE 29. *C. sirtensis.* Left P^{2-3}; Muruarot, Kenya, UCB.V.4899/42058: × 0.94. Occlusal view.

FIGURE 30. *C. sirtensis.* Anterior region of mandible with canine; Muruarot, Kenya, UCB.V.4899/42058: × 2.50. Left lateral view.

FIGURE 31. *Palaeotragus primaevus.* Right P_4; Baringo, Kenya, KNM.BN.287: × 2.43. Occlusal view.

FIGURE 32. *P. primaevus.* Left P_4; Fort Ternan, Kenya, KNM.FT.3045: × 2.43. Occlusal view.


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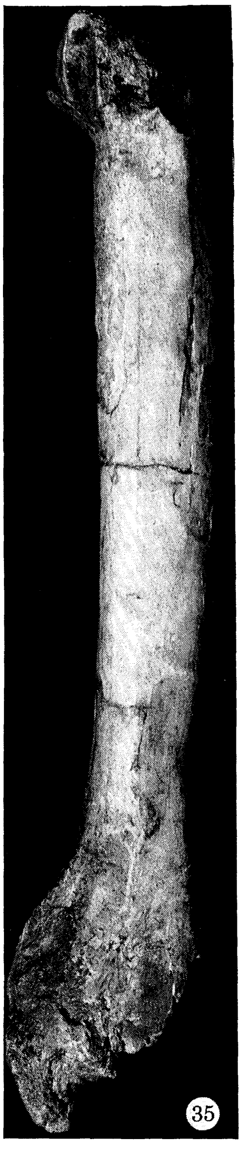
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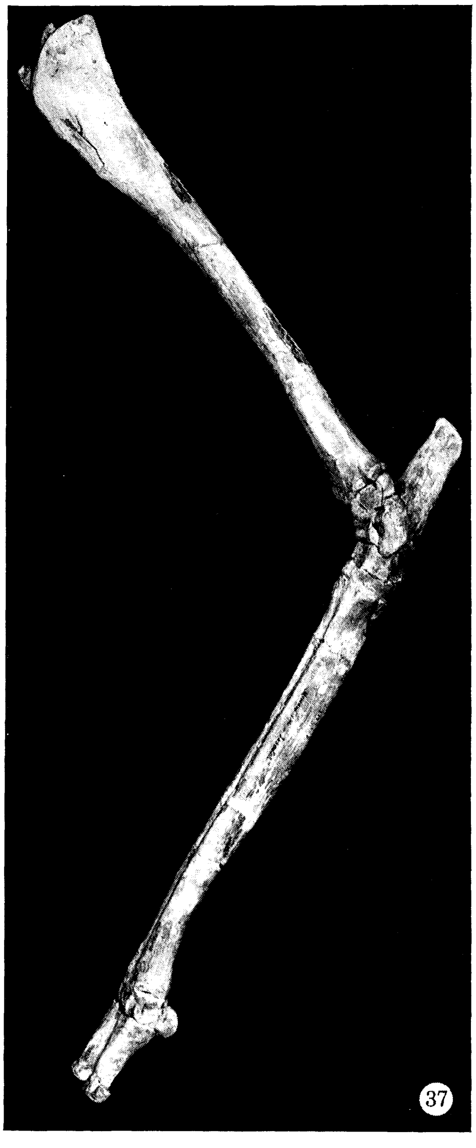
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FIGURES 33–37. For description see opposite.

DESCRIPTION OF PLATE 4

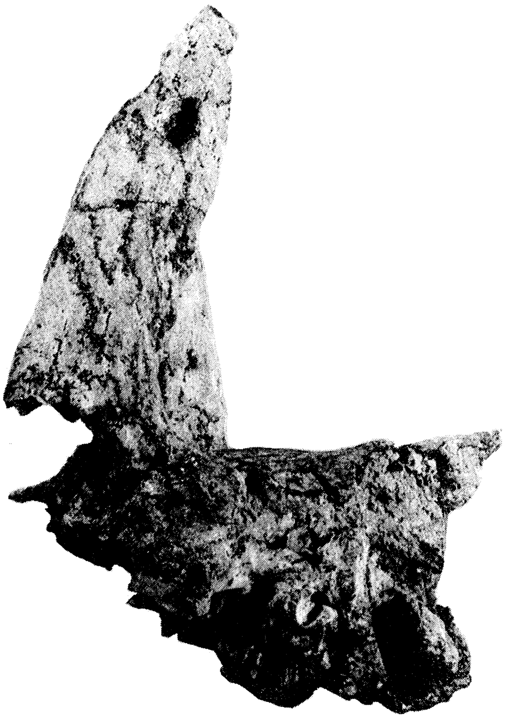
FIGURE 33. *Canthumeryx sirtensis*. Right radio-ulna; Muruarot, Kenya, IPP.1933–9: × 0.46. Lateral view.

FIGURE 34. *C. sirtensis*. Right pelvis; Muruarot, Kenya, UCB.V.4899/42058: × 0.60. Lateral view.

FIGURE 35. *C. sirtensis*. Left femur; Muruarot, Kenya, IPP.1933–9: × 0.62. Lateral view.

FIGURE 36. *C. sirtensis*. Right femur; Muruarot, Kenya, UCB.V.4899/42058: × 0.62. Anterior view.

FIGURE 37. *C. sirtensis*. Left tibia, ankle, cannon-bone and phalanges; Muruarot, Kenya, IPP.1933–9: × 0.25. Lateral view.



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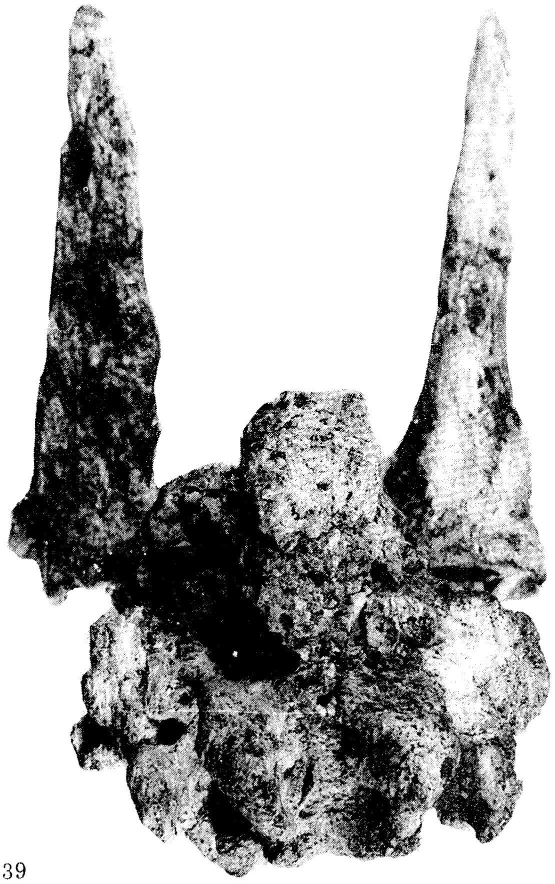

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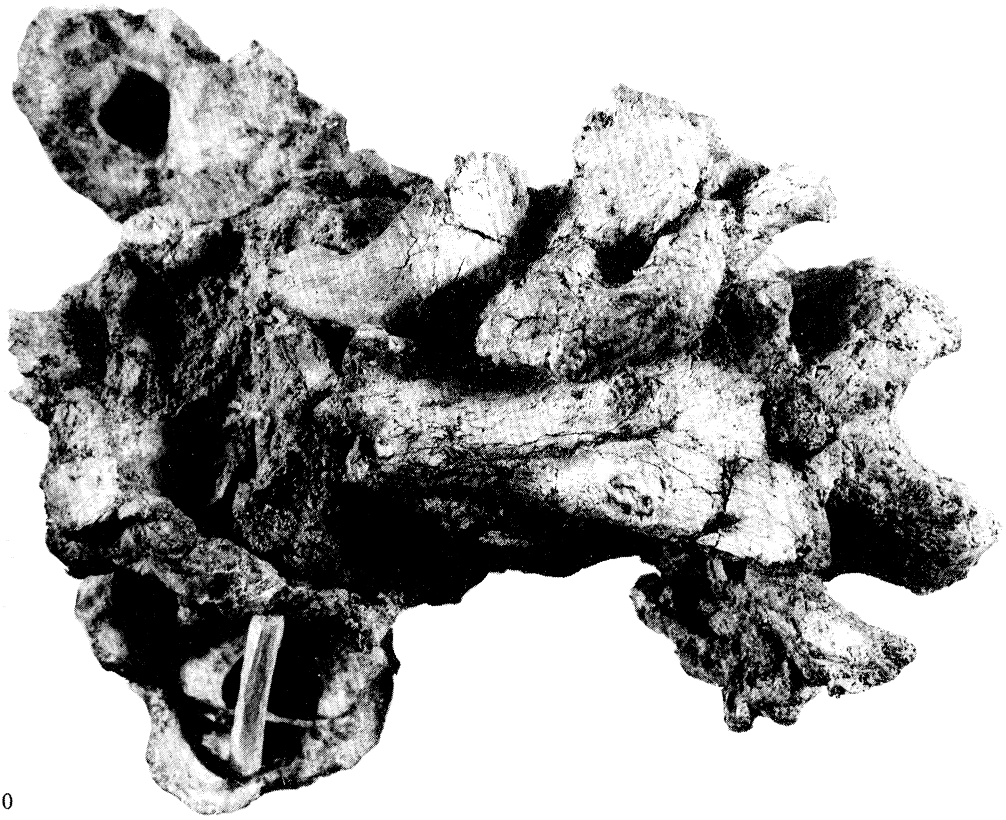

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FIGURE 38. *Palaeotragus primaevus*. Skull fragment with ossicones; Baringo, Kenya, KNM.BN.1446: × 0.50. Left lateral view.

FIGURE 39. *P. primaevus*. Skull fragment with ossicones; Baringo, Kenya, KNM.BN.1446: × 0.64. Posterior view.

FIGURE 40. *P. primaevus*. Skull fragment with ossicones; Baringo, Kenya, KNM.BN.1446: × 1.00. Basicranial view.

Subfamily SAMOTHERIINAE	
	'Palaeotragus' expectans
	'P.' decipiens
	Samotherium neumayri
	S. boissieri (S. sinense)
Incertae sedis	*S. eminens*
	S. tafeli
	S. africanum
Subfamily GIRAFFINAE	
	'Palaeotragus' tungurensis ('P.' primaevus)
	Honanotherium schlosseri
	Bohlinia attica
	Giraffa gracilis
	G. jumae
	G. camelopardalis
Incertae sedis	*'Giraffa' sinensis*
Subfamily PALAEOTRAGINAE	
	Palaeotragus quadricornis
	P. coelophrys
	P. rouenii (P. microdon)
Incertae sedis	*P. germani*
Subfamily INCERTAE SEDIS	
	Decennatherium pachecoi
Family INCERTAE SEDIS	
	Progiraffa exigua

APPENDIX 1. TRAGULIDS FROM BARINGO AND FORT TERNAN

Family TRAGULIDAE Milne-Edwards 1864

Genus ***Dorcatherium*** Kaup 1833

Diagnosis. A diagnosis of this genus is given by Whitworth (1958, p. 3).

Material. KNM.BN.830: right lower molar, lacking anterior end. KNM.BN.1159: right mandible fragment with M_2 and fragments of M_1 and M_3. KNM.BN.1324: anterior lobe of a lower molar. KNM.BN.1030: right mandible with M_{1-2} and unerupted P_{3-4}. KNM.BN.1146: left upper first or second molar. KNM.FT.3138: right mandible with D_{2-4} and M_1. KNM.FT.3140: right mandible with D_{2-4} and M_{1-2}. KNM.FT.3182: right M_3. KNM.FT.3283: left M_3. KNM.FT.3290: right M_2. KNM.FT.3279: right D_4. KNM.FT.3240: anterior two lobes of left D_4. KNM.FT.3292: right P_4. KNM.FT.3294: back of right P_4. KNM.FT.3284: left P_4. KNM.FT.3293: right D_3. KNM.FT.3286: left D_2. KNM.FT.3142: right M^{1-3}. KNM.FT.3139: right M^{1-2}. KNM.FT.3288: right M^2. KNM.FT.3282: left upper molar. KNM.FT.3285: right M^1. KNM.FT.3281: left upper molar lacking lingual parts of crescents. KNM.FT.3215: right M^3. KNM.FT.3291: right D^3. KNM.FT.3287: left D^3. KNM.FT.3295: left P^4. KNM.FT.3144: right upper molar. KNM.FT.3298: left P^{2-3}. KNM.FT.3410: lower molar. KNM.FT.3411: P^4.

Description. Tragulids are common in the East African Miocene collections and are described by Whitworth (1958, pp. 3-16) and Hamilton (1973, pp. 139-142). They are

TABLE 40. *DORCATHERIUM*; PERMANENT LOWER CHEEK TEETH

premolars

	D. chappuisi KNM.FT.3292		*D. chappuisi* KNM.FT.3194		*D. chappuisi* KNM.FT.3284		*D. chappuisi* KNM.BN.1030		*D. chappuisi* BMM 30197		*D. pigotti* BMM 21350		*D. parvum* Whitworth (1958)	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
P_3	—	—	—	—	—	—	11	—	13.3	5	7.5	3.2	7.0	2.5
P_4	12.5	6	—	5.5	12	5	11	—	12.2	6	7.8	3.8	6.8	2.7

lower molars

	D. chappuisi KNM.FT. 3140		*D. chappuisi* KNM.FT. 3168		*D. chappuisi* KNM.FT. 3283		*D. chappuisi* KNM.FT. 3290		*D. chappuisi* KNM.BN. 1030		*D. chappuisi* KNM.BN. 1324		*D. pigotti* KNM.BN. 1159		*D. pigotti* KNM.BN. 830		*D. chappuisi* BMM 30197		*D. pigotti* BMM 21350	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
M_1	11.5	6.3	10	6.5	—	—	—	—	10	—	—	—	—	—	—	—	10.3	6.0	7.2	3.8
M_2	12.5	7.3	—	—	—	—	12.5	8	11	6.5	—	8	8.0	4.5	9	5	11.7	7.2	8.9	4.5
M_3	—	—	—	—	20.8	9.5	—	—	16.5	7.5	—	—	—	—	—	—	18.5	8.2	12.1	5.1

TABLE 41. *DORCATHERIUM*; DECIDUOUS LOWER CHEEK TEETH

	KNM.FT.3140		KNM.FT.3168		KNM.FT.3279		KNM.FT.3293		*D. chappuisi* BM.M.30198		*D. pigotti*		*D. parvum*		KNM.FT.3286	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
D_4	15	5.5	14	5.5	14.8	6	—	—	13.5	5.0	12.0	5.2	6.0	2.0	—	—
D_3	14	4.3	14.5	4.0	—	—	14.5	4.5	—	—	—	—	5.4	1.5	—	—
D_2	13	3.5	13	3.5	—	—	—	—	—	—	—	—	—	—	12.8	3.5

particularly abundant in the earlier Miocene sites of Rusinga and Songhor. Gentry (1970, pp. 301-303) mentions the presence of tragulids in the Fort Ternan collections.

Lower molars from Fort Ternan are bunodont and have the usual '*Dorcatherium* fold' of the metaconid and the protoconid fold. They agree closely in all features with specimens of *Dorcatherium chappuisi* from Rusinga. KNM.BN.1030 has only the M_{1-2} erupted but these agree in size and details with the molars of *Dorcatherium chappuisi* (table 40). The isolated lower molar KNM.BN.1324 is probably an M_2 and is also identified with this species.

Lower molars KNM.BN.1159 and KNM.BN.830 are much smaller than those of *Dorcatherium chappuisi* and agree in size (table 40) with those of *Dorcatherium pigotti* (BMM 21350) being larger than those of *Dorcatherium parvum* (table 40). These molars have the characteristic tragulid pattern with well developed '*Dorcatherium*' and protoconid folds. An isolated M^1 (KNM.BN.1146) is also identified with this species.

The D_4 described by Whitworth (1958, p. 6. BMM 30198) has central and posterior lobes agreeing closely with those of the M_1 or M_2 even to the extent of carrying *Dorcatherium* and protoconid folds. The anterior lobe consists of labial and lingual points both showing transverse flattening but neither is developed as a true crescent or selene. This tooth agrees very closely with the D_4 on KNM.FT.3168 and 3140.

The D_3 is very elongate and narrow. It consists of anterior, central and posterior regions, each defined by a deep notch in profile and carrying a high, transversely flattened point. The anterior crest of the first point flexes lingually at its anterior end. The central point is the highest and widest. It has anterior and posterior crests and on KNM.FT.3140, 3138 and 3293 it also has a short postero-lingual wing. The crest of the posterior region curves diagonally across the back face of the tooth with a shorter labial wing also produced.

The D_2 also consists of three lobes and is very long and narrow. The first point lies at the front tip of the tooth and produces only a very short anterior to antero-lingual crest. The central point is again the highest part of the tooth and each specimen has a short postero-lingual ridge as well as a posterior ridge that runs into the back notch. The back point produces a short postero-lingual ridge and a strong posterior crest which curves lingually across the back of the tooth.

The anterior region of the P_4 (KNM.FT.3292) consists of a single crest that runs anteriorly from the central point before flexing lingually in its anterior region. The central point is high and wide; it produces a weak postero-lingual crest and a strong posterior crest that forms the labial face of the tooth and flexes to form the postero-labial corner of the back wall. From the face of this crest a lingual to postero-lingual crest is produced. This encloses a very short antero-posterior valley which opens lingually and which I will call the 'posterior median valley'. This P_4 crest pattern is found in KNM.FT.3292, 3284 and 3299. *Dorcatherium chappuisi* (Arambourg 1933, pl. 12, fig. 9 and 9*a*) has a P_4 in which the posterior median valley runs from the central point almost to the back of the tooth. The lingual crest is strong and forms most of the postero-lingual face so that the valley opens postero-lingually. *Dorcatherium naui* (BMM 40632. Kaup 1832; Mottl 1966, pl. 2) and *Dorcatherium vindobonense* (Mottl 1961, pl. 9, fig. 15; pl. 7, fig. 10) also have well developed posterior median valleys with a strong wing on the posterior lingual part of the tooth.

Upper cheek teeth. On the upper molars the parastyle and paracone ribs are very strong and very close together. The mesostyle and metacone ribs are also strong. Both labial cusps are transversely wide and similar to the usual form of these cusps in *Dorcatherium chappuisi* and

Hyemoschus. The protocone is not fully crescentic as it lacks a well-developed posterior wing which is again similar to *Dorcatherium chappuisi* and *Hyemoschus*. There is a well-developed basal lingual cingulum around the protocone.

The P^4 has a well-developed parastyle, paracone rib and mesostyle. The lingual crescent is developed anteriorly but the posterior part of the crest is flexed and supplemented by a strong, very high posterior cingulum. There is also a complete cingulum around the base of the lingual region. The posterior part of the D^3 is molariform with a labial selene and a lingual crescent which is pointed with a well-developed anterior wing, but the posterior wing is low and weak. The anterior style of the labial posterior selene is strong. The central point is high and transversely wide with a posterior crescent but it is rounded anteriorly. The front lobe consists of a

Table 42. *Dorcatherium*; upper cheek teeth

premolars

	KNM.FT.3295		KNM.FT.3298		KNM.FT.3411		*D. chappuisi*		*D. pigotti*		*D. parvum*	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
P^4	8.5	10.8	—	—	10.3	11.5	9.6	9.3	6.5	7.9	5.6	5.4
P^3	—	—	6.5	3.3	—	—	12.2	7.5	8.2	5.3	5.5	3.2
P^2	—	—	7	3	—	—	13.0	6.2	—	—	5.5	2.3

molars

	KNM.FT.3142		KNM.FT.3139		KNM.FT.3288		KNM.FT.3281		KNM.FT.3215		KNM.FT.3285		KNM.FT.3282	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
M^1	9.8	11.5	10.5	10.8	—	—	—	—	—	—	11	10.5	—	—
M^2	11.5	13.5	11	12.5	—	—	—	—	—	—	—	—	—	—
M^3	*ca.* 12	—	—	—	12.5	15.5	12.5	—	—	15	—	—	11.5	*ca.* 15

	KNM.FT.1086		KNM.FT.3144		KNM.BN.1146		*D. chappuisi*		*D. pigotti*		*D. parvum*	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
M^1	10.3	10	5.3	6.3	7	9	11.1	12.2	8.1	9.6	5.6	5.6
M^2	—	—	—	—	—	—	12.4	14.5	9.0	10.8	6.7	6.2
M^3	—	—	—	—	—	—	12.2	14.6	9.6	11.5	6.1	6.

Table 43. Post-cranial material of *Dorcatherium*

radius	KNM.FT.3167	KNM.FT.3170
length	99.5	—
width of proximal end	16.5	16.5
depth of proximal end	10.3	10.5
width of distal end	17	—
depth of distal end	12	—
minimum width of shaft	11.5	10.5
minimum depth of shaft	6.5	6.5

first phalange (KNM.FT.3172)	
length	11.8
depth of proximal end	9.3
minimum width of shaft	6.5
minimum depth of shaft	8
width of distal end	8
depth of distal end	7

tibia (KNM.FT.3166)	
estimated length	116
minimum width of shaft	11.5
minimum depth of shaft	12
width of distal end	19
depth of distal end	15.5

humerus (KNM.FT.3168)	
width of distal end	17
depth of distal end	14

sharp-edged crest that curves antero-lingually at the front. There is a labial cingulum on the central and anterior lobes and a lingual cingulum from the front of the tooth to the face of the posterior crescent.

Gentry (1970, pp. 301–305) identified as: 'a small non-tragulid ruminant', ' . . . a right deciduous P^4 62.49 (=KNM.FT.3144) 0.58 cm long'. This specimen is too small to be identified with *Walangania* which was Gentry's suggestion as the D^4 of *Walangania africanus* is 9.0 mm long (BMM 21379). Also the labial rib of the metaconid and the metastylid are weak which suggests that this tooth is not a D^4. However, the tooth agrees very closely in size with the molars of *Dorcatherium parvum* (BMM 30199 and 30203). It has the strong parastyle, paracone rib and mesostyle found in the upper molars of this species and it lacks the labial rib of the metacone as in this species. A right maxilla fragment with P^{2-3} (KNM.FT.3298) is also identified with *Dorcatherium parvum.* The two premolars are heavily worn but they are very elongate and narrow with only slight expansion of the lingual regions. This is a characteristically tragulid premolar form and the specimens are identified with *Dorcatherium parvum* on a size basis.

Post-cranial material. Some post-cranial elements in the Fort Ternan collections are also identified as tragulid and measurements are given in table 43.

I should like to thank the following people who have allowed me to study collections in their care: J. T. Gregory, E. Heintz, R. Leakey, W. W. Bishop.

Professor Bishop allowed me to study the Baringo collections that were made under his leadership. A. W. Gentry gave me valuable comment on this work and C. Patterson gave advice on Hennigian methods of phylogeny.

The Trustees of the British Museum (Natural History) provided funds for my visits to Nairobi and Berkeley.

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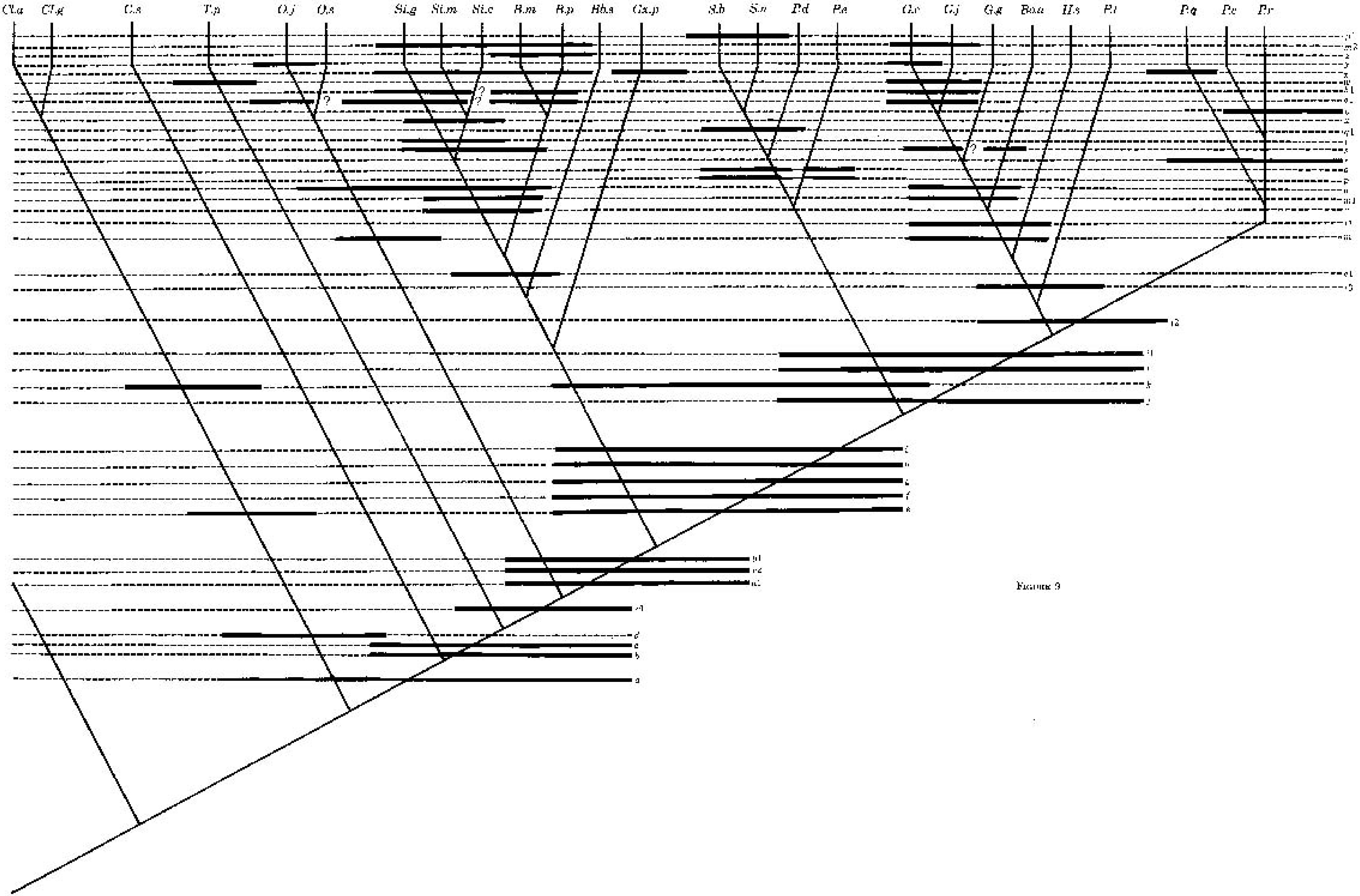
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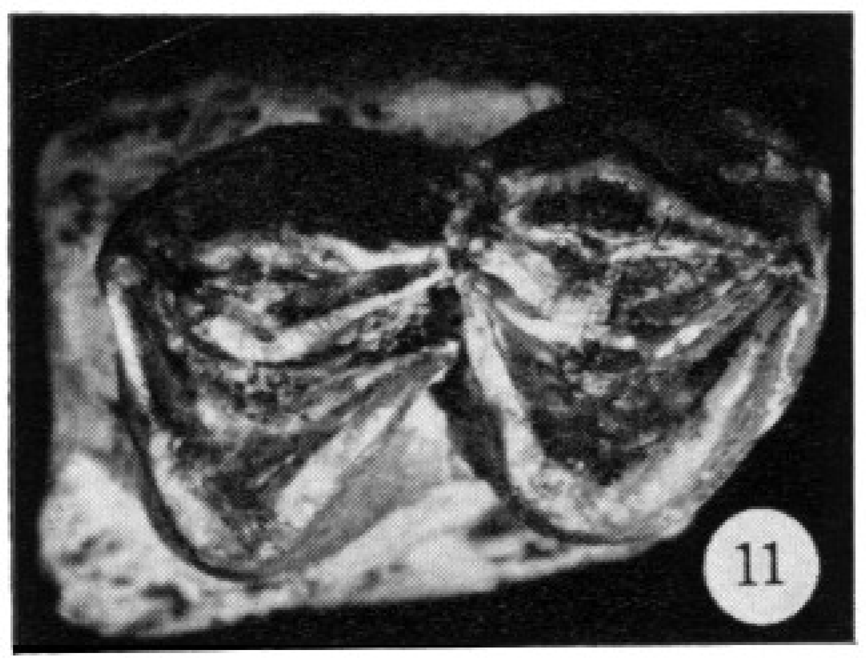
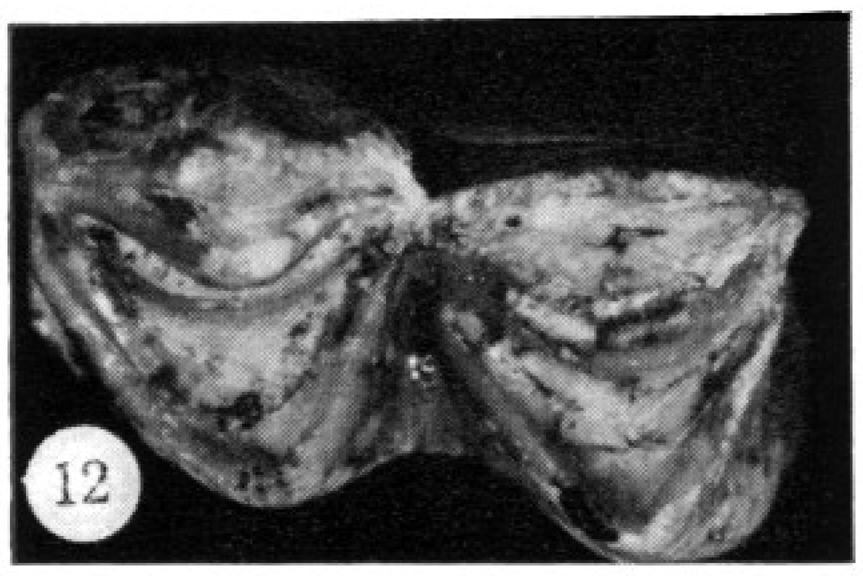
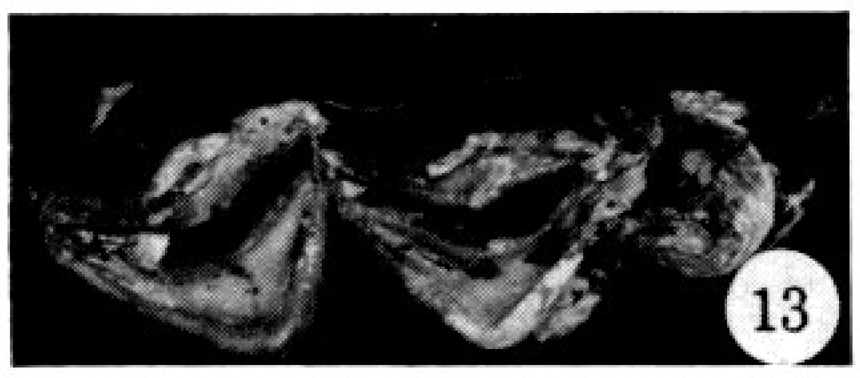
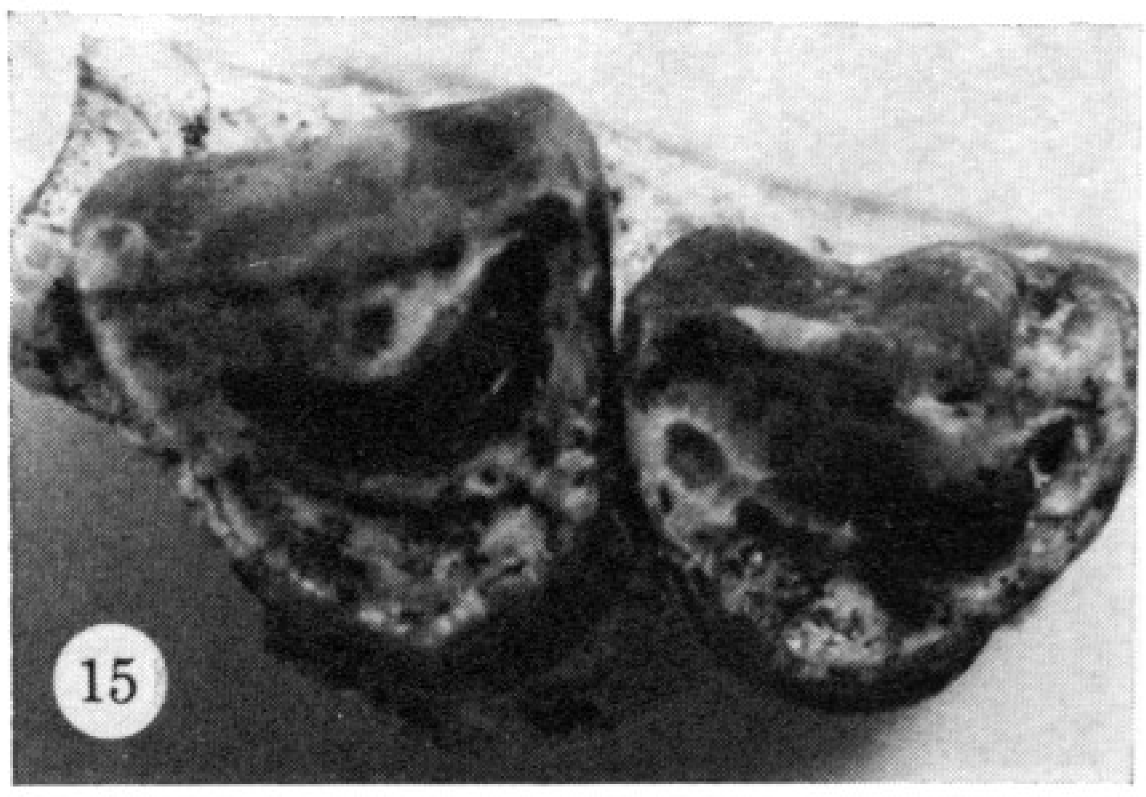
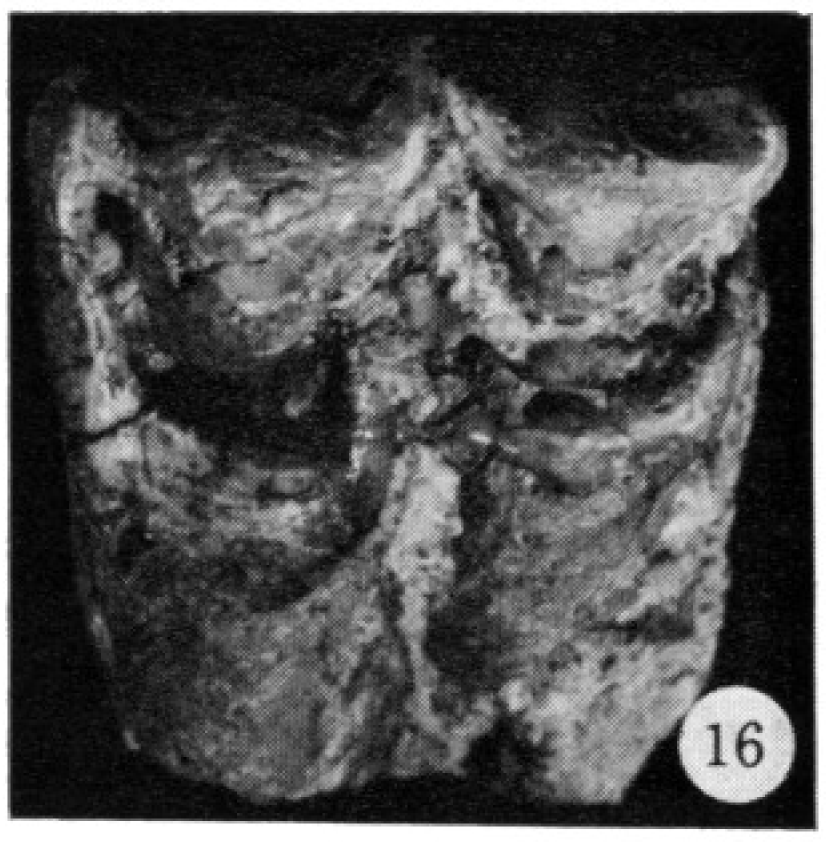
FIGURE 9











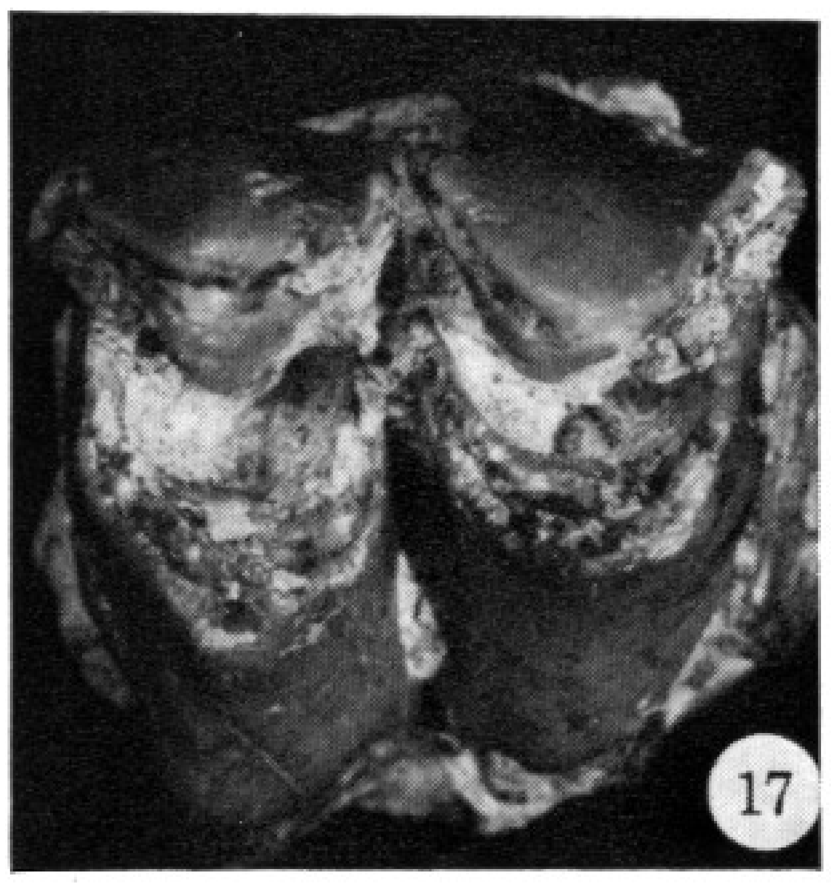


FIGURE 11. *Climacoceras africanus*. Right M$_2$; Maboko, Kenya, BMM 15311: × 2.06.

FIGURE 12. *C. africanus*. Left M$_2$; Maboko, Kenya, BMM 15312: × 2.26.

FIGURE 13. *C. africanus*. Left M$_3$; Maboko, Kenya, BMM 15313: × 1.60.

FIGURE 14. *C. africanus*. Left P$_4$; Maboko, Kenya, BMM 21367: × 3.12.

FIGURE 15. *C. africanus*. Right P$^{3-4}$; Maboko, Kenya, KNM.Mb.552: × 2.59. Occlusal view.

FIGURE 16. *C. africanus*. Left M^2; Maboko, Kenya, BMM 15314b: × 2.24.

FIGURE 17. *C. africanus*. Left M^2; Maboko, Kenya, BMM 15314a: × 2.31.

FIGURE 18. *C. africanus*. Right P$^{3-4}$; Maboko, Kenya, KNM.Mb.552: × 2.59. Labial view.

FIGURE 19. *C. africanus*. Left ossicone; Maboko, Kenya, BMM 15301, (holotype): × 0.83.

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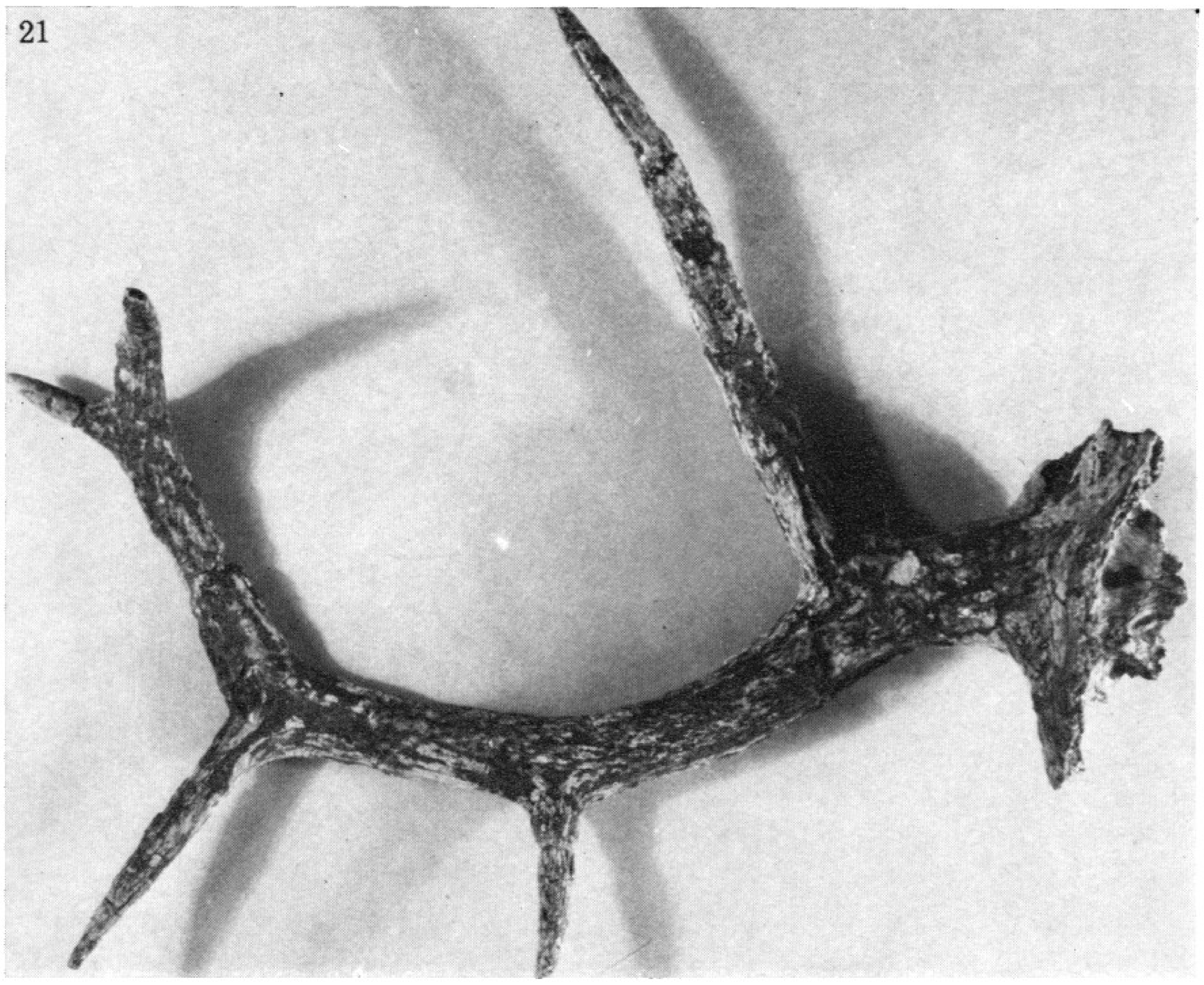

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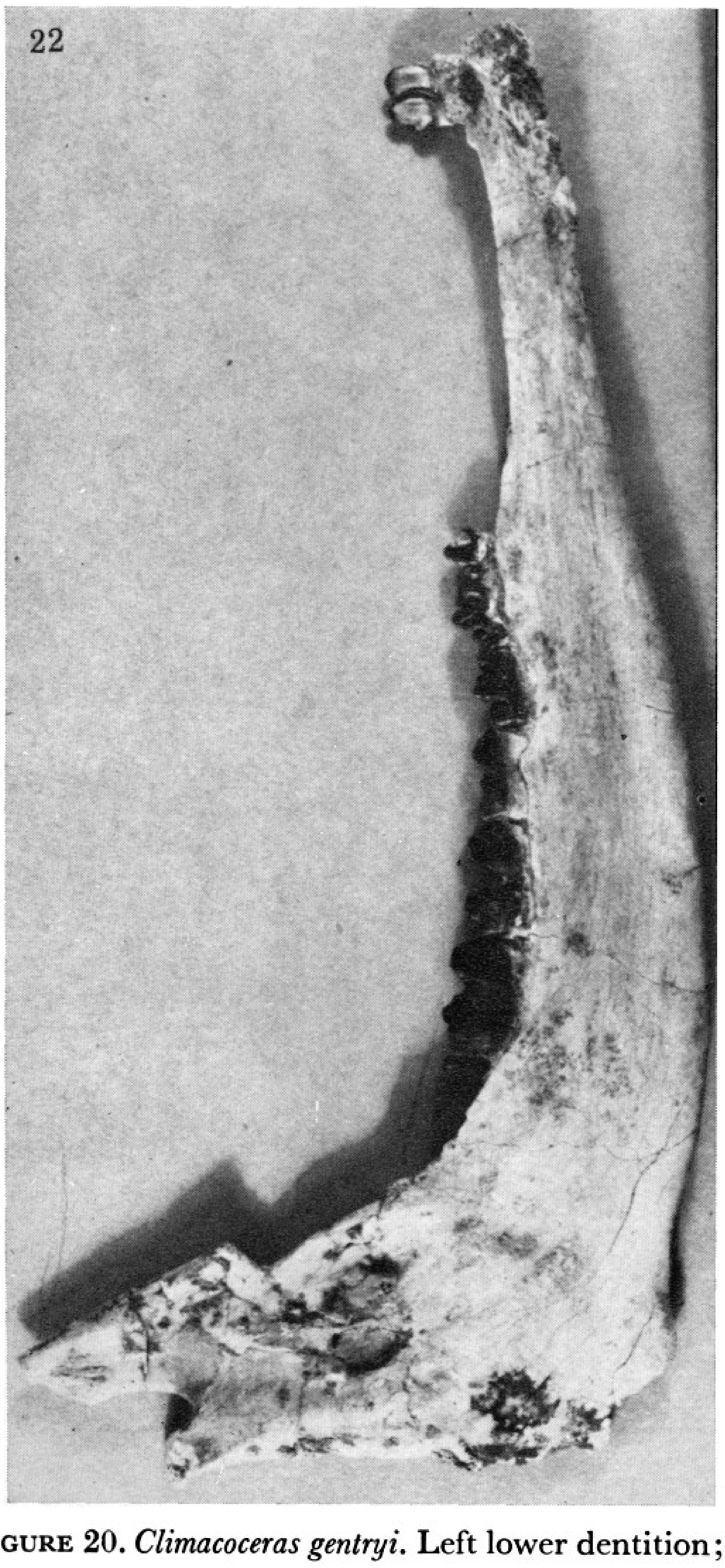

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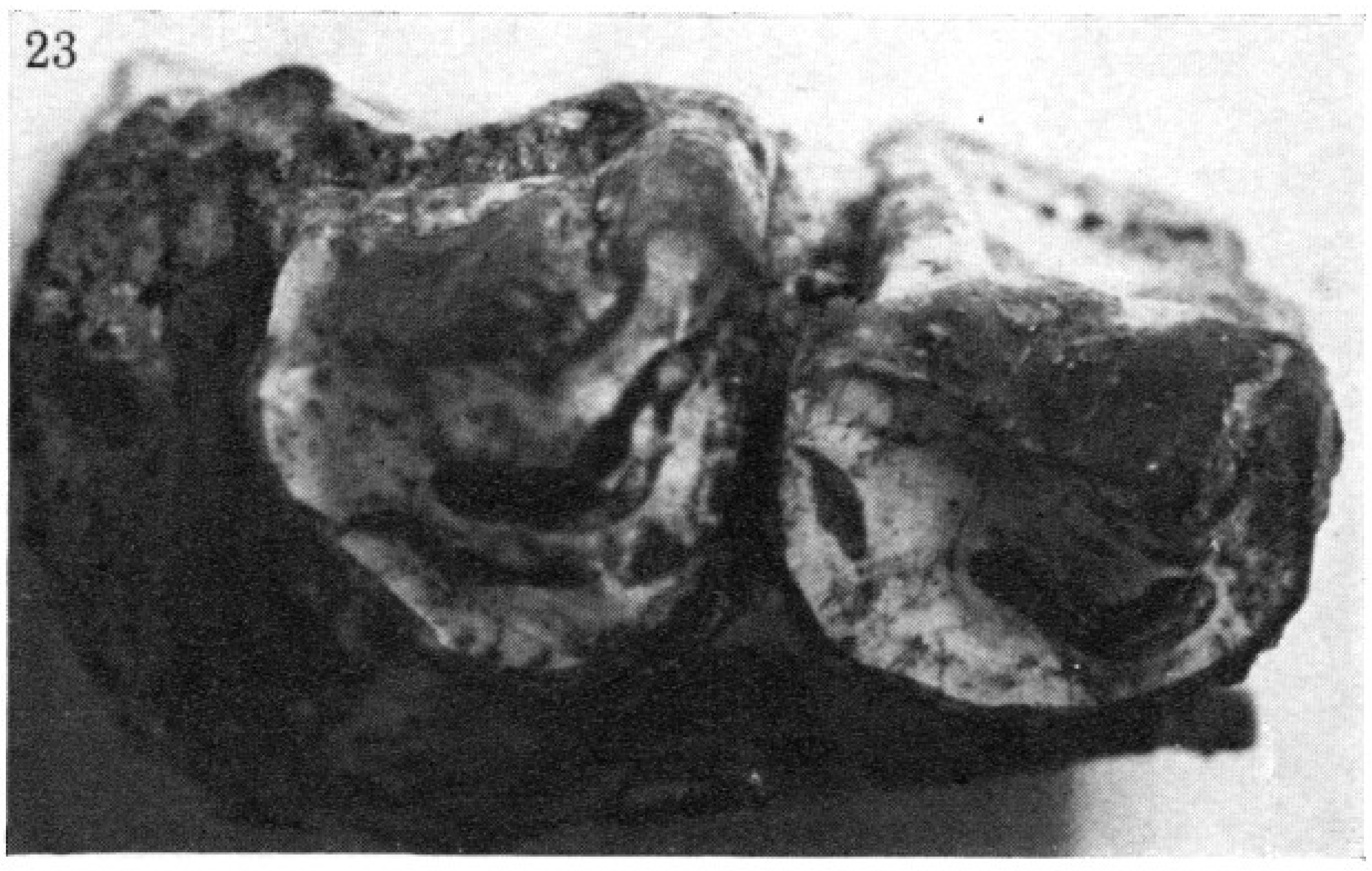

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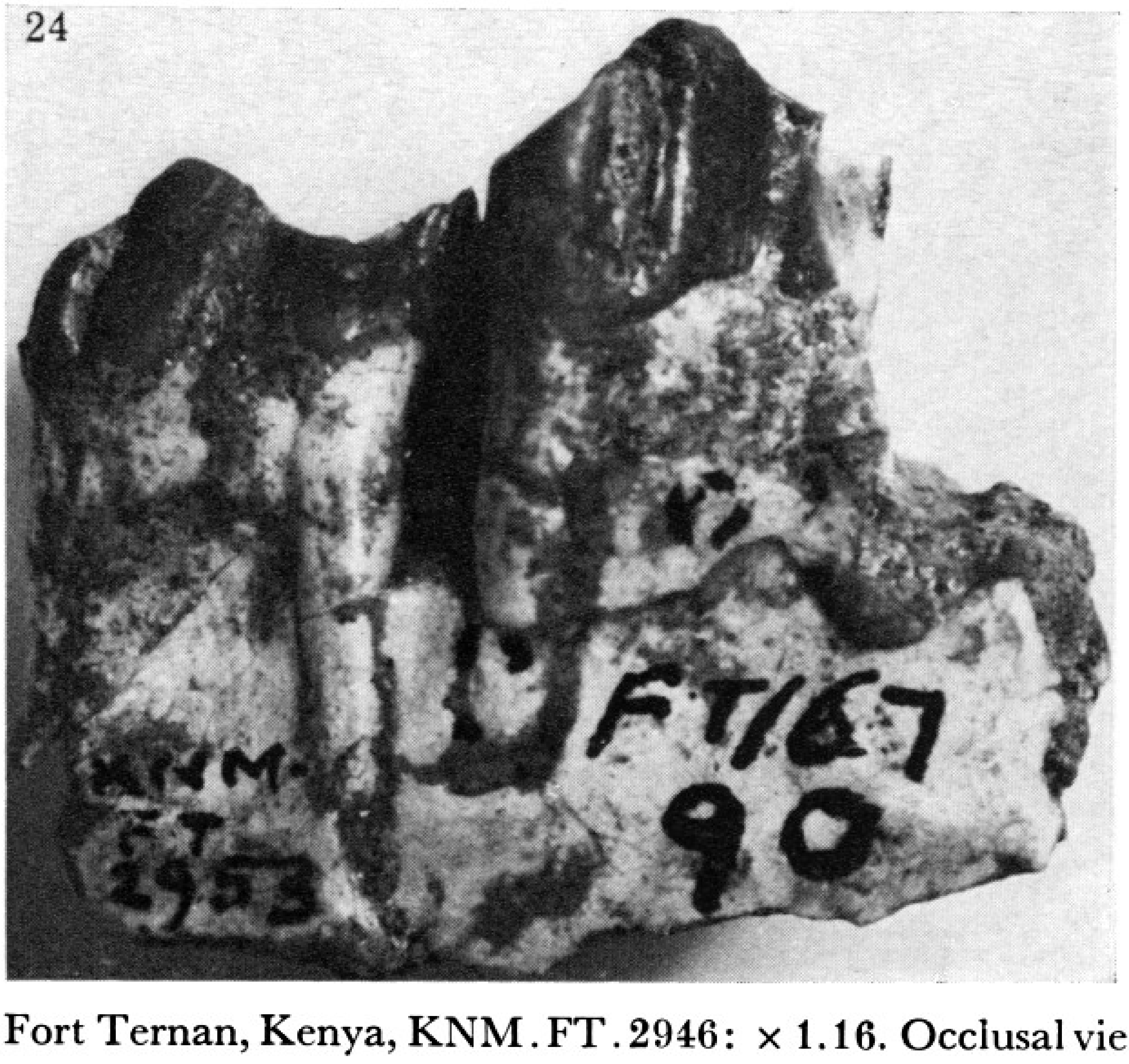


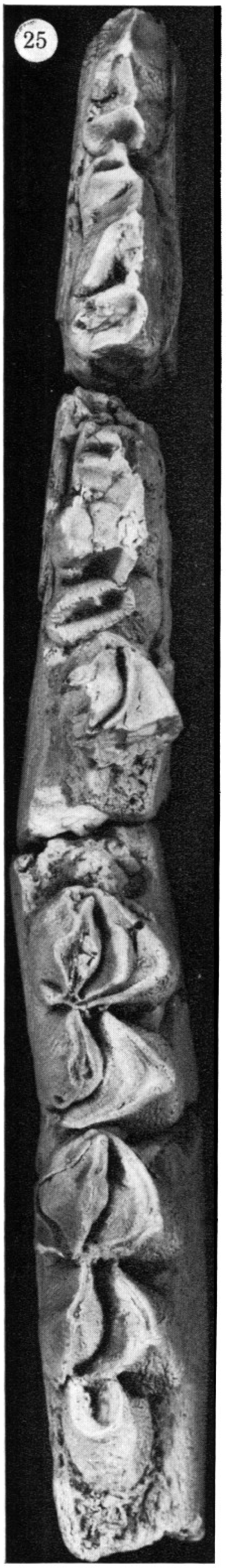
Figure 20. *Climacoceras gentryi.* Left lower dentition; Fort Ternan, Kenya, KNM.FT.2946: × 1.16. Occlusal view.

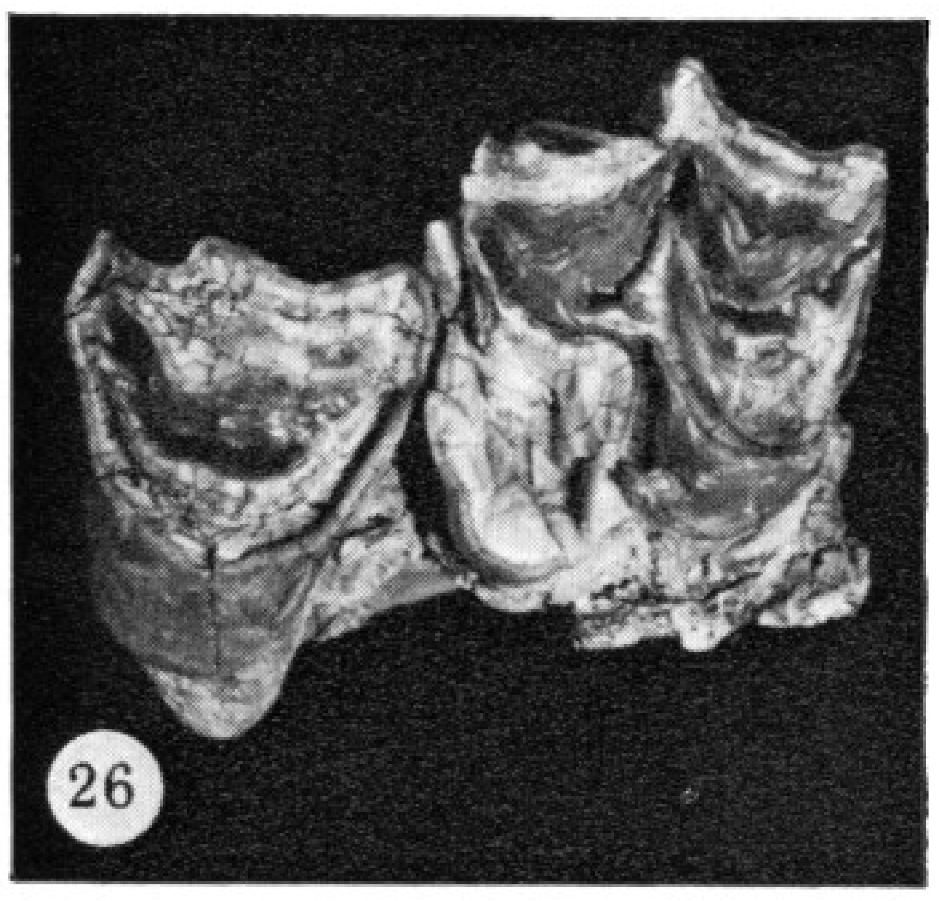
Figure 21. *C. gentryi.* Left ossicone; Fort Ternan, Kenya, KNM.FT.3146: × 0.38. Medial view.

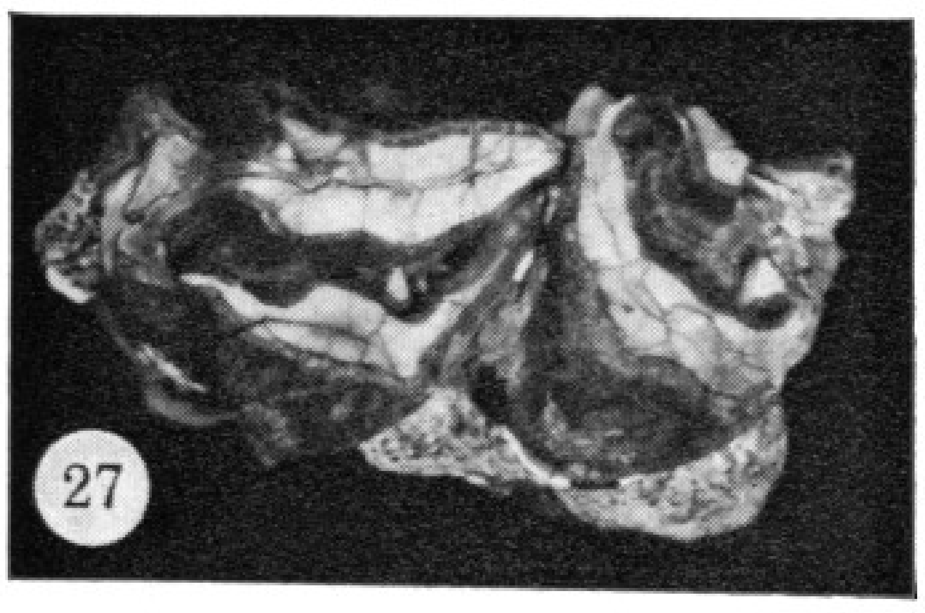
Figure 22. *C. gentryi.* Left mandible; Fort Ternan, Kenya, KNM.FT.2946: × 0.60. Medial view.

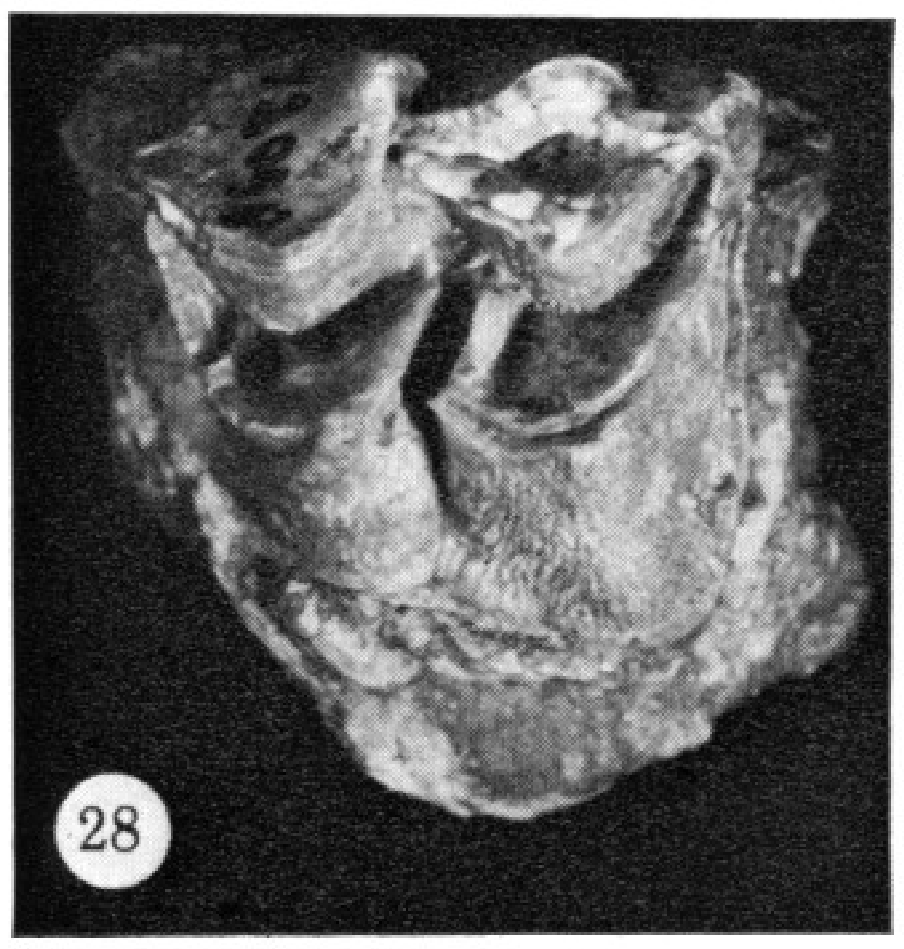
Figure 23. *C. gentryi.* Right P^{3-4}; Fort Ternan, Kenya, KNM.FT.2953: × 2.56. Occlusal view.

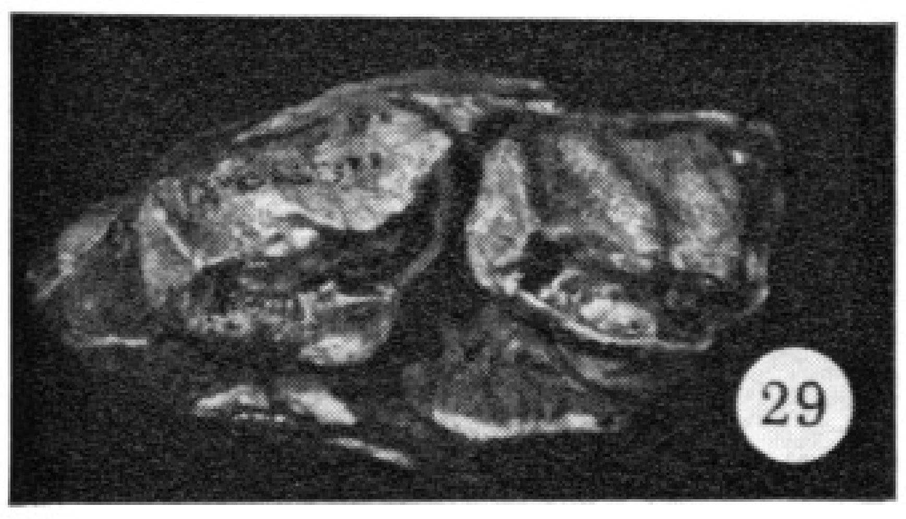
Figure 24. *C. gentryi.* Right P^{3-4}; Fort Ternan, Kenya, KNM.FT.2953: × 2.56. Labial view.

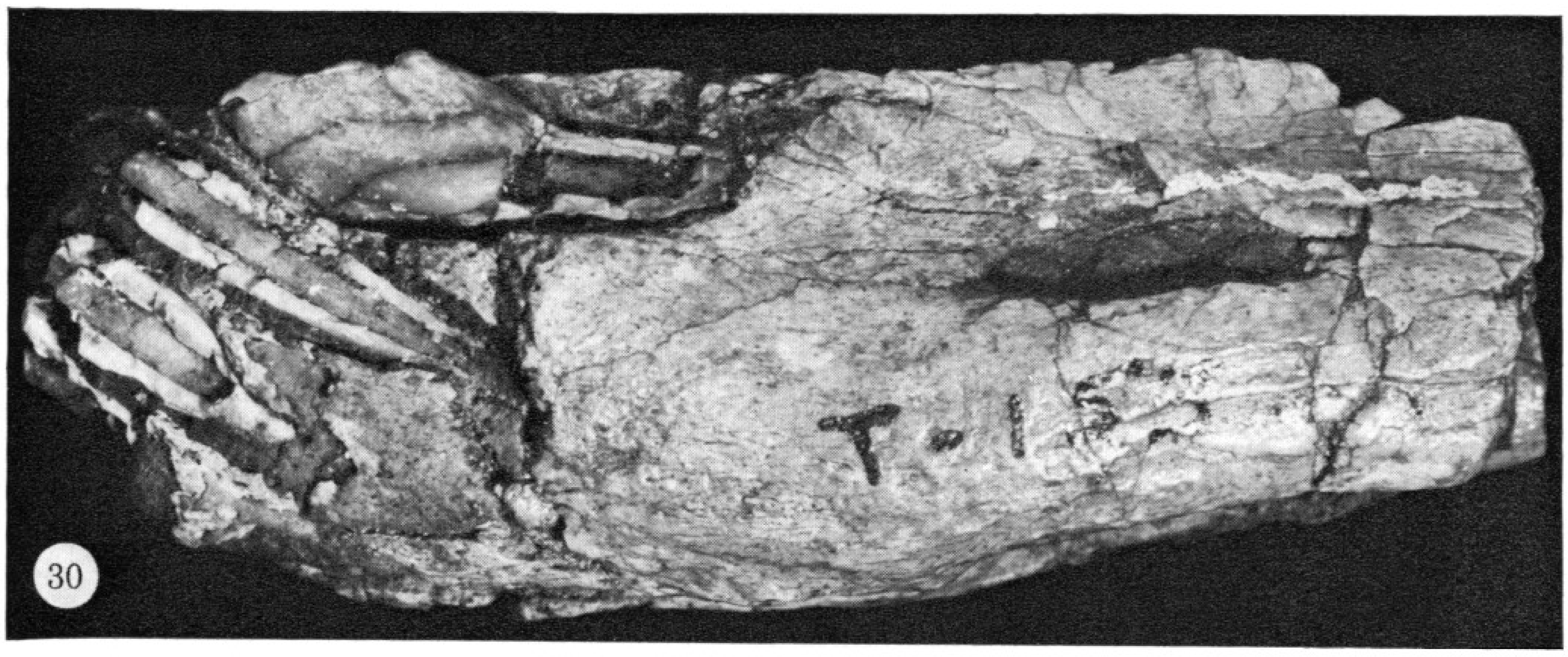


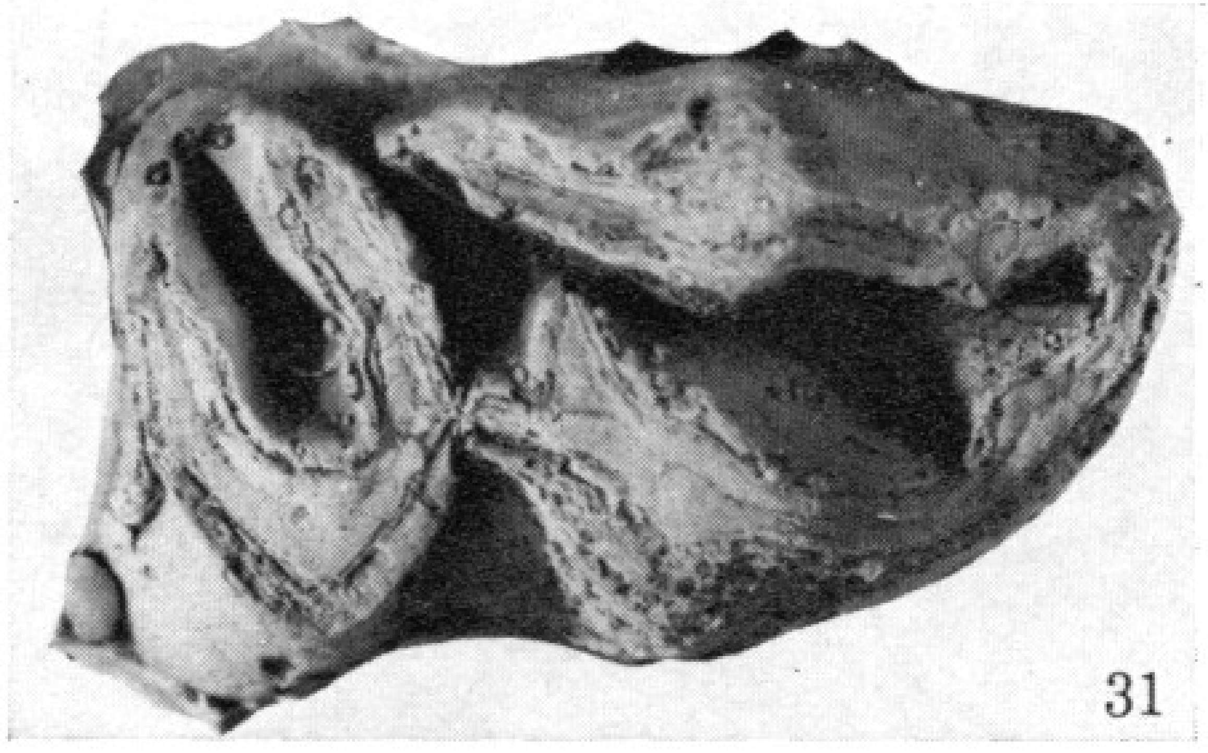












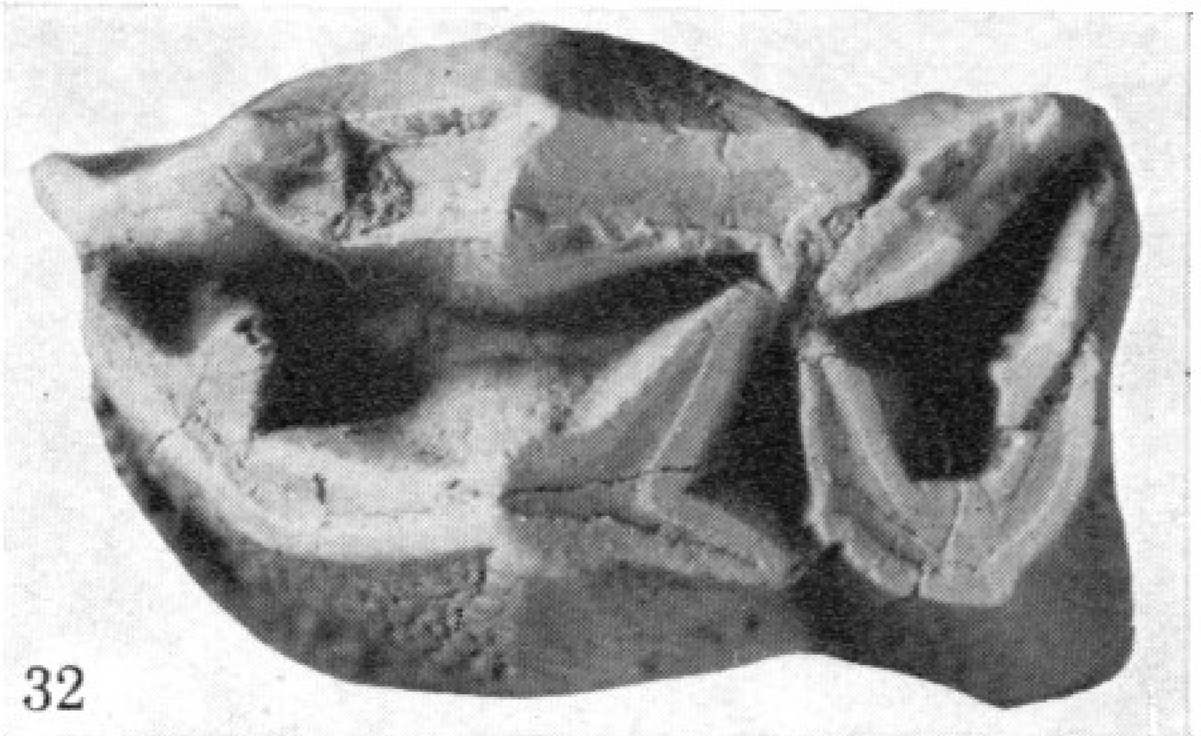


FIGURE 25. *Canthumeryx sirtensis.* Right mandible with P_2–M_3; Muruarot, Kenya, UCB.V.4899/42058: × 1.61. Occlusal view.

FIGURE 26. *C. sirtensis.* Left P^4 and M^1; Muruarot, Kenya, UCB.V.4898/41981: × 1.15. Occlusal view.

FIGURE 27. *C. sirtensis.* Left P^{3-4}; Muruarot, Kenya, UCB.V.4898/41873: × 1.16. Occlusal view.

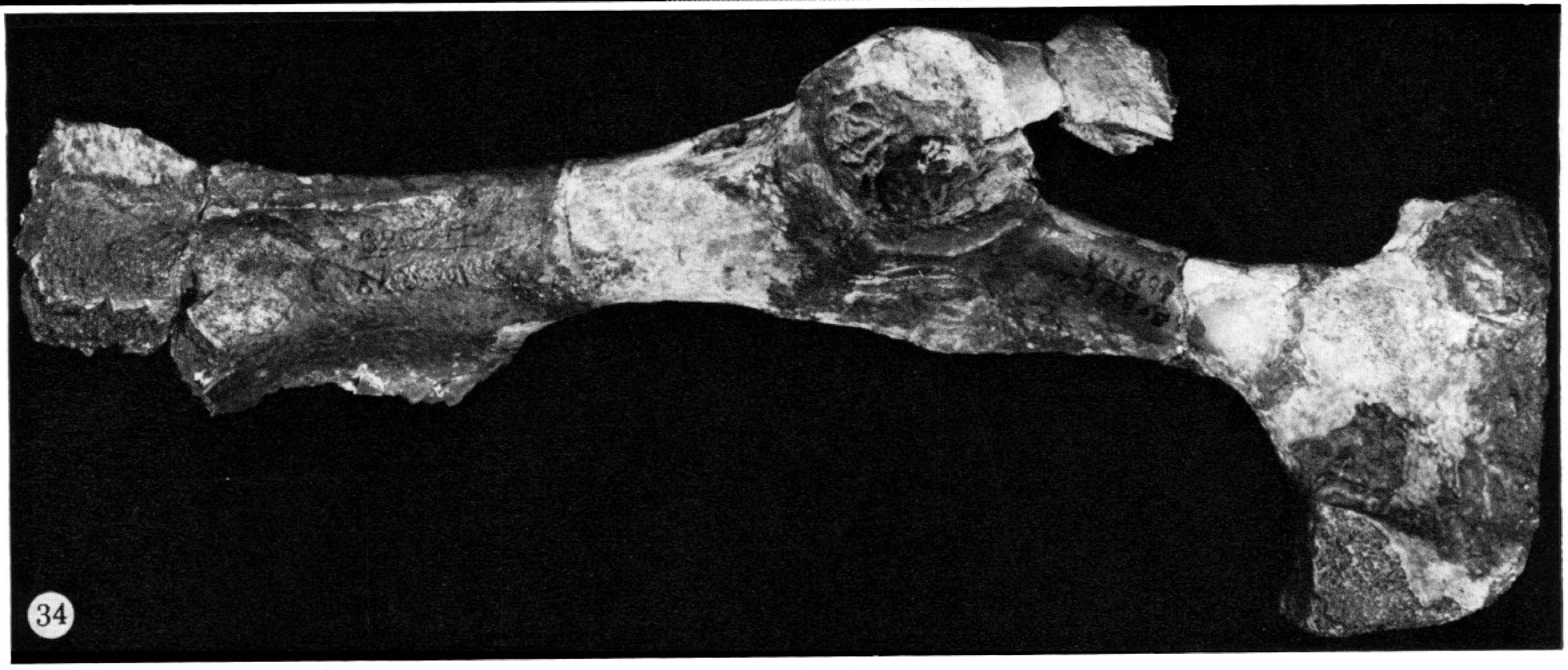
FIGURE 28. *C. sirtensis.* Right M^3; Muruarot, Kenya, UCB.V.4899/42058: × 1.63. Occlusal view.

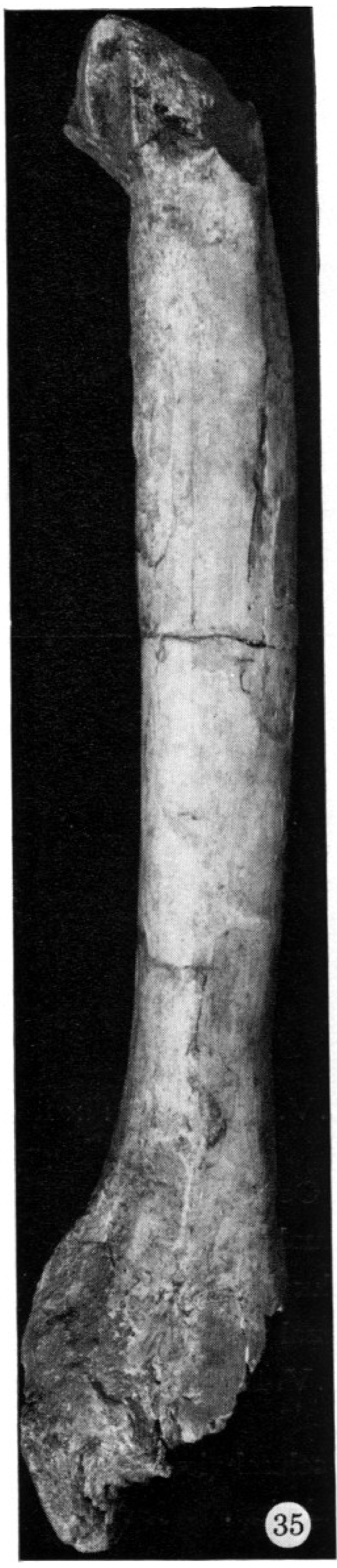
FIGURE 29. *C. sirtensis.* Left P^{2-3}; Muruarot, Kenya, UCB.V.4899/42058: × 0.94. Occlusal view.

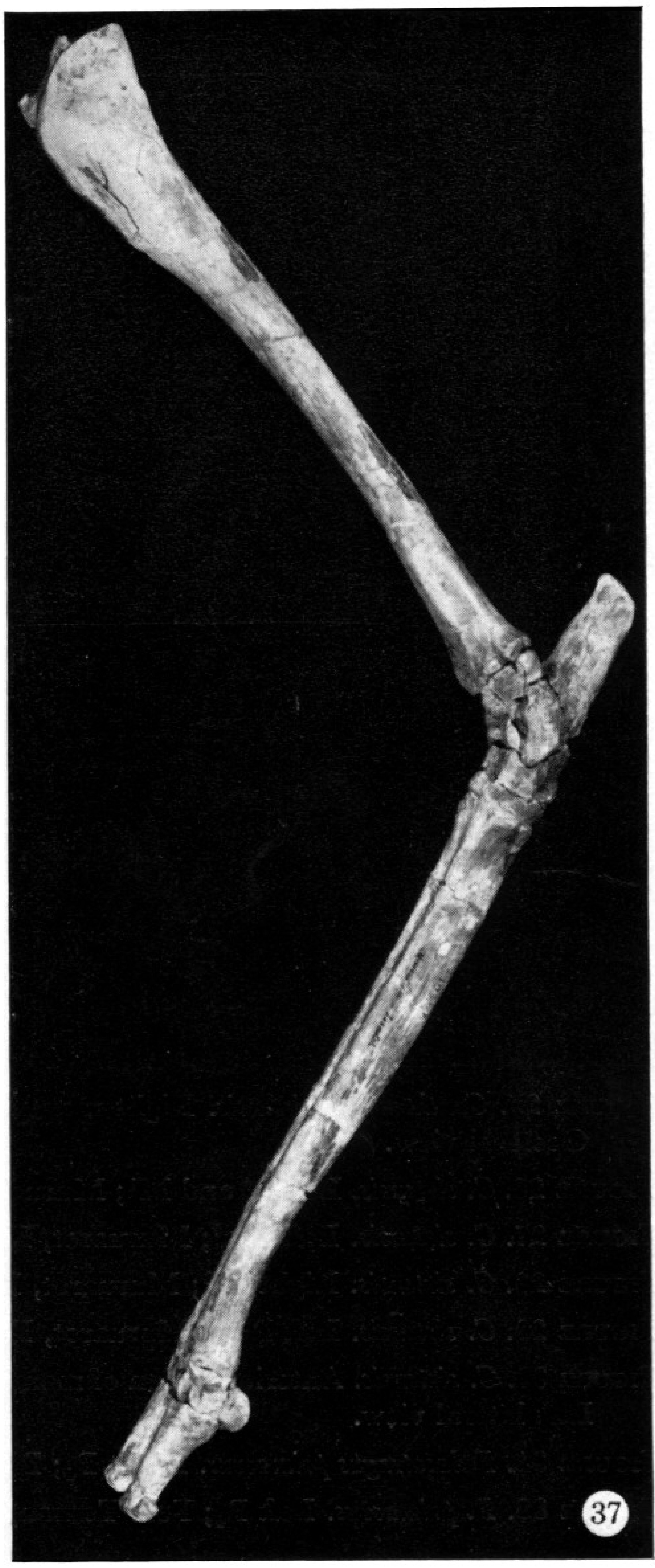
FIGURE 30. *C. sirtensis.* Anterior region of mandible with canine; Muruarot, Kenya, UCB.V.4899/42058: × 2.50. Left lateral view.

FIGURE 31. *Palaeotragus primaevus.* Right P_4; Baringo, Kenya, KNM.BN.287: × 2.43. Occlusal view.

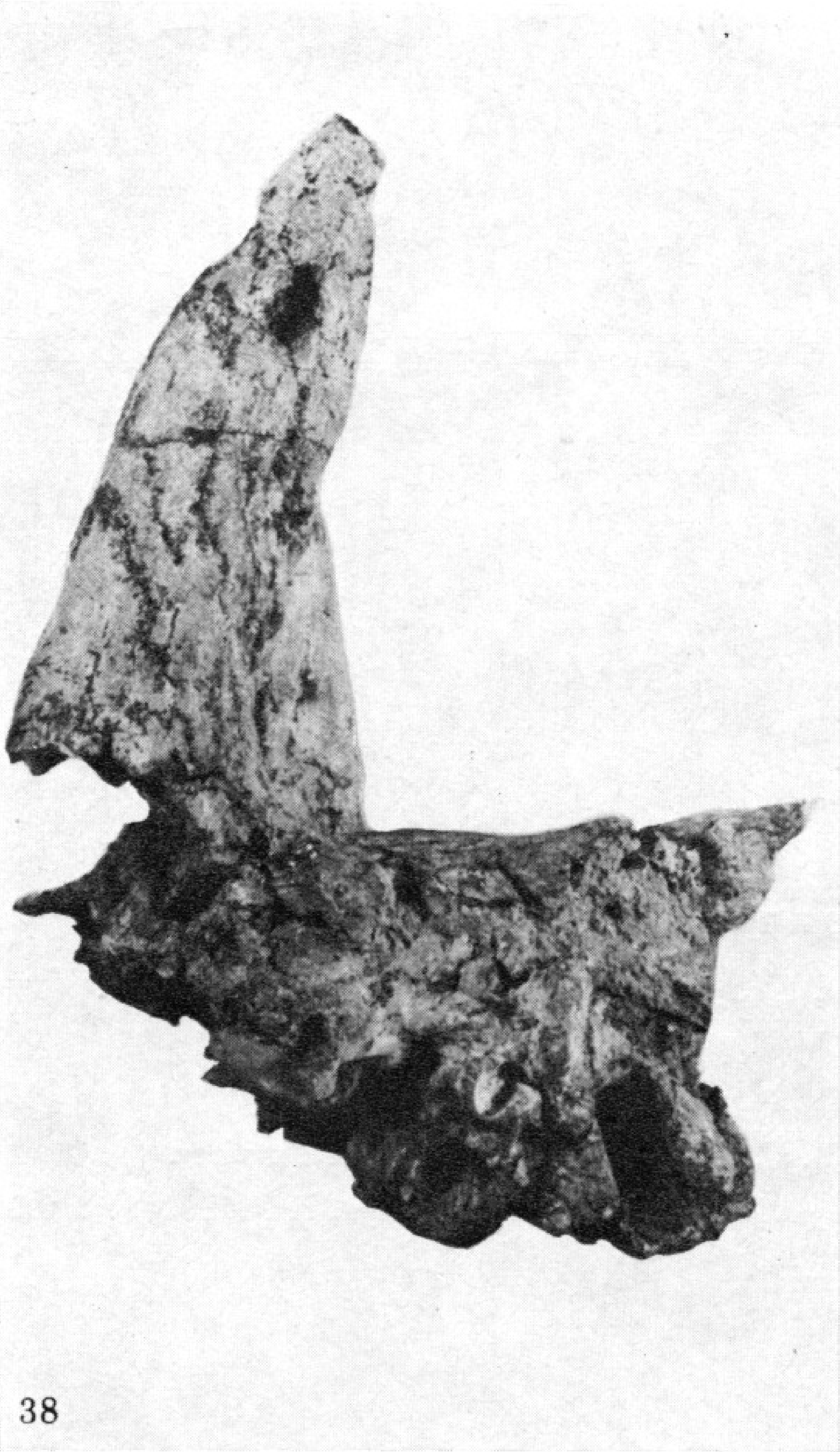
FIGURE 32. *P. primaevus.* Left P_4; Fort Ternan, Kenya, KNM.FT.3045: × 2.43. Occlusal view.







FIGURES 33–37. For description see opposite.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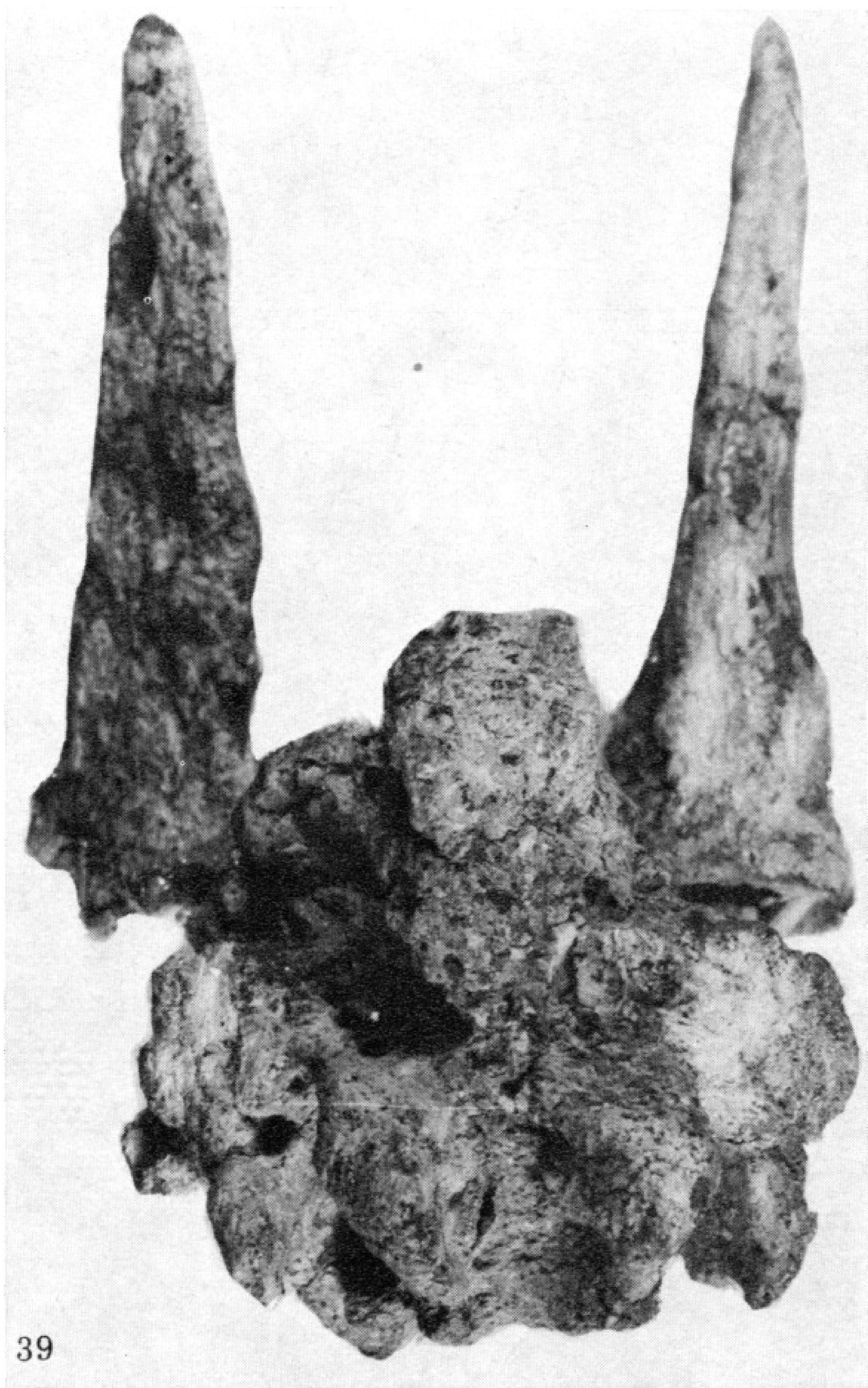
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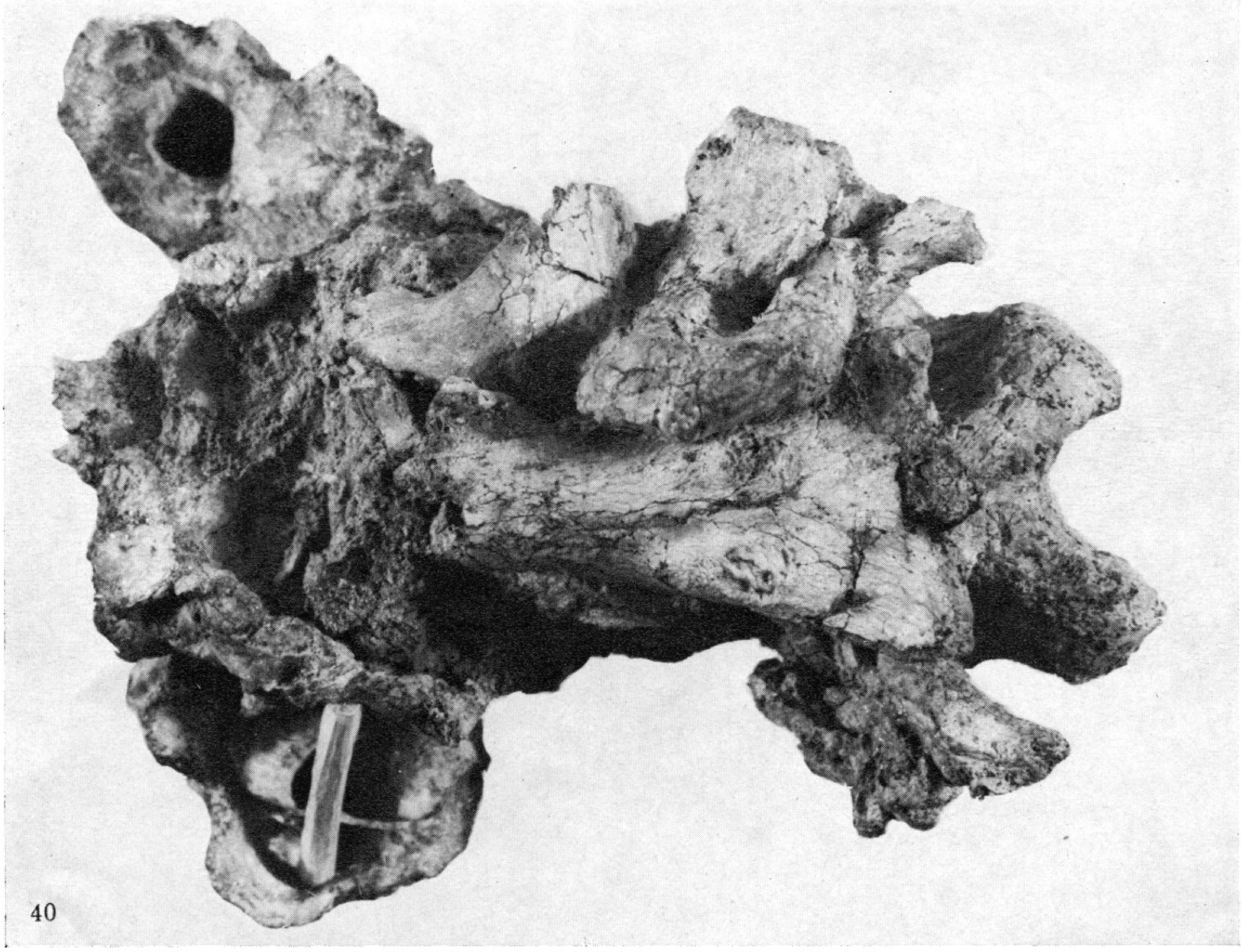
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FIGURE 38. *Palaeotragus primaevus*. Skull fragment with ossicones; Baringo, Kenya, KNM.BN.1446: × 0.50. Left lateral view.

FIGURE 39. *P. primaevus*. Skull fragment with ossicones; Baringo, Kenya, KNM.BN.1446: × 0.64. Posterior view.

FIGURE 40. *P. primaevus*. Skull fragment with ossicones; Baringo, Kenya, KNM.BN.1446: × 1.00. Basicranial view.