FOSSIL BOVIDAE FROM THE LIMEWORKS QUARRY, MAKAPANSGAT, POTGIETERSRUS

By L. H. Wells* and H. B. S. Cooke**

ABSTRACT

A short history of palaeontological work in the Makapan Valley is given and the setting of the fossil material is briefly described. Many hundreds of bovid cranial and dental fragments have been recovered, in addition to thousands of bones and bone fragments. The post-cranial material is not considered in the present account. The collection includes a number of species not separable from the living kudu, nyala, eland, Cape buffalo, blue duiker, mountain reedbuck, gemsbok, sassaby, brindled gnu and impala. Known extinct species include cf. *Alcelaphus robustus,* cf. *Pelorocerus helmei* and *Oreotragus major*. A new genus of aberrant Alcelaphine is described as *Makapania broomi.* Other new species are *Cephalophus pricei, Redunca darti, Gazella gracilior,* and *Phenacotragus vanhoepeni.* A feature of the assemblage is the tendency for species to be larger than their living counterparts. The whole described fauna of the deposits is discussed and it is considered that a lower Pleistocene (probably Villafranchian) age is most likely.

HISTORY

The occurrence in the Makapan valley of consolidated bone-bearing cave deposits was first mentioned by Dart in 1925 and some specimens were collected by him two years later at a site now known as the "Limeworks Quarry". In 1937 Broom described a dwarf buffalo *"Bos" makapani* from a cemented bone breccia on the opposite side of the valley and this location has come to be called "Buffalo Cave". A year later Van Riet Lowe (1938) drew attention to further sealed cave deposits near the head of the valley, adjoining an open cave associated with historic incidents. One of these deposits comprises banded layers of coloured ash and bat guano, containing Middle Stone Age artifacts, and it was named the "Rainbow Cave"; the other deposit contains Earlier Stone Age (hand-axe) tools and shows a basal ash and guano layer which led to the name "Cave of Hearths". Additional sites have also been found in the valley and their relative positions are shown in the accompanying map (Fig. 1).

In 1945 and 1946 senior students and staff from the Department of Anatomy of the Medical School in Johannesburg collected fossil material from dumps of waste at the Limeworks quarry. Several extinct species were recognised, some of them new, and it was realised that the fauna had affinities with that of the australopithecine-bearing cave breccias of the Sterkfontein area. Accounts ware published describing some of this material and dealth with Primates (Broom and Jensen, 1946; Mollet, 1947; Kitching, Wells and Westphal, 1948, Suidae (Dale and Tobiansky, 1947; Dale 1948), Giraffidae (Cooke and Wells, 1947) and a rodent mole (Broom 1948).

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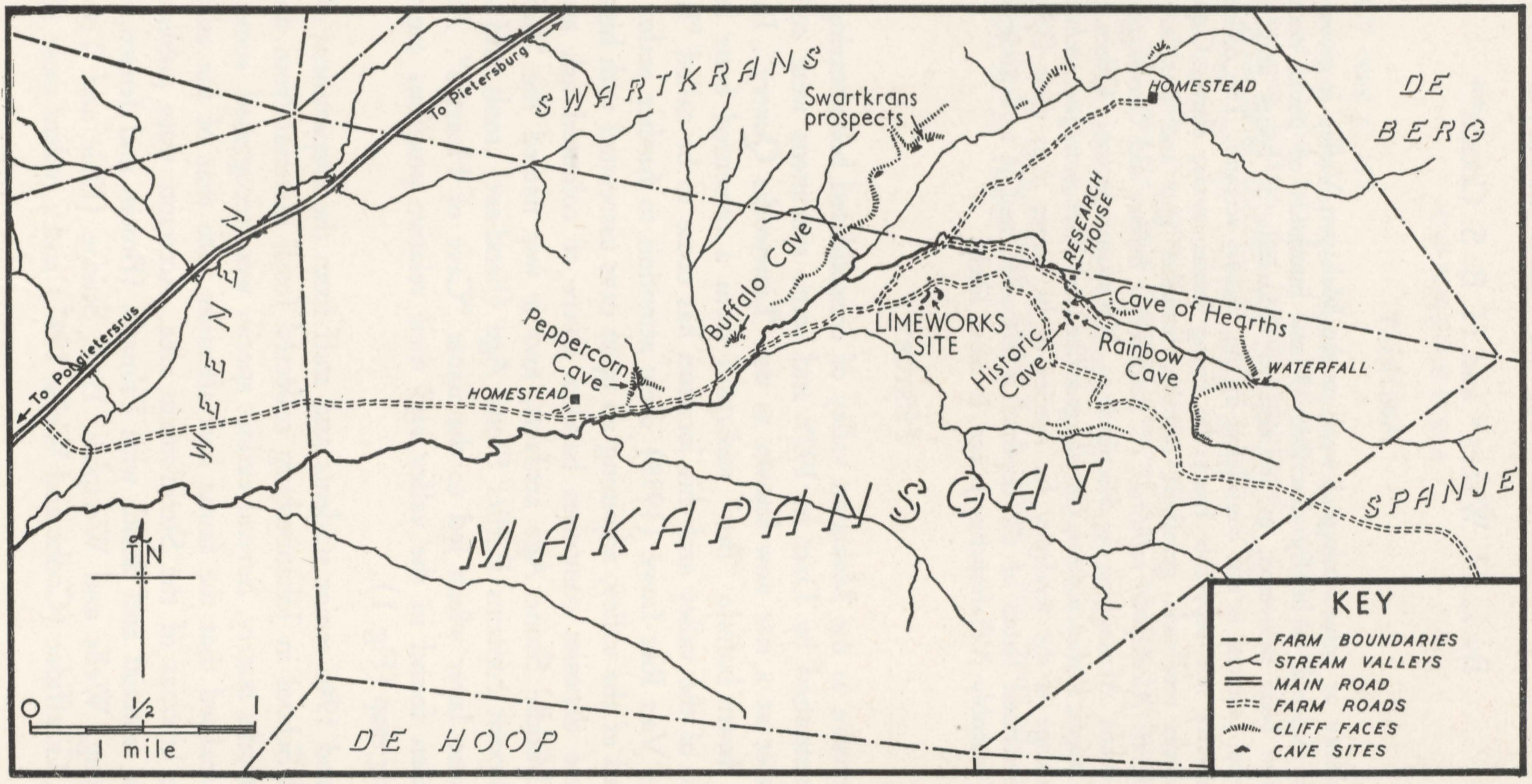

Fig. 1—Plan of Makapan valley showing location of main sites. (Based on survey by H. B. S. Cooke 1939, 1947.)

A paper on the Bovidae was presented to the Royal Society of South Africa by one of us (L.H.W.) in 1947, but it was withdrawn for revision in the light of a rapid increase in the quantity of material collected.

Archaeological excavations began at the Cave of Hearths in 1947 with the aid of funds provided by Dr Bernard Price and in the following year a human mandible was recovered (Dart 1948 e). The availability of a base camp in the area facilitated work on the waste dumps at the Limeworks quarry and in 1948 were recovered an australopithecine occiput (*Australopithecus prometheus;* Dart 1948 a, c) and, subsequently, an adolescent mandible (Dart 1948 b, d). Excavations at the Cave of Hearths stopped at the end of the 1949 winter season and were resumed only in 1953 with funds made available by the Wenner-Gren Foundation. At the Limeworks, however, sorting of the dump material has been continued each winter season (except in 1952) and additional australopithecine fragments have been described (Dart 1949 a, b, c; 1954; Boné, 1955). Some further accounts have appeared of baboons (Broom and Hughes 1949; Kitching 1952, 1953). New descriptions also include a chalicothere (George 1950), a klipspringer (Wells 1951), a hippopotamus (Kitching 1951), carnivores (Toerien 1952, 1955), hystricomorphs (Greenwood 1955) and hyracoids (Churcher 1956). At present, the baboons are being re-considered by Freedman (1955) and the carnivores and Suidae are under review by Ewer.

GEOLOGICAL SETTING

The general physiography of the Makapan valley has been described by Barbour (1949 a, b) and its geology by King (1951) with additional details furnished by Van Riet Lowe (1938, 1943, 1948), Bosazza, Adie and Brenner (1946), Cooke (1952), Dart (1952) and Oakley (1954 a, b). Haughhton (1947) has discussed the cave breccias in general. King provides an excellent factual account of the sequence of deposits observed at each of the major sites. He gives a geological map of the upper part of the valley and sketch plan of the Limeworks site. While his descriptions cannot be questioned, his interpretations of the successions and his correlations are subject to dispute. His conclusions differ from those of Barbour and have been criticised in some respects by Robinson (1952).

Like those of the Sterkfontein area, the original caves (now largely represented only by the consolidated fillings) were formed by solution in dolomitic limestones of the Transvaal system, some of them selectively along old crush zones. Such caves tend to follow in depth the shallow southerly dip of the bedding planes of this formation. Before the cavities became opened to the surface, travertines or dripstones of rather pure calcium carbonate were formed on the floor, walls and roof of the cavern. As an opening to the surface developed and grew in size, increasing amounts of detrital soil, wind-blown dust and other material were carried in. Thinning of the retreating roof or lip of the cave ultimately led to the development, in many cases, of a covering of collapsed rock breccia or rubble. The detrital material has been cemented to a greater or lesser degree by the infiltration of calcium carbonate.*

At some localities continued erosion has led to secondary cavernation of deposits of the first cycle, followed by a subsequent cycle of infilling. Complete removal of the original cave roof and surface erosion of the already cemented cave deposit is characteristic of the older sites. As this general cycle is largely inherent in the process of cavern formation and filling, it is clear that similar lithological sequences of detrital cave deposits may vary widely in age. The age is controlled to a great extent by (1) the moment at which a surface opening developed and (2) the rate of introduction of detritus, which is likely to begin slowly and increase in tempo. While the cave opening is small, the "cave climate" must exert a considerable influence on the character of the deposit but the detrital material introduced reflects in its physical state the impress of the external or regional climate. Tedious mineralogical and analytical studies being pursued by Brain at the Transvaal Museum, Pretoria, are yielding most interesting results and promise to provide a valuable tool for use in correlation together with the palaeontological evidence. Detailed results are unpublished but a brief note has appeared recently (Brain, Van Riet Lowe and Dart 1955).

Except in the case of the Historic Cave, the deposits have come to light as a result of the activities of lime workers, who sought and mined the valuable basal travertine deposits. The travertine is almost pure calcium carbonate whereas the parent limestone is highly dolomitic and of little commercial value. In consequence of these mining activities, the original cave fillings were undercut by galleries and stopes so that access to the deposits at the present day is normally gained from these workings *below* the detrital filling.

At the Makapan Limeworks, the lime-seekers fortunately discarded much of the material which lay above the pure basal travertine because it was contaminated with introduced sandy material. The waste dumps of sandy limestone and cemented detritus have thus proved a rich source of fossil bone, though many valuable specimens must also have gone to the kilns. With very few exceptions the fossils previously described (and also nearly all those discussed in the present account) have come from the dumps at the Limeworks quarry and their horizons of derivation in the deposit cannot be determined precisely. Certain information can be deduced from the matrix material.

A simplified plan of the Limeworks quarry area is given in Figure 2. A road separates the northern area of dumps and old kilns from the open quarry and underground galleries. Entrance to the workings is usually gained from the western open cutting. The first part of the inner gallery is roofless and has a northwestern wall of crudely stratified red or pink sand with bones visible in the lower part.

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* King's suggestion of consolidation due to recrystallization of original calcite dust is here regarded as improbable.

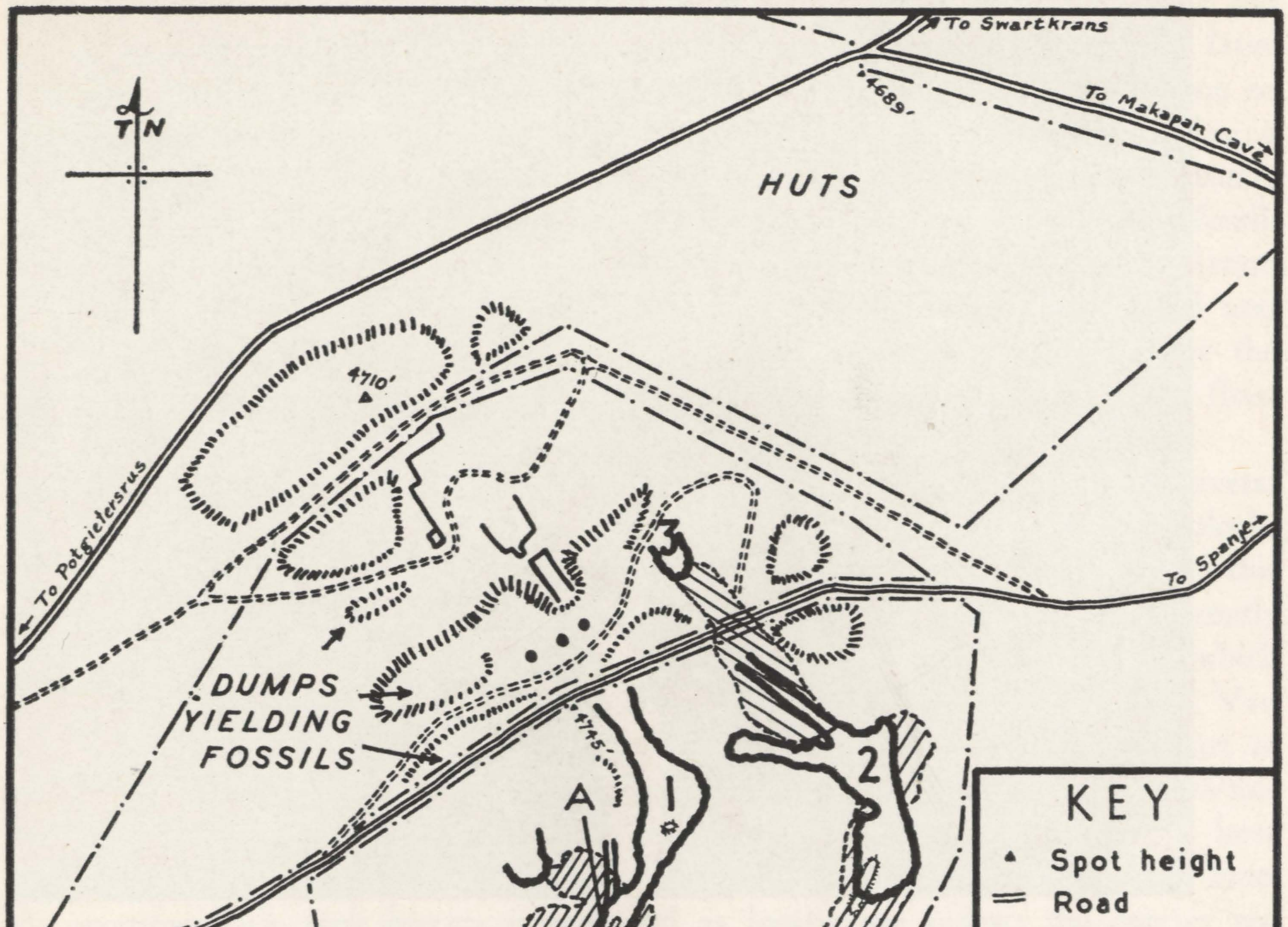

Fig. 2—Simplified plan of the Makapan Limeworks site and a North-South section illustrating the geological succession of the fossil-bearing deposits. In the plan, 1 is the western quarry, 2 the eastern quarry and 3 a quarry and cave known as the "Horse mandible Cave". (Based on surveys by H. B. S. Cooke 1939, 1947 and A. R. Hughes 1948.)

The original floor travertine has been removed almost entirely leaving the old filling overhead (Figure 3). Resting on the old travertine was a manganous layer of mixed travertine and very fine pink sand. This gives place to stratified pink or red breccia with occasional dark bone fragments and is then overlain, after a variable distance, by a grey layer of cemented marl rich in bone, sometimes actually in contact with the cave roof. This grey layer is considered to be the main fossil-bearing horizon and its richness is probably due to the very slow rate of accumulation of introduced sediment. The floor of the old workings descends southward and the grey layer rises somewhat on the western wall so that it lies far above the present artificial floor. Eastwards, the grey layer dips sharply above the old floor and vanishes below a large cone of fallen brownish-red sandy breccia (Fig. 4).

In this (southern) portion of the cave system, the grey layer is overlain by several feet of slightly coarser and sandier pink breccia with a good fauna. Collapsed blocks of travertine, presumably fallen from a thinning roof, lie in the upper part of this zone. Overlying it is the coarser brownish-red sandy breccia which forms the recently collapsed cone. This material contains weathered pebbles and gravel from which dubious artefacts of extremely primitive character have been recovered (Brain, Van Riet Lowe and Dart, 1955). Brain regards this brownish-red material as a part of the normal succession and hence as a direct continuation of the grey breccia. While this is probably the case, the browner material might possibly represent a later filled-in sink-hole. Detailed study of this question is awaited but, in the mean time, the stratified pale pink breccia is regarded as locally the oldest; the coarser red breccia with dark bone is considered to be its direct successor, followed by the main fossiliferous grey layer, while the browner deposit is thought to be at least a little younger and possibly a good deal younger. However, the total time span covered is probably limited. The grey layer is rich in bone and is the source of most of the fossil material recovered; the red or pink zone contains only a modest quantity of material; the browner material is scarcely studied and there is considerable uncertainty regarding the reference of dump material to this zone.

Fig. 3—View of the stratified pink and red sandy breccia with dark bones, resting on remnants of floor travertine, the mining of which produced the gallery. Photograph taken from dolomite hummock near centre of section AB of Fig. 2, looking towards A.

Fig. 4—Cone of collapsed brown breccia, containing weathered pebbles and gravel in its lower portion. On the left of the picture is the downward-projecting solid mass of cave deposit shown in the centre of the section in Fig. 2.

Classification and Nomenclature

Various classifications of the Bovidae have been put forward by numerous authors, notably Schlosser (1925), Schwarz (1937), Pilgrim (1939) and Simpson (1945). Simpson degrades the sub-families of most authors to the more reasonable rank of tribes, recognising thirteen and grouping them into five subfamilies as follows:—

Subfamily BOVINAE:	Tribes	Strepsicerotini
		Boselaphini
		Bovini
Subfamily CEPHALOPHINAE:	Tribe	Cephalophini
Subfamily HIPPOTRAGINAE:	Tribes	Reduncini
		Hippotragini
		Alcelaphini
Subfamily ANTILOPINAE:	Tribes	Neotragini
		Antilopini
Subfamily CAPRINAE:	Tribes	Saigini
		Rupicaprini
		Ovibovini
		Caprini

Although this classification may be subject to minor objections, it is simple, essentially reasonable and is adopted here. Neither the recent fauna of southern Africa nor the fossil assemblage from the Limeworks quarry includes any Caprinae* or Boselaphini. Of the remaining eight tribes, at least one representative of each has so far been identified in this fossil assemblage.

For the nomenclature of recent genera and species, Allen's "Checklist of African Mammals" (1939) is followed in the main, subject to such modification as is required by Simpson's classification. For the fossil species from Africa, the list given by Hopwood and Hollyfield (1954) serves as a useful guide. In describing the teeth, the terminology used by Pilgrim (1939) is employed in preference to the Cope-Osborn nomenclature. The abbreviations I, C, P and M will be used to indicate incisor, canine, premolar and molar teeth respectively; the prefix D is used for decidious (milk) teeth and the prefixes R and L indicate the right and left jaws.

In the paper communicated to the Royal Society of South Africa in 1947, a number of new names were proposed. Although these names were given in a circulated abstract, they were unaccompanied by any description and are here regarded as *nomina nuda*. The earlier names are entirely superseded in the present account.

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* Two extinct African genera (*Pultiphagonides* and *Pelorocerus*) assigned to the Caprinae by Hopwood and Hollyfield (1954) belong in reality to the Alcelaphini (*vide infra*).

Systematic Description

Subfamily BOVINAE

Tribe Strepsicerotini

Strepsiceros cf *strepsiceros* (Pallas)

Koedoe.

A number of partial upper and lower dentitions cannot be separated from the living kudu, though many of the teeth lie at or above the upper limit of size variation noted in living material. The best specimen (M 2)* is a right maxillary fragment with P^4 - M^3 and part of P^3 in advanced wear. The intact teeth measure 82 mm, the length of the three molars being 69 mm. These measurements correspond exactly with those of a male kudu skull in the Transvaal Museum. The anterior and middle external folds of the molars are very reduced so that they lie practically flush with the face of the lobe behind them. In correspondingly worn teeth of the living kudu, these folds are also reduced, though not to quite the same degree. Similar reduction is also apparent in a more worn third molar, 26 mm in length, which occurs in a maxillary fragment together with part of the second molar. A well worn upper right dentition is a good deal larger, the three premolars having a combined length of 52 mm and the three molars a length of 77 mm compared with 44 mm and 71 mm in the largest living specimen studied. The folds are more normal in this specimen (M 3).

Also assigned to this species are: a partial palate with well-worn RP^3 - RM^1 and LP^4, LM^1 and part of LM^2; half a dozen isolated upper teeth; five mandibular fragments with one or two teeth in each; five loose lower molars; and a partial left lower jaw of a juvenile with DM_2- DM_4 and parts of M_1 and M_2, the latter still in alveolus. This last specimen (M 4) belongs to the collection made by Dart in 1927.

The back half of a skull, broken across in front of the orbits, shows no trace of horns and agrees closely with the skull of the female kudu, except that the width across the mastoid region is greater than in living material. This specimen (M 1111) is filled with firmly cemented fine bright pink silt and the bone is unusually dark, suggesting that the specimen did not come from the usual grey breccia.

A frontlet with a cavity for the right horn core and with a much damaged hind portion of the left core resembles the kudu in size and erection of the horns but the condition of the specimen (M 1112) prevents more exact comparison.

A large fragment of the back part of a skull (M 555), though badly damaged, agrees in all essential features with the corresponding portion of the skull of a recent kudu. It is therefore placed tentatively in this group.

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* Specimen number in the catalogues of the Bernard Price Institute for Palaeontological Research, Johannesburg.

Bosbok.

Strepsiceros (*Tragelaphus*) cf *angasi* (Gray)

Four partial upper dentitions, a loose RM^2, two partial lower jaws, a few loose lower molars and three fragments of horn core cannot at present be separated from the living nyala, though the fossil is somewhat larger. The best upper series is a right maxillary fragment with moderately worn M^1 - M^3, 55 mm in length (M 5), compared with 52 mm in the largest specimen available for comparison. A good lower left jaw has P$_4$ - M$_3$ in fairly early wear (M 6), the premolar being 16 mm long and the molar series 64 mm, compared with 14 mm and 58 mm in the living species. These dimensions thus exceed the observed upper limit of variation in the nyala and are comparable with typical material of the mountain nyala (*T. buxtoni*). The lower molars all show a moderately well-developed external basal pillar, strongest in M$_1$ and weakest in M$_2$.

The three horn core fragments represent the tip, upper median and basal parts of at least two different horns. The somewhat triangular cross-section and spiral keel characteristic of this group are clearly shown. The size of the basal portion is about normal for the nyala and smaller than in the mountain nyala.

Arambourg (1941, 1947) described an extinct species *Tragelaphus nakuae* from Omo which he regarded as related to the bongo. Both the teeth and the horns of the Omo form are larger than is the case with the Makapan material and specific identity seems improbable.

Taurotragus cf *oryx* (Pallas) Eland.

Remains not at present distinguishable from the existing eland are fairly plentiful, though a feature of the material is the youth of the individuals represented.

The most considerable specimen is a right maxillary fragment with DM^2 - M^2, lacking the outer walls of all the teeth except the last. Three other maxillae (two right and one left), carry DM^2 - M^1 and there are five fragments with milk teeth only. One partial right palate possesses M^1 and M^2; a damaged left maxilla (M 7) has P^4 (unworn), M^1 and M^2. There are also a piece of left maxilla with P^2 and P^3 in moderate wear and some half dozen isolated upper molars in varying degrees of attrition.

The upper permanent molars correspond exactly with those of *T. oryx* in size and in the broadly rounded form of the medial lobes. In the isolated upper teeth the strong folds and weak ribs of the external wall are identical in development with those of the living eland. A feature of the upper permanent molars which is not common in *T. oryx* is the presence in M^1 and sometimes in M^2 of a weak basal pillar extending as much as half the height of the crown. In the upper milk molars the basal pillar is rudimentary.

Two left mandibular fragments, with DM$_2$ - DM$_4$ and DM$_2$ - M$_2$ respectively, can also be assigned to this species. A jaw fragment with P$_3$ and P$_4$ and two isolated unworn lower first molars may be included.

Tribe Bovini

cf *Syncerus caffer* (Sparrman)

Buffels.

A left maxillary fragment (M 10) with DM^2 - M^1 in early wear is considerably larger than the remains ascribed to *Taurotragus* cf *oryx,* the three milk molars measuring 75 mm as compared with 64 mm in the eland. A right maxillary fragment carries unworn DM^3 and DM^4 and there are also six isolated milk molars and four first molars of similar character. All are practically unworn. These teeth are further distinguished from *Taurotragus* by prominent external ribs. DM^4 has a well-developed basal pillar, but this is not continued into a cingulum fold around the medial lobes as is the case in *Hippotragus.*

Allowing for their very early state of wear, these teeth agree with those of the only juvenile specimen of *Syncerus caffer* at our disposal. They are actually somewhat larger than the recent dentition, in which the three milk molars measure 66 mm. This is due at least partially to the less worn condition of the fossil teeth. The basal pillars of DM^4 and M^1 are more slender, and that of M^1 possibly shorter, in the fossil than in the recent dentition; also there is no rudimentary basal pillar in DM^3. These features may prove to be outside the range of variation of *S. caffer* but the evidence on this point is at present too uncertain to justify specific distinction.

A portion of a right mandible (M 15) carries M$_2$ and a damaged and almost unworn M$_3$, the combined length being 74 mm, which is 7 mm larger than the biggest available living specimen. Two mandible fragments have DM$_4$, unworn, in each. Another piece shows the crown of M$_1$, still unerupted, and there is a fragment of jaw with a slightly worn first molar. Isolated lower teeth include three complete fourth milk molars, a fragment of one, and a first molar, all unworn. All these teeth are very similar in size and in structure to the corresponding teeth in *S. caffer,* though on the whole they tend to be a little larger than in the specimens available for comparison.

None of these teeth is large enough to be assigned to *Homoioceras bainii* (Seeley) or even to *"Bubalus"* (? = *Syncerus*) *andersoni* Scott. *"Bos makapaani"* Broom comes from a different site in the area and is almost certainly much more recent in age than the Limeworks fossils; it is most unlikely that any of the Limeworks buffalo teeth belong to this dwarf species.

Also probably representing the buffalo is a portion of an occiput (M 950) lacking the upper part of the braincase.

As is the case with the other large species already considered, a feature of the buffalo material is the youth of the individuals represented.

Subfamily CEPHALOPHINAE

Duikers.

Tribe Cephalophini

Cephalophus pricei sp. nov.

Diagnosis: A cephalophine about thirty-five per cent larger than *Cephalophus natalensis* and with relatively shorter premolars.

Holotype: Left mandible with moderately worn cheek teeth P_2 - M_3 (M 18; Fig. 5).

Paratypes: Right mandible with P_2 - M_3 in early wear (M 17; Fig. 5); right mandible with P_2 - M_3 in advanced wear (M 19; Fig. 5); left mandibular fragment with DM_2 - M_1 (M 9; Fig. 5); right horn core (M 478; Fig. 6).

Measurements (in mm):

	Holotype	Paratypes		
	M 18	M 17	M 19	M 9
DM_2 length				6
DM_3 length				8
DM_4 length				14
Series DM_2 - DM_4	—	—	—	28
P_2 length	5	7	5½	
P_3 length	8	10	8	
P_4 length	10	11	10½	
Series P_2 - P_4	23	28	24	—
M_1 length	11½	12	12	12
M_2 length	12	14	13	—
M_3 length	18	18	19	
Series M_1 - M_3	42	44	44	—
Ratio $\frac{P \times 100}{M}$	55	62½	54½	—
Jaw height at P_4/M_1	23	20	23	21

Eighteen lower jaws and jaw fragments resemble closely the living duikers but the teeth are a good deal larger than in the biggest living South African specimens of *Cephalophus natalensis* (red duiker) or *Sylvicapra grimmia* (Cape duiker). The fossil material is somewhat larger even than the Bay Duiker of West Africa *Cephalophus castaneus* but is considerably smaller than the Yellow-backed Duiker *C. sylvicultor*. Comparative average measurements are given in the following tables:

	Fossil	Sylvicapra grimmia	Cephalophus natalensis	Cephalophus castaneus	Cephalophus sylvicultor
DM_2 length	6	6	5	7½	11
DM_3 length	8	7	6½	7½	13
DM_4 length	14	11½	9½	13½	19½
Series DM_2 - DM_4	28	24½	21	28½	43½
P_2 length	6	6½	5½	7½	12
P_3 length	9	7½	6½	8	12
P_4 length	10½	8	8	9	12½
Series P_2 - P_4	25½	22	20	24½	36½
M_1 length	12	9	8	9½	13
M_2 length	13	10½	10	12	17½
M_3 length	18½	13½	13	15	23
Series M_1 - M_3	43½	33	31	36½	53½
Ratio $\frac{P \times 100}{M}$	58½	67	64½	67	68
Jaw height at P_4/M_1	22	16	15	20	29

In the fossil form the average length of the cheek tooth series is thirty-five per cent. greater than in *C. natalensis* and twenty-five per cent. greater than in *Sylvicapra grimmia.* In the living forms premolar length is close to two thirds that of the molars, but in the fossil the molars are proportionally more elongated, the third molar being particularly long.

The lower molars are distinguished from those of the gazelles by being much lower crowned and shortening very rapidly with wear. They have prominent, tapering, somewhat oblique external lobes which are rounded at the apex. The anterior and posterior internal folds are prominent and persistent but the middle fold soon disappears with wear. There are also well marked internal ribs. In P_4 the medial cusp is prolonged forwards to unite with the anterior wing but is separated from the posterior wing by an open valley. This last feature, as well as the relatively low crown, distinguishes the tooth from that of *Aepyceros;* in having the medial cusp united with the anterior wing it resembles the red rather than the Cape duiker. The anterior premolars, on the other hand, are less compressed and sectorial than in *C. natalensis* and more nearly resemble those of *S. grimmia.*

Also in the collection are three horn-cores of duiker-like character. The best specimen belongs to the right side (M 478; Fig. 6). It lacks the extreme tip and

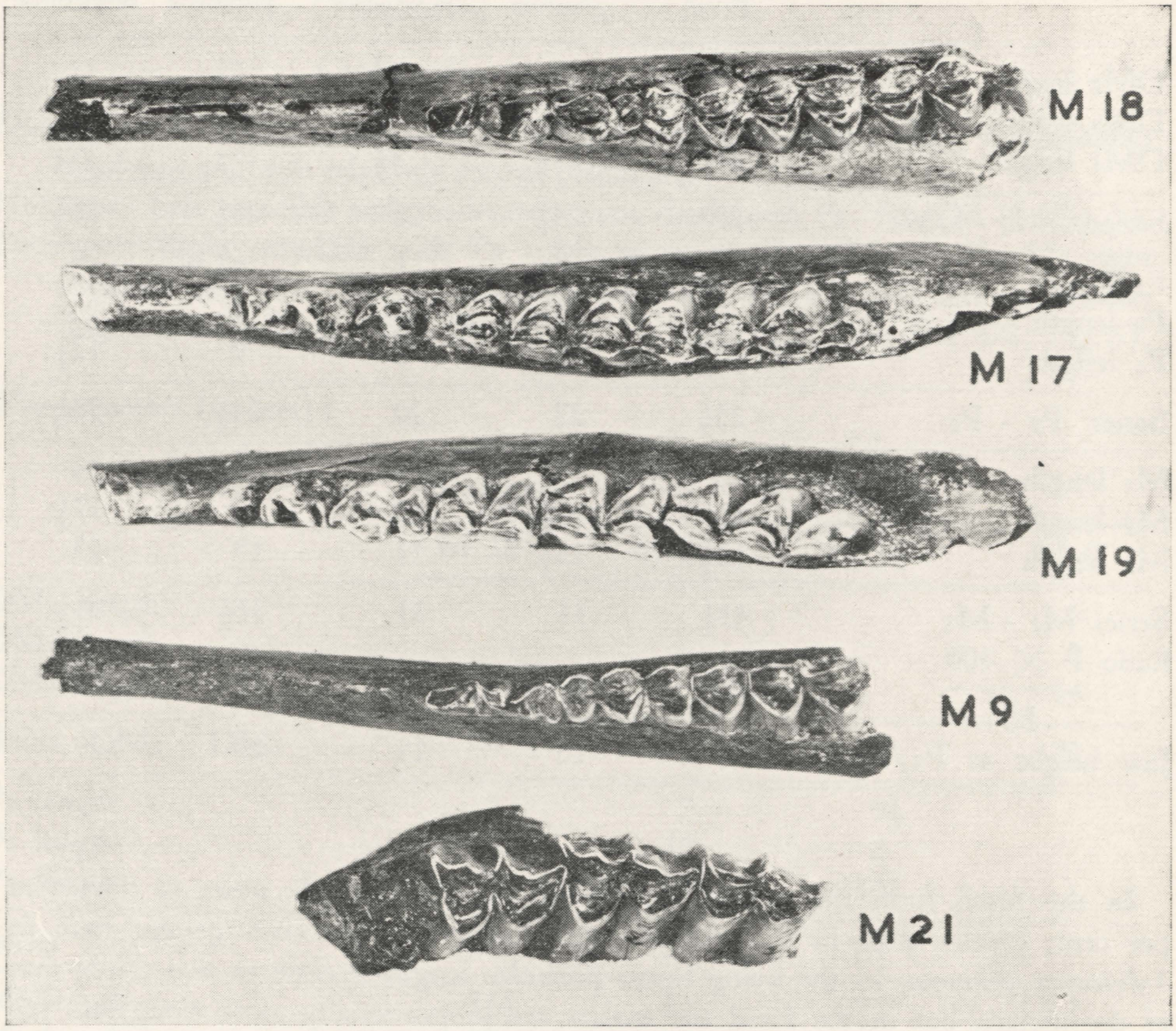

Fig. 5—Cephalophus pricei. M.18; holotype left mandible with P_2 - M_3 in moderate wear; M 17: paratype right mandible with P_2 - M_3 in early wear; M 19: paratype right mandible with P_2 - M_3 in advanced wear; M 9: paratype left mandibular fragment with DM_2 - M_1; M 21: referred partial maxilla with M_1 - M_3 in early wear. Natural size.

must have been about 85 mm long when complete. It is slightly oval at the base, the elongation being transverse to the axis of the skull. The greatest diameter is 18 mm and the least 15 mm. The largest red duiker horn core available is 80 mm long and 12 to 16 mm in diameter at the base; the Cape duiker has horn cores up to 90 mm in length with the base almost circular, having a diameter of 12-15 mm. The fossil core is somewhat stouter than in the red duiker but is very similar in proportions and rises from the frontal bones in the same manner and at the same angle. Its resemblance to the horn core of *Sylvicapra* is less marked and this fact, together with the features of the lower fourth premolar, suggests that the new species be placed in *Cephalophus* rather than *Sylvicapra*.

Fig. 6 — Cephalophus pricei. **Paratype right horn core, M478,** facial aspect. Natural size.

Probably also to be referred to this new species is a partial left maxilla with M^1 - M^3 in early wear (M 21; Fig. 5). The teeth are low-crowned, the almost unworn third molar being only 19 mm high, compared with 25-30 mm in the very similar teeth of the gazelle *Phenacotragus vanhoepeni* to be described below. The outer walls have strong folds and definite, though weak, ribs. The molar series is 42 mm long, compared with 27-28 mm in *C. natalensis* and 29.30 mm in *S. grimmia*. Four isolated third molars may also belong to this species.

This new species has been named in honour of the late Dr Bernard Price.

cf *Cephalophus* (*Guevei*) *caerulus* (Hamilton-Smith)

A fragment of right mandible with P_4 - M_2 in fairly advanced wear is indistinguishable from corresponding teeth of the living blue duiker. An upper left third molar, with part of the maxilla, is also inseparable from this species. The fragments constitute the smallest bovid elements of the fauna.

Subfamily HIPPOTRAGINAE

Tribe Reduncini

Remains of reduncines constitute the most abundant element in the collection, fairly closely rivalled by the gazelle *Phenacotragus*. There are about fifty partial skulls and horn cores, twenty palates or maxillary fragments, thirty loose upper molars, fifty lower jaws or jaw fragments and twenty isolated lower molars. Two species are clearly present, one being very similar in size to the reedbuck *R. arundinum* but at least specifically distinct while the other is sufficiently close to the mountain reedbuck *R. fulvorufula* not to justify separation. The latter is relatively rare. It was thought, at first, that the smaller horn cores and skull represented merely young individuals of the larger species but this possibility has been excluded for reasons which will be given below.

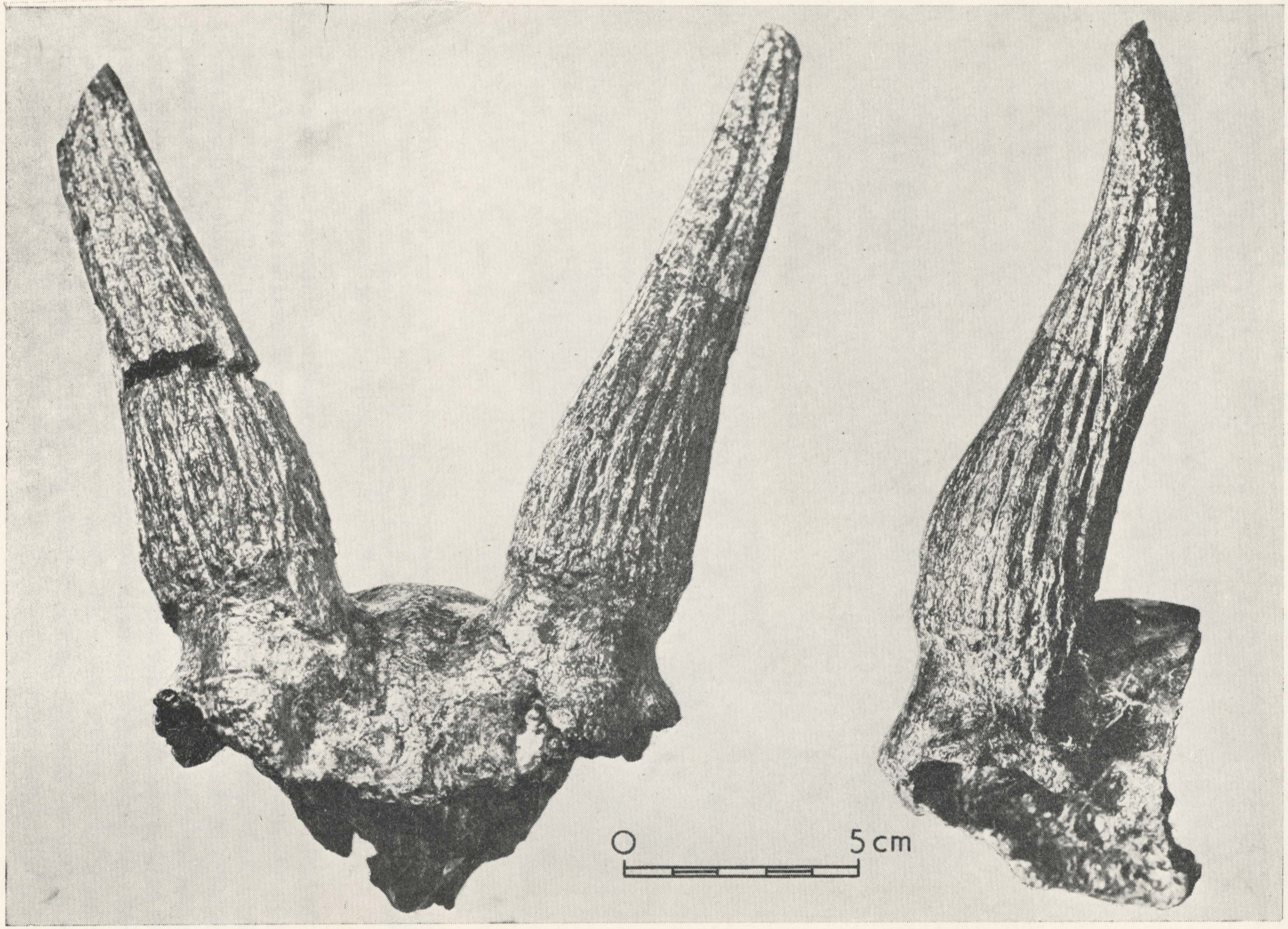

Fig. 7—Redunca darti. Holotype frontlet, M 446, facial and left lateral aspects. Two-thirds natural size.

Redunca darti sp. nov. Rietbok

Diagnosis: A reduncine the size of *Redunca arundinum* but possessing more massive horn cores with a distinctly sigmoid profile.

Holotype: A frontlet with well-preserved horns (M 446; Fig. 7).

Paratypes: A brain case and occiput with one horn core (M 447); a damaged skull lacking braincase and horns but with palate and teeth (M 690; Fig. 8).

The frontlet (M 446) belongs to an adult male animal and the horn cores are nearly complete, only the extreme tip being missing in the left core and a few centimetres lacking on the right core (Fig. 7). Compared with the horn cores of *R. arundinum,* those of the fossil are massive and relatively short; their total length measured on the anterior curve cannot have exceeded 150 mm. At their bases the cores are oval in cross-section with a maximum diameter of 44 mm and minimum of 36 mm; the long axis is directed obliquely backward and laterally.

The cores diverge at an angle of about 60° and rise abruptly from the frontals instead of sweeping back at an acute angle almost parallel to the skull surface as in *R. arundinum.* In profile they have a distinctly sigmoid curvature, the massive basal portion being convex anteriorly and the tapering upper portion concave anteriorly. The horns of *R. arundium* have a simple anterior concavity and those of *R. fulvorufula* are almost straight.

The braincase (M 447) has the occiput and pterygoid region well-preserved. The block from which the specimen was recovered was broken across at the base of the horn core, which was almost detached and has had to be reinforced. In form it resembles the holotype frontlet very closely and specific identity appears certain. The occipital crest is higher above the foramen magnum than in *R. arundinum*, giving a slightly different appearance to the nuchal view. In the living species the braincase of the male has a maximum width of 73-81 mm; in this fossil specimen the breadth is 84 mm. In two other specimens, the width of the braincase is close to 80 mm.

The skull lacks most of the braincase and the nasal region but the palatal aspect is almost complete (M 690; Fig. 8), except for the loss of the snout and some damage to the crests formed by the pterygoid process of the sphenoid and palatine bones. The left bulla is missing and there is some damage in the mastoid region and to the zygomatic arches. The occiput and pterygoid regions agree in every way with the corresponding portions of the brain case specimen described above and there is no doubt that both belong to a single species.

The upper aspect of the skull appears very incomplete owing to the lack of the braincase and nasal region. Parts of the malar and lacrimal bones are present on both sides. The anterior parts of the nasals are preserved and they show the flattening so characteristic of *Redunca*. In all dimensions, the skull agrees very closely with *R. arundinum*. Both sides of the palate carry M^1 - M^3 in moderate wear. The teeth are very similar to those of the reedbuck but are a little wider.

Fig. 8—Redunca darti. Paratype skull, M 690, palatal aspect. Natural size.

An excellent palate (M 24; Fig. 9) shows the entire set of cheek teeth on both sides, agreement with the teeth in the skull being most exact. Comparative measurements are given below:—

	Paratype (M 690)		Palate (M 24)	
	Left	Right	Left	Right
P^2 length			7½	7 est
P^3 length			9	9
P^4 length			9½	9½
Series P^2 - P^4			26	25½
M^1 length	13½	14	13	13
M^2 length	15	15	16	16
M^3 length	17	17	17½	17
Series M^1 - M^3	45½	46	46½	46
Ratio $\frac{P \times 100}{M}$	—	—	56	55½

P^2 is somewhat larger than in the reedbuck and the cheek teeth are relatively and absolutely broader than in *R. arundinum.* In this respect there is some resemblance to the puku and, in fact, the fossil gives the impression of being in some respects intermediate between the puku and the reedbuck. The molar teeth have their inner lobes more rounded than in either puku or reedbuck, in both of which there is a slight kink as if the lobe had been gently pinched near its tip. In the plentiful additional material available no significant variation either in size or in pattern of the upper teeth has been observed.

Four lower jaws have been selected from the abundant collection to illustrate the lower dentition of the new species. The teeth are closely similar to those of *R. arundinum* but, as with the uppers, they lie at the upper limit of size variation of the living form. The dimensions of these four specimens are given below and they are shown in Fig. 9.

	M. 27	M. 26	M. 25	M.948
	L. (juvenile)	L. (early wear)	R. (moderate)	L. (advanced)
DM_2 length	6*			
DM_3 length	9½*			
DM_4 length	17			
Series DM_2 - DM_4	32	—	—	—

	M. 27 L. (juvenile)	M. 26 L. (early wear)	M. 25 R. (moderate)	M.948 L. (advanced)
P_2 length		6½	7*	7 est
P_3 length		10	10*	8
P_4 length		12	11½*	10½
Series P_2 - P_4	—	28½	27	25½
M_1 length	15	15½	13*	11½*
M_2 length		16½	15	15*
M_3 length		21	19½	21
Series M_1 - M_3	—	53	47½	47
Ratio $\frac{P \times 100}{M}$	—	54	57	54
Height of jaw at P_4/M_1	24	26	24	26

* overlapping

Amongst the remaining material referable to this species is a good braincase with both the occiput and one horn core well preserved. The specimen (M 494) is curiously associated with a very good frontlet of the gazelle *Phenacotragus vanhoepeni*. Most of the remaining horn cores lack the extreme tips but it can be seen that the sharp curvature of the upper part of the core is characteristic. There are a few imperfect cores of juveniles and in these also the curvature is apparent. It is noted in the living *R. arundinum* that youthful specimens already possess the curvature exhibited at the tip in the adult form, though not always so markedly and it thus seems reasonable to exclude from *R. darti* the few shorter horn cores which correspond so closely in their almost straight character with the normal horns of *R. fulvorufula*.

From the West African bohor *R. redunca,* the fossil species differs in the massiveness and anterior convexity of the horn cores, and also in the greater actual length of the molar series and relative reduction of the premolars in *R. darti*. The fossil species *R. ancystrocera,* described by Arambourg (1947) from the lower Pleistocene Omo beds of southern Abyssinia, has simply curved horn cores resembling those of *R. arundinum* but being considerably longer. The only other extinct reduncine recorded from South Africa is *"Kobus" venterae* Broom from Florisbad but this is larger than *R. darti* and has very widely divergent horns.

In some respects the Makapan fossil resembles the Puku (*Adenota vardoni*) but these two species cannot be placed in the same genus unless the Puku is to be separated generically from the Kobs. Failing this, the fossil species is better retained in *Redunca*. The specific name is given in honour of Professor R. A. Dart, who initiated the exploration of this remarkable site.

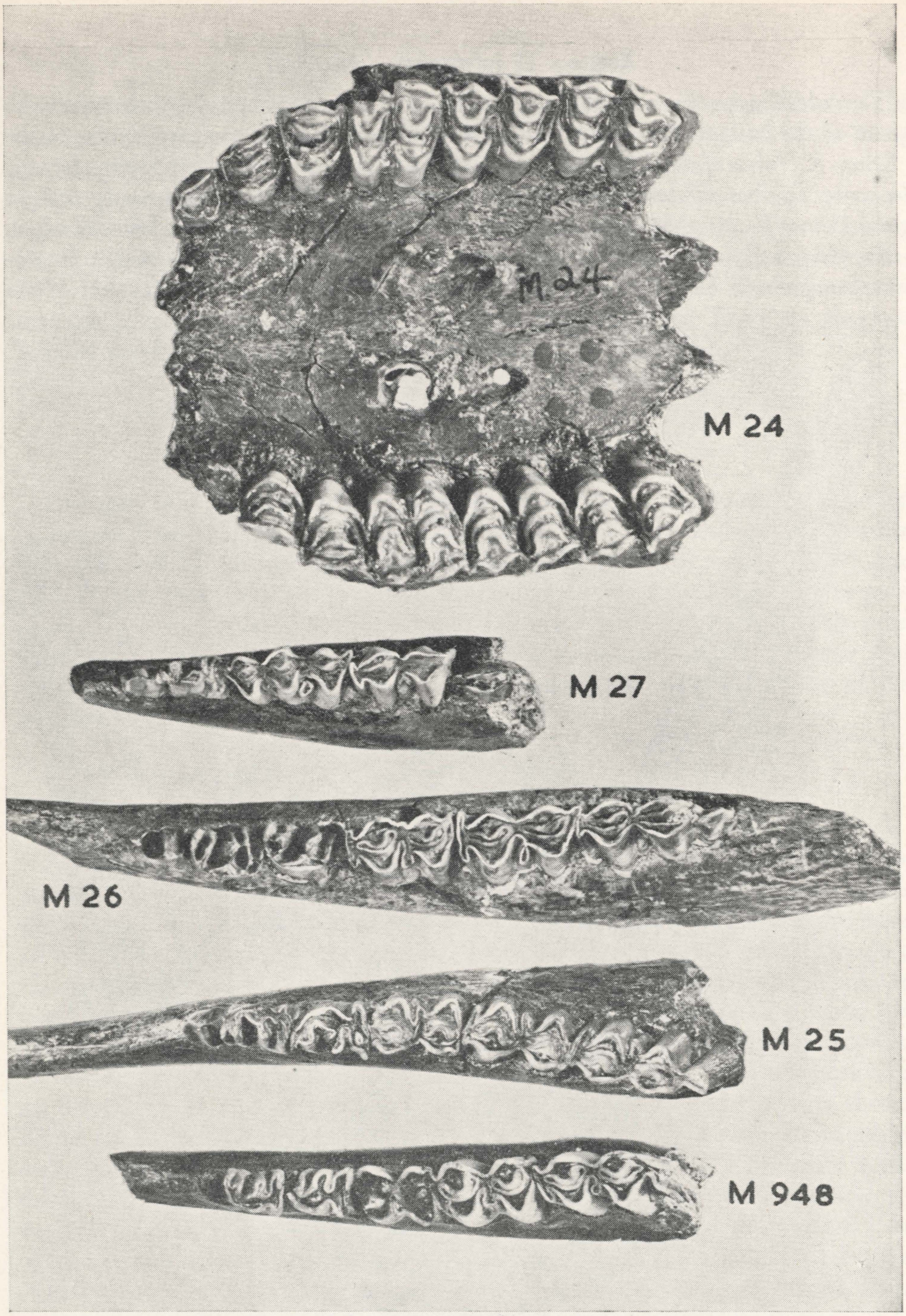

Fig.9—Redunca darti. Referred dentitions. M 24: palate with cheek teeth in moderate wear; M 27: left mandibular fragment with DM$_2$ - M$_1$; M 26: left mandible with P$_2$ - M$_3$ in early wear; M 25: right mandible with P$_2$ - M$_3$ in moderate wear; M 948: left mandible with P$_3$ - M$_3$ in advanced wear. Natural size.

Redunca cf *fulvorufula* (Afzelius)

In addition to seven partial horn cores, the collection includes a frontlet with part of the braincase and both horns (M 465), all of which are very similar to the living *R. fulvorufula.* The right core of the frontlet is complete, except for the extreme tip, but the left core lacks the top one third. The horns are nearly straight and cannot be assigned to *R. darti,* especially as sutures suggest an adult individual. The deep sculpturing of the frontal bone below the supraorbital foramen is notable in the specimen (Fig. 10) and is characteristic of *Redunca.* Similar features of the

Fig. 10—Redunca cf fulvorufula. **Frontlet, M 465, facial aspect.** Natural size.

face are shown in another specimen (M 507), which is a hornless female. The braincase and occiput are well preserved and agree closely with material of the living species; possibly the fossil is a little larger than is usual.

The presence of a reduncine which is not *R. darti* is confirmed by a piece of right maxilla and palate with P^4 - M^3 in moderate wear (M 28). The following are the lengths of the teeth: $P^4 = 8\frac{1}{2}$ mm; $M^1 = 12\frac{1}{2}$ mm; $M^2 = 12\frac{1}{2}$ mm; $M^3 = 13$ mm; $P^4 - M^3 = 46\frac{1}{2}$ mm; $M^1 - M^3 = 38$ mm. These dimensions and the pattern of the teeth conform closely to *R. fulvorufula*. There are also two isolated upper third molars which appear to belong to this species.

Tribe Hippotragini

cf *Oryx gazella* (Linnaeus)

Gemsbok

Five specimens in the collection are hippotragine in form and cannot be separated at present from the living gemsbok. The best specimen is a portion of left maxilla with M^2 and M^3 in moderate wear (M 34). The teeth are respectively 30 mm and 29 mm long, which is slightly larger than in living examples. An internal basal pillar rises to the crown in M^2 and half way up the side in M^3. Two worn upper right third molars also belong here and a moderately worn right lower first molar (M 8) $30\frac{1}{2}$ mm long and 29 mm high agrees also with lower teeth of the gemsbok.

Tribe Alcelaphini

Damaliscus sp. (aff *albifrons*)

Blesbok

A frontlet with the bases of the two horn cores (M 781; Fig. 11) indicates the presence of a *Damaliscus* which resembles the living blesbok but displays features which might be regarded as excluding it from that species. In the fossil the bases of the horn cores are strongly oval and measure 33 mm and 45 mm across their minor and major axes compared with 31 by 43 mm in a large living blesbok. In the fossil form the better preserved (right) core shows a rapid upward taper and at a height 75 mm above the base of the rugose core, the dimensions are reduced to 17 mm by 29 mm; in a typical living specimen at the same height, these dimensions are 18 mm by 31 mm; thus the base is a little larger and the taper is more abrupt in the fossil than in the living form. In the living species the axis of elongation makes an angle with the median line of the skull very close to 45°; in the fossil this line is more strongly transverse and approaches 60°. The spiral twisting of the core is sharper in the fossil than in the living form. The pedicle at the base of the horn is also stouter and less elevated in the fossil specimen. The inference is that the horns of the fossil resemble those of the blesbok but are shorter, taper and twist more abruptly and stand on a wider, stouter and lower frontlet.

A partial braincase and occiput (M 510) is typically Damaliscine in form but is rather more massive, having a very heavy occipital condyle and higher occiput than the living blesbok. As the frontlet suggests a more robust skull, the occiput probably belongs to the same species.

Two upper third molar teeth resemble those of the blesbok very closely and are comparable in size, as also is a right lower jaw with P_4 (erupting below a fragment of DM_4), M_1 and M_2 being in early wear (M 778).

Blou Wildebees

cf *Gorgon taurinus* (Burchell)

A fair number of partial dentitions and isolated upper and lower cheek teeth agree very closely with those of the living brindled gnu. The best specimen is a partial palate with well worn LM^1, LM^2, RM^2 and RM^3 (M 857). At the front lobe of M^2 the palate is 58 mm wide and the lengths of the individual teeth are: $LM^1 = 21\frac{1}{2}$ mm; $LM^2 = 25\frac{1}{2}$ mm; $RM^2 = 26$ mm; $RM^3 = 22\frac{1}{2}$ mm.

The best lower jaw (M 858) belongs to the right side and there is a less complete

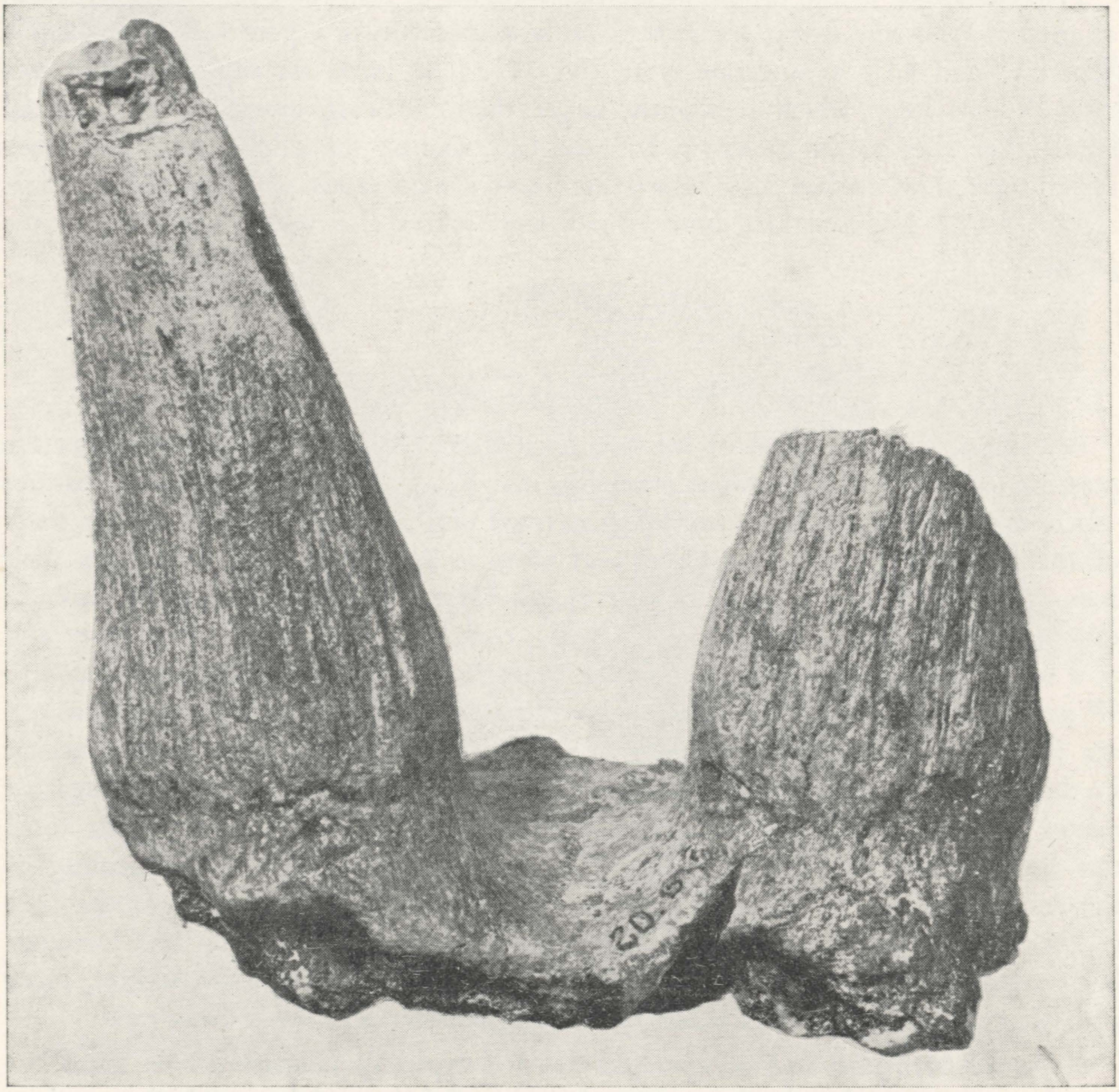

Fig. 11—Damaliscus sp. (aff albifrons). Frontlet, M 781, facial aspect. Natural size.

fragment of the left side which is probably its mate. In both specimens P_3 — M_3 are preserved and M_1 - M_3 has a total length of $69\frac{1}{2}$ mm.

Five other partial lower jaws, three partial upper dentitions, a dozen loose lower molars and three dozen isolated upper molars may also be assigned to this species. There are, in addition, a number of juvenile dentitions which cannot with certainty be distinguished from those of *Makapania broomi,* which is described below.

cf *Alcelaphus robustus* Cooke

Hartbees.

Two upper third molars and one lower molar are typically alcelaphine in structure but are larger than the living species. They are shown in Fig. 12 and may be compared with similar specimens from the Vaal river gravels which were named *Alcelaphus robustus* (Cooke 1949).

cf *Pelorocerus helmei* (Lyle)

Three well-worn upper molars of alcelaphine type (Fig. 12) are even larger than those tentatively placed in *Alcelaphus robustus* and are closely comparable with teeth previously referred by the present authors to *Pelorocerus helmei* (Lyle).

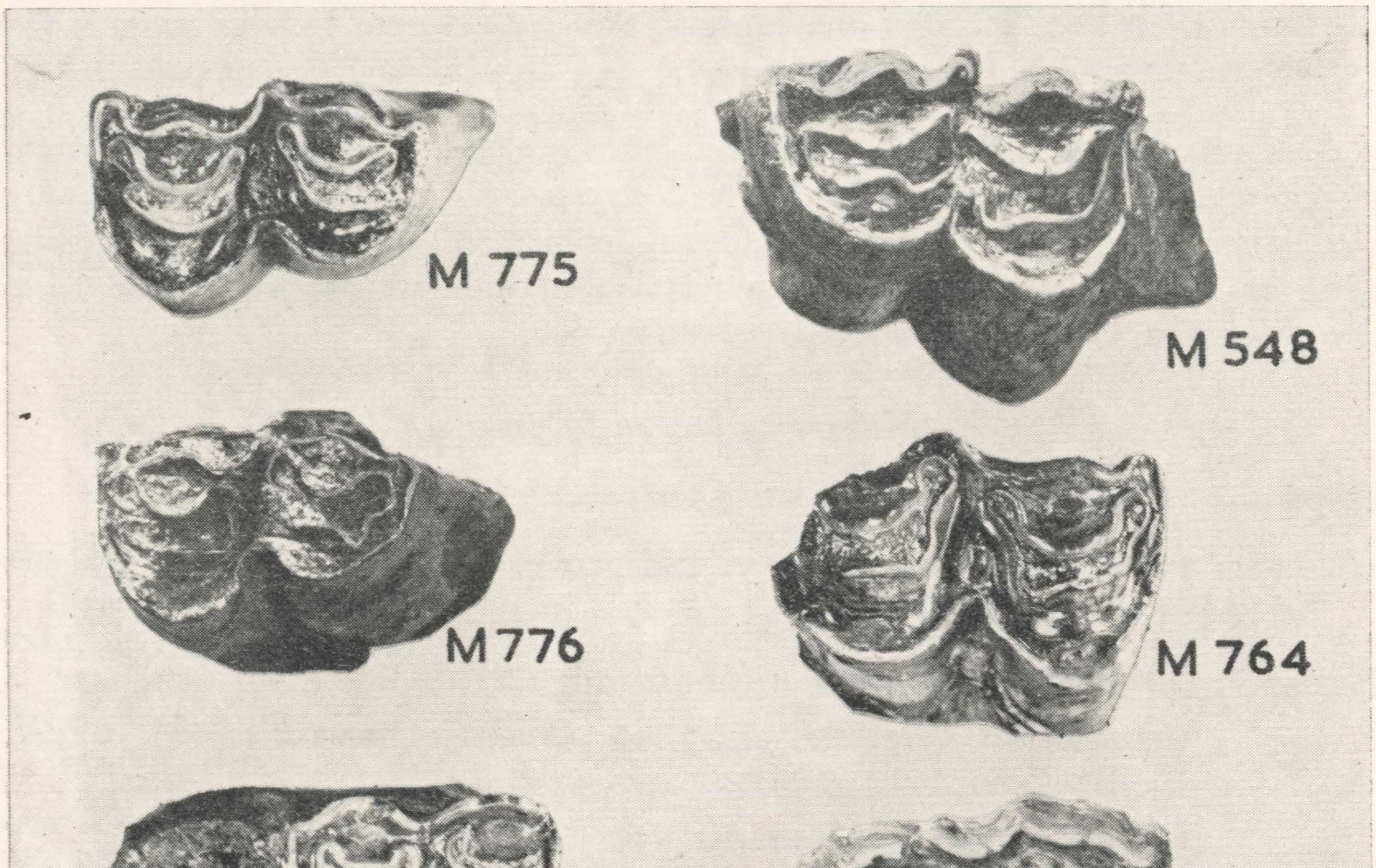

Fig. 12—**LEFT:** cf Alcelaphus robustus. **Two left upper third molars (M775, M776) and a lower right first molar (M 777) RIGHT:** cf Pelorocerus helmei. **An upper right third molar (M 548), a damaged upper right second molar (M 764) and an upper left first molar (M 765).** Natural size.

Hoffman (1953) provides confirmatory evidence for the size of the teeth of that species but indicates that a related form, which he regards as generically separate and calls *Lunatoceras mirum,* has almost identical teeth. The reference of the scanty Makapan material must, therefore, be very tentative at this stage.

A left mandibular fragment with the three milk molars in advanced wear (which is one of the specimens recovered by Professor Dart in 1927) clearly belongs to this group. DM_4 measures 30 mm in length, compared with 25 mm for an equally worn tooth of a large *Gorgon taurinus,* a ratio comparable with that between *Gorgon* and *Pelorocerus* in adult third molars.

Hopwood and Hollyfield (1954) have erroneously included *Pelorocerus* among the Caprinae. It is true that in the form of the horn-cores *Pelorocerus* is quite similar to the extinct genus *Pultiphagonides* from Olduvai, which Hopwood and Hollyfield also regard as caprine. Through Dr Hopwood's kindness we have been able to examine the type skull of *Pultiphagonides africanus* Hopwood in the British Museum (Nat. Hist.); on dental characters we consider it to be unquestionably alcelaphine. There appears therefore no good reason to depart from the view that *Pelorocerus* is also alcelaphine.

MAKAPANIA gen. nov.

Alcelaphini of medium to large size, with horns arising close to the posterior orbital margin and directed strongly laterally; teeth hypsodont; upper molars with typically alcelaphine outer ribs and folds but medial lobes more V-shaped and resembling those of *Tragelaphus;* lower molars alcelaphine in structure but with lateral lobes more V-shaped. Genotype *Makapania broomi* sp. nov.

Makapania broomi sp. nov.

Diagnosis: A *Makapania* approximately the size of *Gorgon taurinus.*

Holotype: Partial skull with horn cores and part of palate bearing LM^3 and part of LM^2 (M 162; Figs. 13, 14).

Paratypes: (a) Slightly crushed snout (M 163; Fig. 15);
(b) Crushed snout and associated portions of mandibles (M 652 A, B, C, Fig. 16);
(c) Portion of right mandible with P_2 - M_3 (M 655; Fig. 16).

The holotype specimen consists of the anterior portion of the brain case, with parts of both horn cores, and the hinder portion of the palate. The facial region is damaged.

A low transverse elevation on the roof of the brain case represents the horn-pedicle of *Alcelaphus.* The horn cores, which spring from the extremities of this elevation, are at first directed somewhat upwards and then pass almost horizontally outwards in the transverse plane; they appear to have been upcurved towards their tips. This form differs both from *Alcelaphus* and from *Connochaetes* in having the root of the horn core very close to the posterior border of the orbit. The preserved portion of the more complete (right) horn core measures approximately 17 cm in length, and probably at least 10 cm of the tip is missing. At its base the core is oval in cross-section, measuring 62 mm in transverse diameter and 48 mm in anteroposterior diameter; at 15 cm from the base it is nearly circular in section, measuring 32 x 33 mm.

The bony palate is unusual in having its median portion (between the pterygoid plates) prolonged further posteriorly than the lateral portions. LM^3 and the hinder portion of LM^2 and of RM^3 in early wear are preserved. The breadth of the palate between the third molar teeth is approximately 60 mm. The intact LM^3 is 28 mm long and 18 mm broad.

The peculiar formation of the palate and also the pattern of the teeth in the holotype make it possible to identify with this species a crushed snout with LP^3 - M^3 in early wear (M 163). Another crushed snout (M 652A) with LM^2 and M^3 in early wear also clearly belongs to this species and is associated in a single block with damaged left and right mandibles. The right mandible (M 652C) has the outer lobes of the molars rather damaged and only the root of P_4 remains. The left mandible (M 652B) has LP_3 - M_3 well preserved, the premolars being unworn. The upper and lower dentitions are thus definitely associated and it is then possible to identify as belonging to this species a well worn right mandible with P_2 - M_3 in advanced wear (M 655, Fig. 16). The dimensions of the teeth in these specimens are given below.

Measurements of upper and lower cheek teeth (in mm).

	UPPER					LOWER		
	M 162	M 163	M 652A	T.M.†		M 652B	M 652C	M 655
P^2 Length	—	—	—	11	P_2 Length	—	—	10
Breadth	—	—	—	10	Breadth	—	—	6
P^3 Length	—	12	—	14	P_3 Length	15	—	12
Breadth	—	13½	—	13	Breadth	8	—	9
P^4 Length	—	13	—	14	P_4 Length	16	—	15
Breadth	—	15	—	15	Breadth	10	—	11
Series P^2 - P^4	—	—	—	39		—	—	37
M^1 Length	—	21	—	25	M_1 Length	24	22*	19
Breadth	—	19	—	19	Breadth	12	c12*	13
M^2 Length	—	26	26?	27	M_2 Length	26	25½	25
Breadth	—	19	18	19	Breadth	12	c12*	15
M^3 Length	28	31	24+	—	M_3 Length	34?	34	36
Breadth	18	19	15+	—	Breadth	11½	12	14
Series M^1 - M^3	—	78	—	—		84	81	80

† Specimen in Transvaal Museum

* Damaged

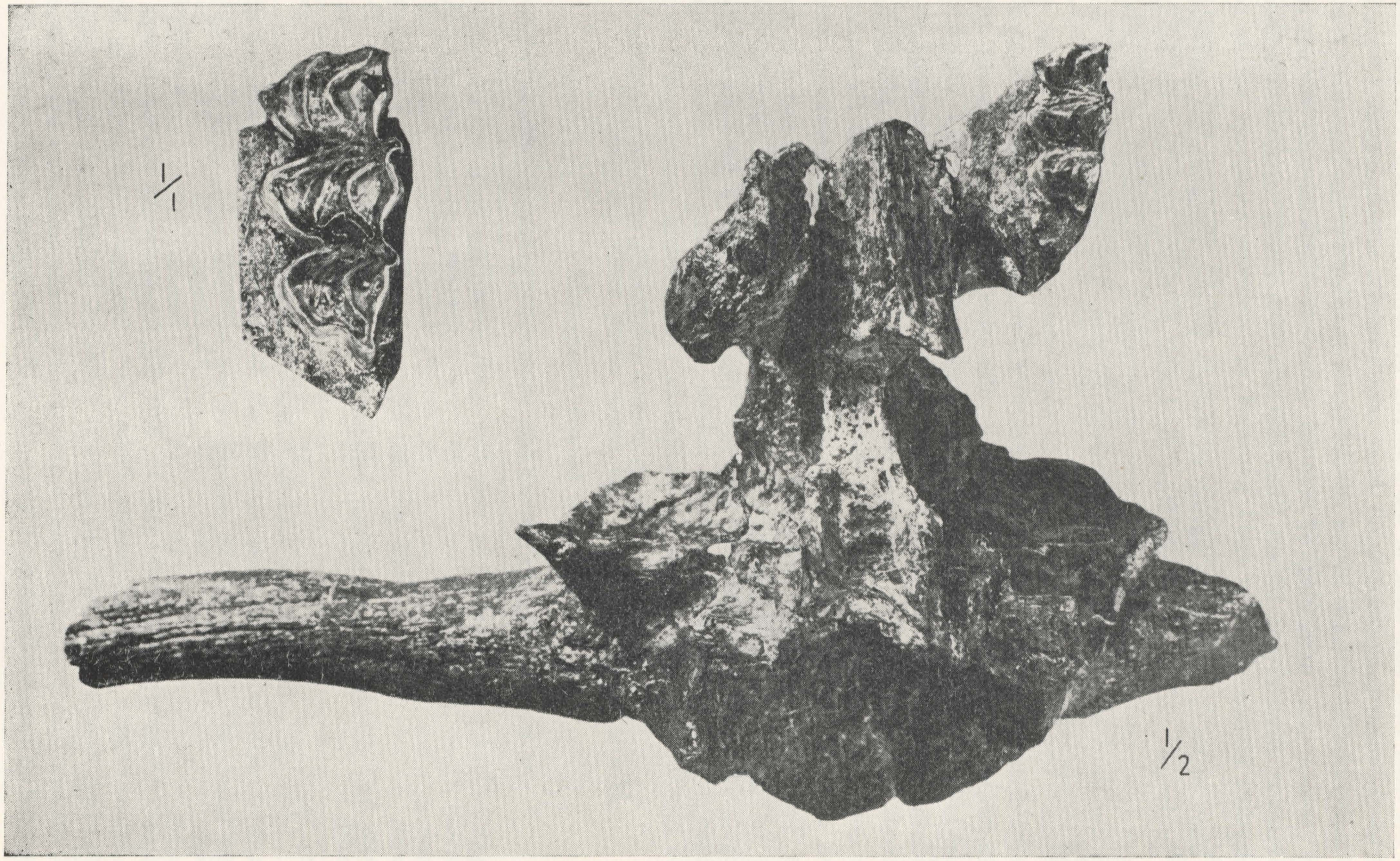

Fig. 13—Makapania broomi. Palatal aspect of holotype skull fragment (M 162). One half natural size. On the left are shown the left third molar and partial second molar, natural size.

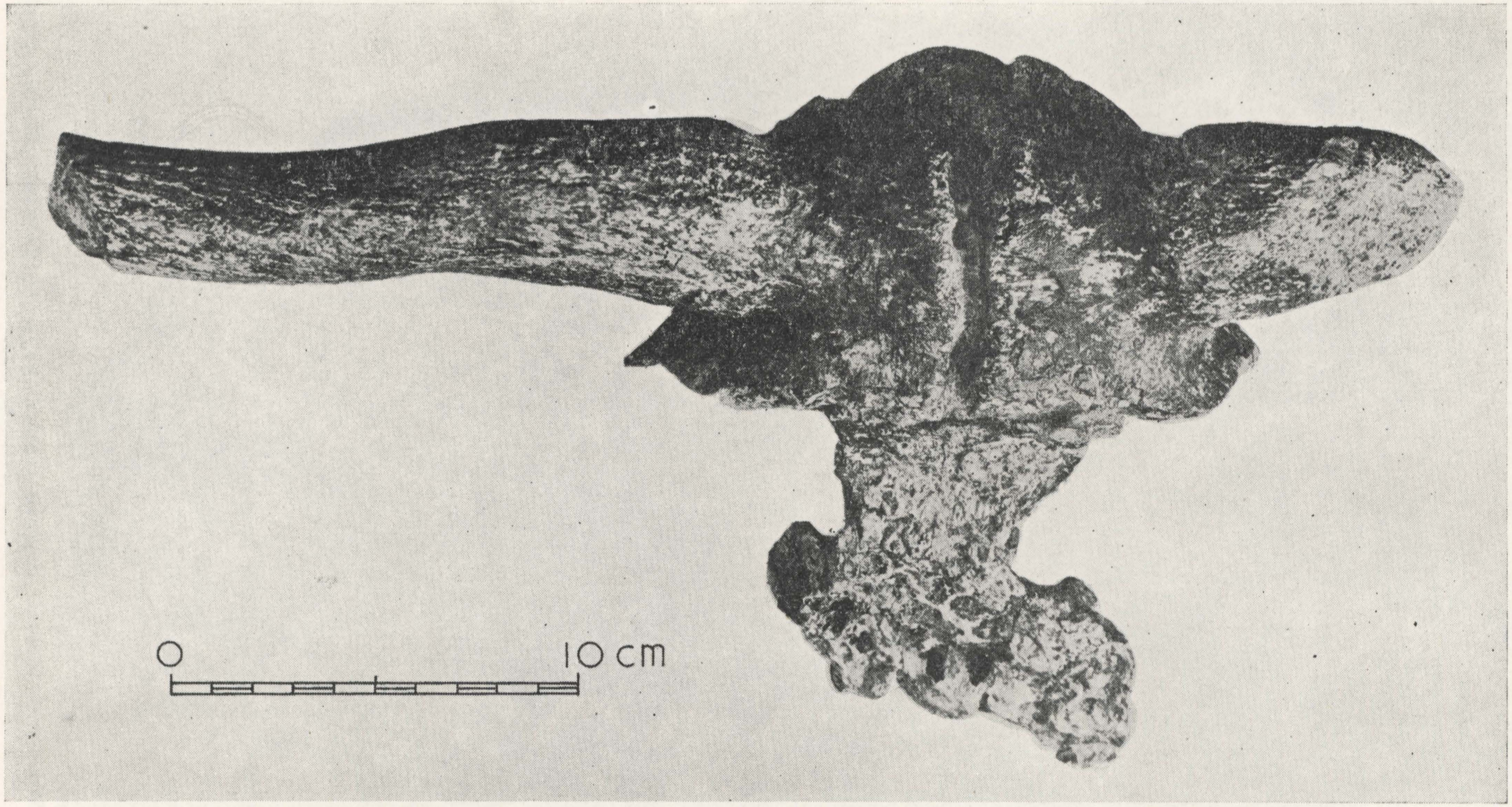

Fig. 14—Makapania broomi. Dorsal aspect of holotype skull fragment (M 162). One half natural size.

Fig. 15—Makapania broomi. **Slightly crushed snout of paratype, M 163, palatal aspect.** Natural size.

The most conspicuous feature of the upper molars is the pronounced V-shape of their medial lobes, in which respect they differ from all living alcelaphines. Superficially the teeth resemble those of *Tragelaphus* but are distinguished by being much more hypsodont; the height of the crown of M^2 in specimen M 652 is 49 mm and of M^3 is 56 mm. The external folds are strongly marked and the ribs moderately developed, giving the outer face of the teeth a typically alcelaphine appearance. As the teeth are worn down, they increase in width much less rapidly than do those of *Tragelaphus;* the groove between the medial lobes is wider and shallower and there is a large central enamel island. There is no basal pillar rising from the cingulum. In the rear enamel island, a posterior spur is sometimes present but in the anterior one this is unusual. The upper premolars are small in proportion to the molars, as in *Connochaetes* and *Gorgon,* but are relatively a little larger than in the gnus.

Similarly, the lower molars differ from those of living Alcelaphines in having angular lateral lobes. They are distinguished from those of *Tragelaphus* by being more hypsodont (M_3 in M 652 having a crown height of 57 mm) and by possessing a rudimentary antero-lateral fold or flange. As in the upper molars there is no basal pillar. P_4 is hypsodont and agrees essentially with P_4 in *Alcelaphus, Connochaetes* and *Gorgon;* P_3 is also hypsodont but of simpler form; P_2 is a simple, compressed, sectorial tooth.

In addition to the type material, there are several other specimens which contribute information regarding the structure of the skull and horns of *Makapania.* A partial brain case, with the occipital region rather eroded (M 499) possesses the posterior portion of the basal part of each horn core and its generic reference is quite certain. The lower edge of the occipital condyles and the basilar tubercles are also preserved. Another specimen (M 952) comprises an occiput with part of the brain case and it seems to agree closely in dimensions and character with the back of the previous specimen. This fragment displays a sharp posterior ridge above the foramen magnum, a feature possessed very markedly also by *Damaliscus* and, to a lesser degree, by *Alcelaphus.*

Three other partial skulls and twenty fragments of horn cores attest to the typical character of the holotype specimen. One fragment (M 487) comes from near the tip of the core and indicates a somewhat gnu-like shape in this region, though the curvature is less marked than in either *Connochaetes gnou* or *Gorgon taurinus.*

Five maxillary fragments with teeth in various stages of wear and some twenty isolated upper molars confirm the features shown in the type. These teeth tend to be slightly larger than those of *G. taurinus.* Seven lower jaw fragments and more than a dozen isolated lower molars also agree with the paratypes but, as the latter are either very worn or relatively unworn, a good specimen with LP_4 - M_2 in normal wear is figured here (M 962; Fig. 16) together with an upper and a lower series of what is believed to be the milk dentition of *Makapania.*

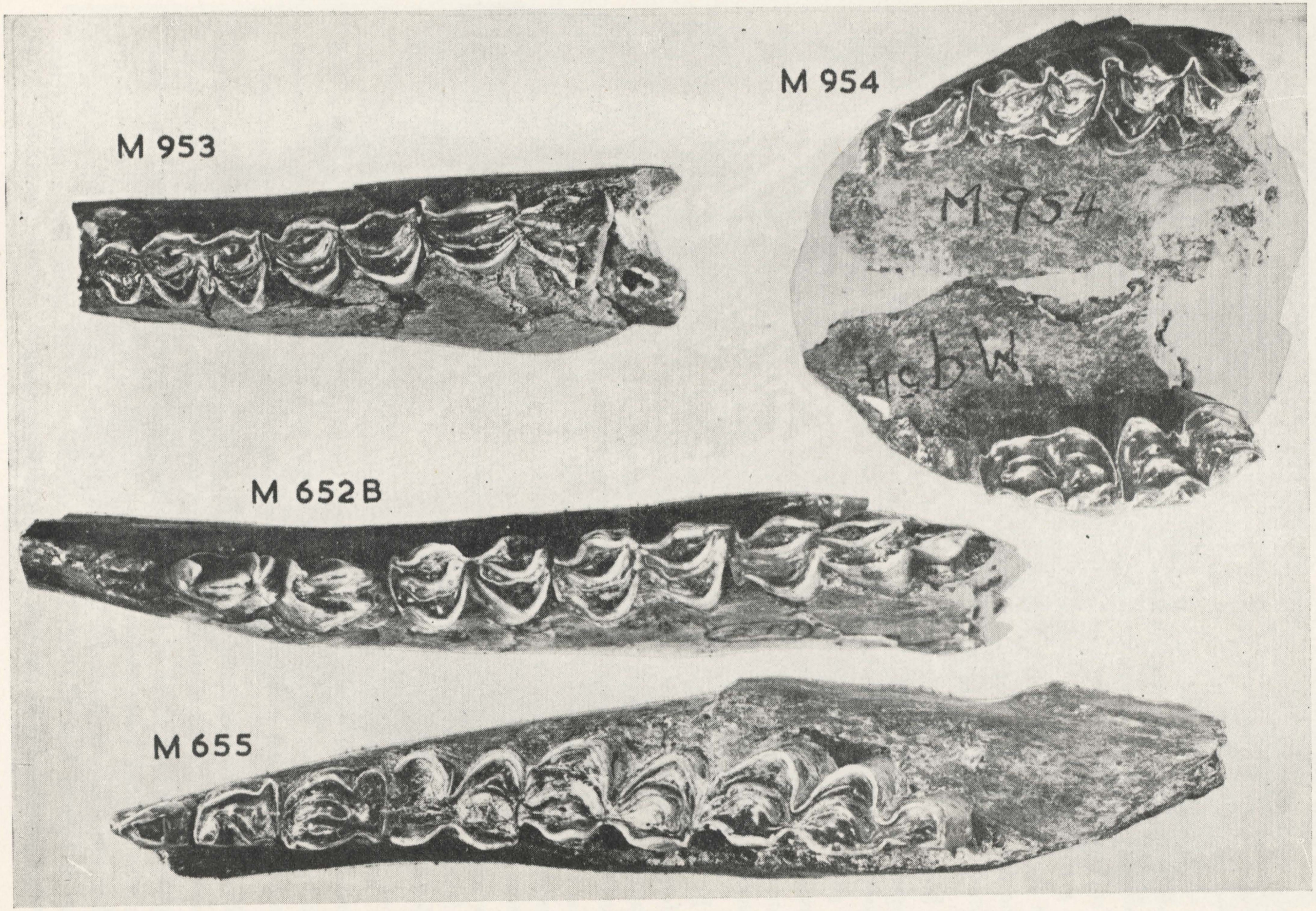

Fig. 16—Makapania broomi. M 954: referred juvenile palate with milk teeth; M 953: referred partial juvenile mandible with LDM$_4$ - M$_2$; M 652B: paratype right mandible with P$_3$ - M$_3$ in early wear; M 655: paratype right mandible with P$_2$ - M$_3$ in moderately advanced wear. Natural size.

A damaged brain case of a very young individual (M 512) has part of the base of the left horn preserved. This specimen resembles fairly closely a gnu skull of similar age but the frontoparietal sutures are different and would fit well with the probable state in Makapania at this early age.

In the collections of the Transvaal Museum, Pretoria, there is a maxillary fragment from the Makapan limeworks, possessing LP^2 - M^2 in early wear, which clearly belongs to *Makapania broomi*. The same species has also been observed in a private collection from deposits in the Sterkfontein area.

By the form of its horn cores this antelope could be regarded as falling between the kongoni (*Alcelaphus cokei*) and its allies on the one hand and *Gorgon taurinus* on the other, but it differs from both in having the horns arising close to the orbits. It might therefore be considered as an offshoot from the common ancestral stock of these two types which has escaped specialisation in the origin of the horn core, but has developed its own "pseudo-tragelaphine" specialisation in the molar teeth. This form cannot therefore be assigned to either *Alcelaphus* or *Connochaetes,* nor can it be placed in any of the described extinct genera, *Pelorocerus* (van Hoepen, 1932), *Parmularius* (Hopwood, 1934), or *Parestigorgon* (Dietrich, 1950). The upper molars somewhat resemble those assigned by Dietrich (1950) to *Praedamalis deturi,* but the character of the associated horn core is wholly different.

Pultiphagonides africanus Hopwood has horn cores of similar character but shorter. It has been mentioned above that *Pultiphagonides* on its dental characters is certainly an alcelaphine; its molars are almost indistinguishable from those of *Alcelaphus*. The Makapan fossil with its very specialised molars cannot be assigned to the Olduvai genus. It has therefore seemed justifiable to create a new genus for which the name *Makapania* appears appropriate; the specific name has been chosen in memory of the late Dr Robert Broom who contributed so much to our knowledge of the Quaternary mammals of South Africa.

Subfamily ANTILOPINAE

Tribe Neotragini

Oreotragus major Wells

Klipspringer.

The collection includes a number of jaws, teeth and horn cores of neotragine type, apparently belonging to a single species. The best representative specimens comprise a frontlet with both horn cores (M 476; Fig. 18), an entire palate with P^2 - M^3 on both sides (M 951; Fig. 17) and two left mandibles with all the cheek teeth (M 997 and M 998; Fig. 17). The teeth of the palate are rather worn but a left maxilla displays all the teeth in early wear (M949; Fig. 17).

These remains agree in all essential characters with the genus *Oreotragus* but their dimensions exceed by fifteen to twenty per cent the limits of the living *O. oreotragus*. A large extinct species *O. major* was founded upon a skull from a read breccia deposit at another site in the Makapan Valley (Wells 1951) and the present collection conforms sufficient closely to be referred to the same species.

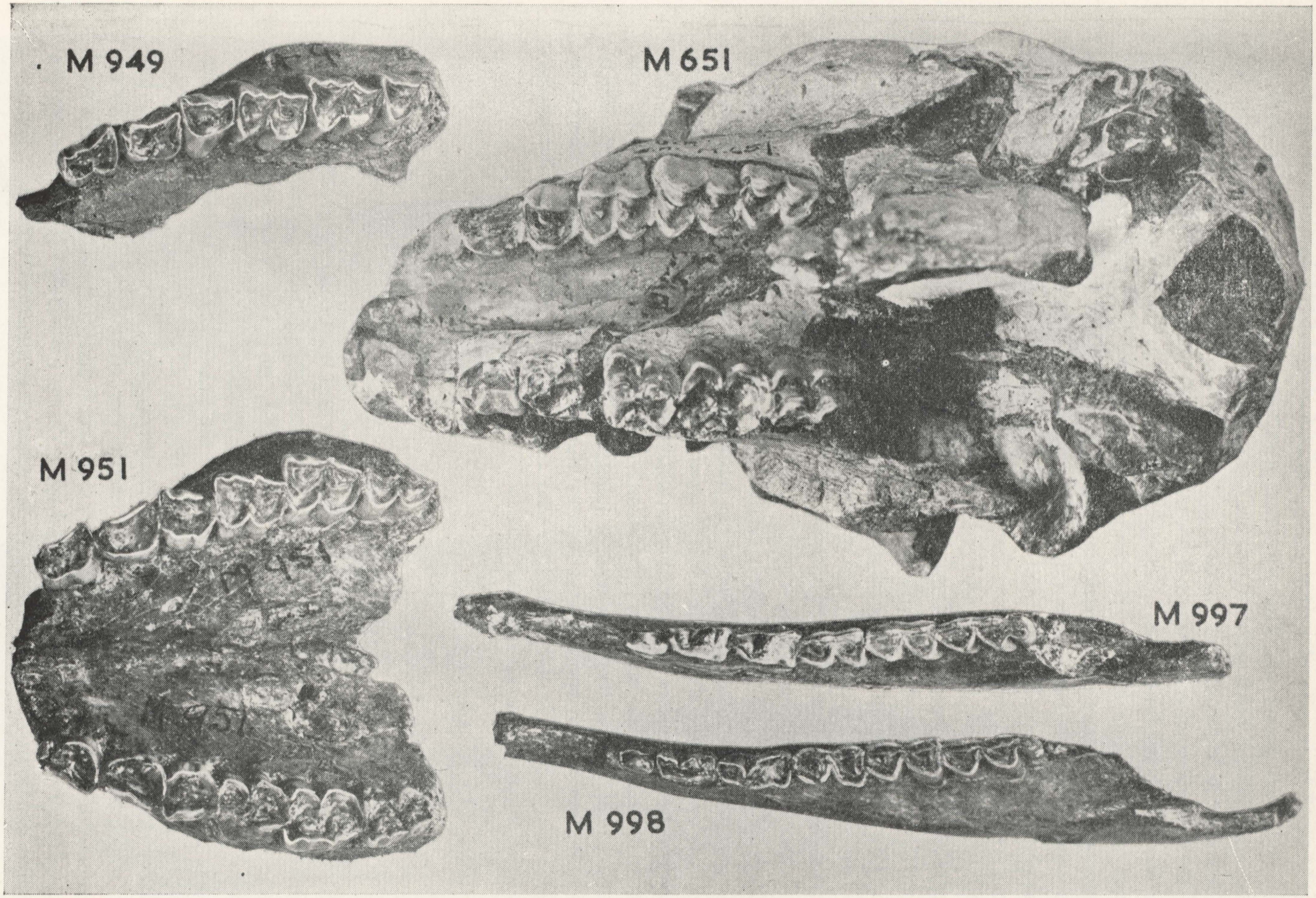

Fig. 17—Oreotragus major. M 651: palatal view of somewhat crushed type skull from the Swartkrans (Makapan) site; M 949: referred partial left maxilla with P^2 - M^3 in early wear; M 951: referred palate with cheek teeth in moderately advanced wear; M 997: left mandible with P_2 - M_3 in fairly early wear; M 998: left mandible with P_2 - M_3 in moderately advanced wear. Natural size.

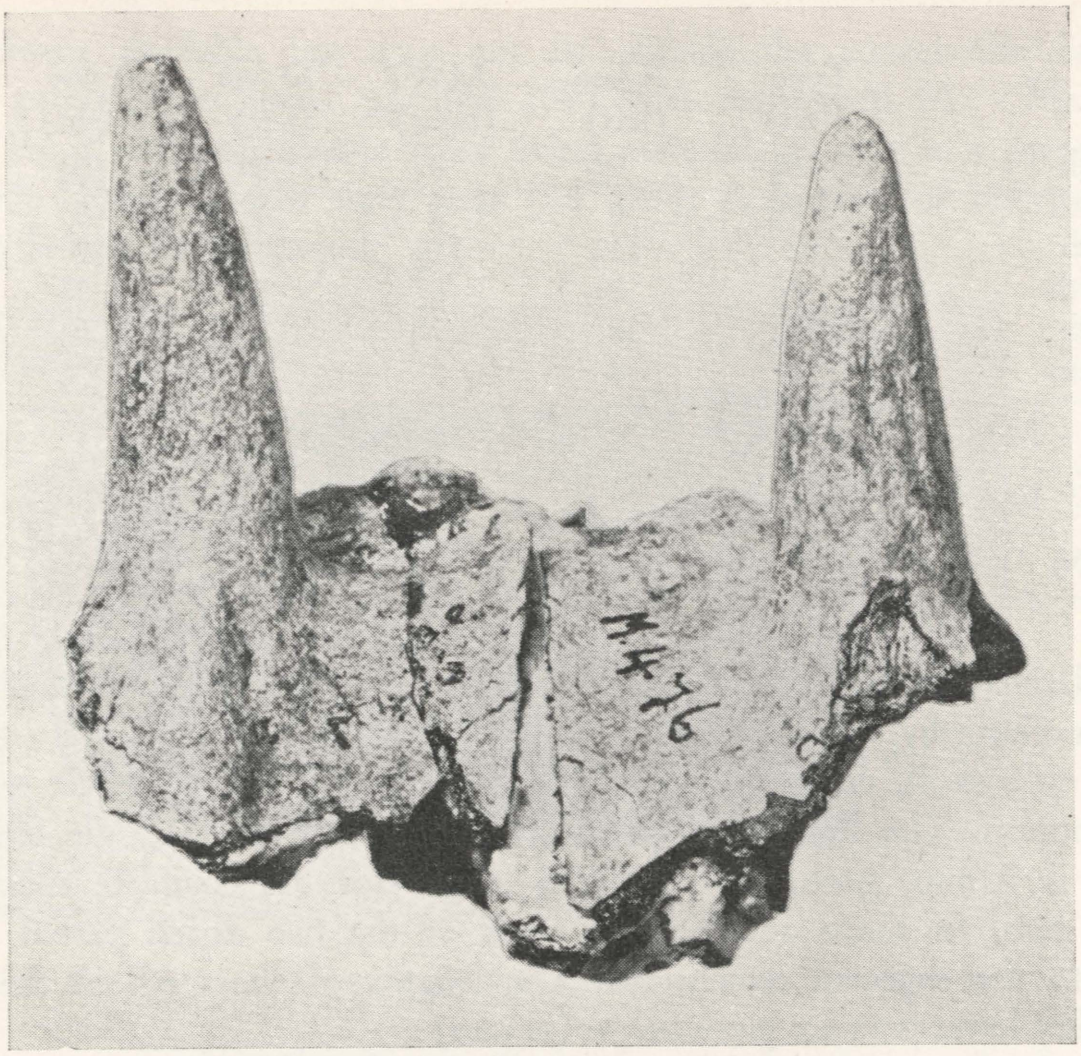

Fig. 18—Oreotragus major. **Frontlet, M 476, facial aspect.** Natural size.

In the type skull only the lower part of the right horn core was present, the left horn having been lost. The frontlet possesses both horns and the distance from the centre of each core to the median suture is 30 mm, exactly the same as in the type; the horn cores are slightly stouter but three isolated cores agree more exactly with the type. The heights of the left and right cores are approximately 43 and 46 mm respectively.

The teeth of the type skull have not been figured and the palatal aspect of the type is illustrated in Fig. 17 for comparison with selected specimens from the Limeworks deposit. The following are the relevant measurements (in mm) :

		Type (left)	Palate (left)	M 951 (right)	M 949 (left)	M 999 (right)	Oreotragus oreotragus (average)
P^2	Length	—	$9\frac{1}{2}$	$9\frac{1}{2}$	9	—	$7\frac{1}{2}$
	Breadth	—	$7\frac{1}{2}$	8	$6\frac{1}{2}$	—	$5\frac{1}{2}$
P^3	Length	10	$9\frac{1}{2}$	9	9	—	8
	Breadth	8	$7\frac{1}{2}$	8	7	—	$6\frac{1}{2}$
P^4	Length	8	8	8	8	$8\frac{1}{2}$	7
	Breadth	8	$7\frac{1}{2}$	$7\frac{1}{2}$	7	7	$6\frac{1}{2}$
Series P^2 - P^4		—	27	$26\frac{1}{2}$	26	—	$22\frac{1}{2}$

	Type (left)	Palate (left)	M 951 (right)	M 949 (left)	M 999 (right)	Oreotragus oreotragus (average)
M^1 Length	10½	9½	9	9	10½	9
Breadth	9½	8	8	8	8	7½
M^2 Length	12	11½	11½	11	12	9½
Breadth	9½	8½	8½	8½	8½	8
M^3 Length	11½	10	9½	9½est	10½	10
Breadth	8	8	8	7½	7½	7½
Series M^1 - M^3	34	31	30	29½	33	28½
Ratio $\frac{P \times 100}{M}$		87	88½	88	—	79

The relatively large size of M^2 in the fossil material as compared with the living species is noteworthy.

In the type skull, only the second and third lobes of the left M_3 represent the lower dentition. The breadth of the second lobe is 6 mm and the length of the fragment is 9 mm, giving an estimated length for the complete third molar of about 14 mm. In shape and size the teeth of the two dozen partial lower jaws conform to the expected dimensions. The lengths of the teeth in the two most complete left lower jaws are given below (in mm) :—

	P_2	P_3	P_4	P_2 - P_4	M_1	M_2	M_3	M_1 - M_3	$\frac{P \times 100}{M}$
M 997	6½	9	9½	25	9	10	13	32	78
M 998	5	8½	10½	24	10	10½	14	34½	69½
Oreotragus oreotragus	4	7½	9	20½	8	9½	12½	30	68½

It would appear that the type skull lies close to the upper limit of size variation of the species or, alternatively, that the material from the Limeworks deposit represents a slightly smaller variety or race.

Tribe Antilopini

Aepyceros cf *melampus* (Lichtenstein) Impala

A portion of horn core (M 654) approximately 8 cm in length, shows the characteristic ringing of the impala core (Fig. 19). As far as can be determined from the curvature it belongs to the central part of the horn. It is larger than the cores in any specimens available but may not lie outside the conceivable limits of variation. A partial right lower jaw (M 759) with well worn M_1 - M_3 and a fragment of P_4 is indistinguishable from living material, as also is a juvenile left lower jaw with DM_3 - M_3 in early wear (M 758). A number of isolated upper teeth probably belong to this species.

Fig. 19—Aepyceros cf melampus. Fragment of horn core (M 654)

Gazella gracilior sp. nov.

Gazella's

Diagnosis: A gazelle somewhat resembling *G. rufifrons* but with more delicate horns and having M_1 relatively larger.

Holotype: A frontlet with horn cores, damaged at the tips (M 773; Fig. 20).

Paratype: A left lower jaw fragment with P_4 (damaged) - M_3 (M 767; Fig. 21).

The frontlet comprises part of the parietal bone, the horn cores and the frontals as far as the supraorbital foramen on each side. The horns are fairly close together, the basal separation being 22 - 23 mm, and they rises steeply from the brain case. The heights of the right and left cores as preserved are approximately 60 mm and 70 mm respectively, measured on the inner side; the probable height when complete is about 10 - 11 cm. The horns curve gently outwards and backwards, the condition of the extreme tip being uncertain. In cross-section, the cores are oval with antero-posterior elongation. The greatest and least diameters at the base are 21½ mm and 16½ mm for the left horn and 22 mm and 17½ mm for the right horn; 4 cm higher up, the measurements are 15½ mm and 13 mm on both cores. An isolated broken core (M 772) is closely similar in shape and in basal dimensions but tapers more rapidly upwards.

In the British Museum (Natural History) is an interesting specimen from this locality, taken over by Dr K. P. Oakley for exhibition. It comprises a right horn core thrust into the marrow cavity of a broken long bone (Fig. 20). The tip is

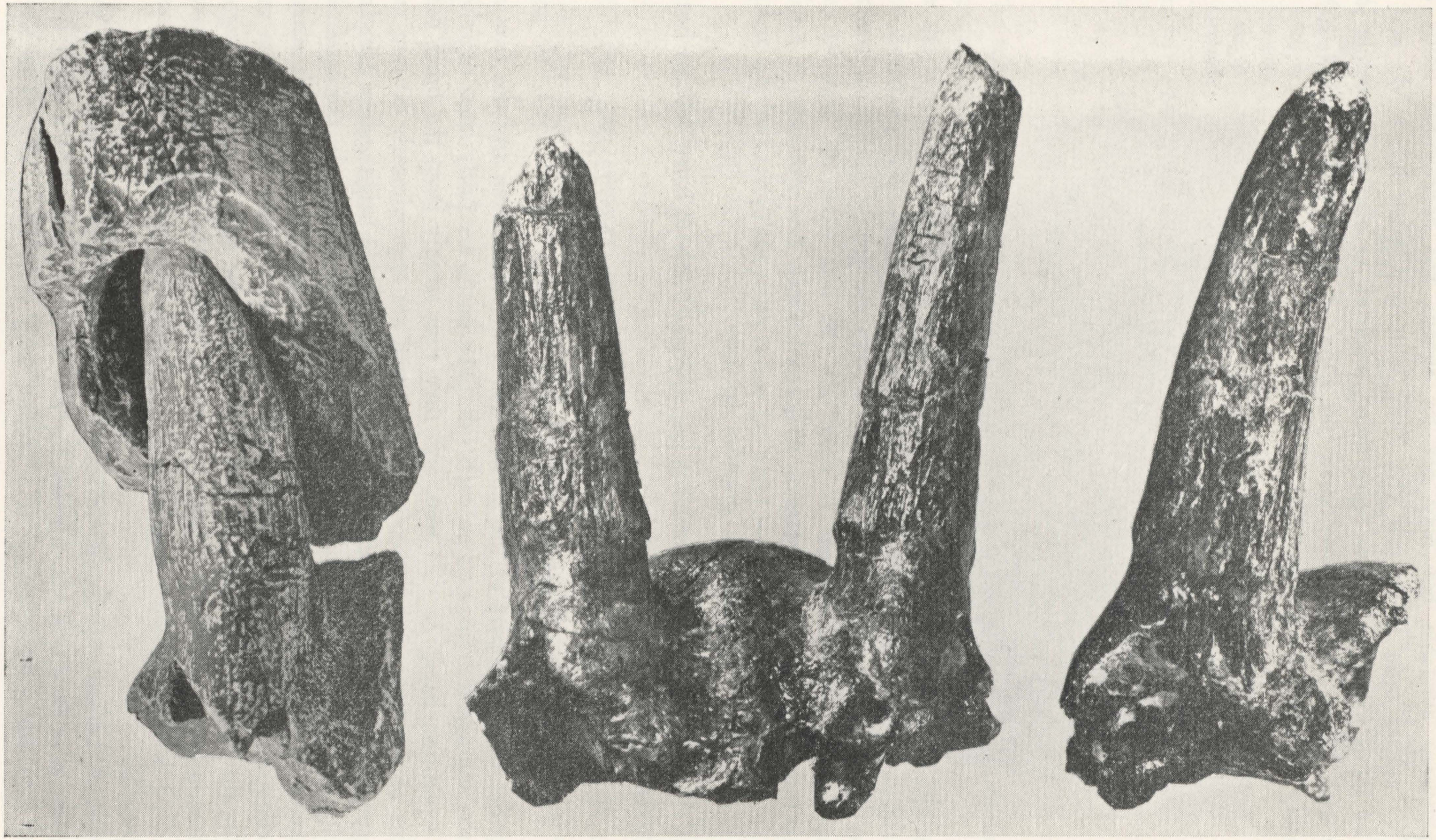

Fig. 20—Gazella gracilior. Holotype frontlet, M 773, facial aspect (centre) and left lateral aspect (right); on the left is a photograph of a cast of the referred specimen in the British Museum (Natural History.) Natural size.

missing and the length of core preserved is 61 mm. The greatest and least diameters at the base are 25 mm and 19 mm respectively and at the broken tip are 17 mm and 12 mm. It is thus slightly larger than the holotype but is otherwise closely similar.

On the brain case, the suture between the frontals lies on a ridge which passes into a raised area on the anterior edge of the parietal. The horn base above the supraorbital foramen is elevated from the surface of the frontals.

In the living African gazelles, the horn bases of males are normally oval in section and those of females are more nearly circular. In *G. granti,* in which the cores of the male are greatly elongated in section, the females also have rather oval horn cores; but this is exceptional and, in any case, the fossil has horns far too short to belong to the *G. granti* female. There is thus good reason to consider the fossil frontlet as belonging to a male animal.

Parallelism of the two horns is exhibited by *G. cuvieri, G. leptoceras, G. rufifrons, G. spekei, G. thomsoni, G. dama* and *G. granti.* The two last named are much too large and the horns of the Dama Gazelle curve too sharply backwards. Speke's Gazelle is of comparable size, though rather larger, but the sharp backward arching of its horns serve to eliminate it. Of the remaining four, the following are average dimensions for the core bases:

G. cuvieri	32 x 22 mm
G. leptoceras	26 x 19 mm
G. rufifrons	27 x 19 mm
G. thomsoni	32 x 22 mm

All are thus somewhat larger than the fossil frontlet. Both *G. rufifrons* and *G. thomsoni* show ridging of the fronto-parietal region and the fossil form resembles these two species more closely than it does any other African gazelle; the fossil clearly had fairly short horns and is more like *G. rufifrons* in this respect than like the long-horned *G. thomsoni.*

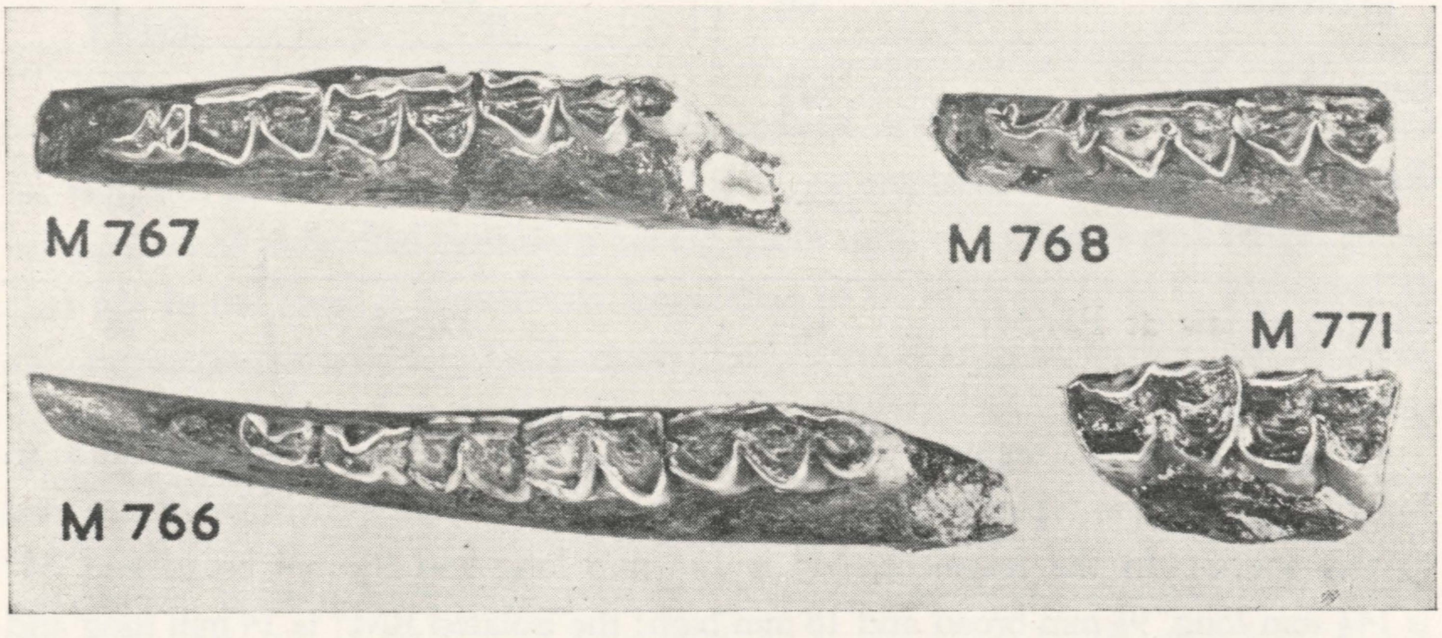

Fig. 21—Gazella gracilior. **M 767: paratype left mandibular fragment with P_4 - M_3 in moderate wear; M 768: referred left mandibular fragment with P_4 - M in moderate wear; M 766: left mandible with P_3 -- M_3 in advanced wear; M 771: maxillary fragment with RM^2 - M^3 in moderate wear.** Natural size.

Four lower dentitions (all of the left side) are gazelle-like in form and of the correct size to be associated with the frontlet described above. One of these (M 767; Fig. 21) has been selected as a paratype of the species. It has the greater part of P_4 preserved and the whole of M_1 - M_3 in moderate wear. A similarly worn fragment (M 768; Fig. 21) has P_4 intact but lacks M_3 and a specimen in advance wear (M 776; Fig. 21) has P_3 - M_3 and the root of P_2 preserved. The measurements of these specimens are given below (in mm) :—

		Paratype M 767	M 768	M 766
P_2	Length	—	—	5½est
	Breadth	—	—	3 est
P_3	Length	—	—	7
	Breadth	—	—	4
P_4	Length	9 est	10	7½
	Breath	5	5	5
Series P_2 - P_4		—	—	20 est
M_1	Length	12	12	10
	Breadth	6½	6	7
M_2	Length	13	13½	12
	Breadth	6½	6½	8
M_3	Length	17½	—	18
	Breadth	6½	—	7
Series M_1 - M_3		42½	—	40
Ratio $\frac{P \times 100}{M}$		—	—	50
Height of jaw at P_4/M_1		17	19 est	18

A right maxillary fragment (M 771; Fig. 21) with M^2 and M^3 and also an isolated RM^3 show typically gazelle-like teeth which may be provisionally assigned to this species. In the fragment, M^2 is 13½ mm long and 9½ mm broad and M^3 is 14½ mm long, 9½ mm broad and 18 mm high; the isolated RM^3 is 14 mm long and 9 mm broad. The table overleaf gives average figures for the dimensions of teeth in the living gazelles of comparable size.

		G. cuvieri	G. leptoceras	G. rufifrons	G. thomsoni	Fossil
P_2	Length	5½	5½	5	5	5½?
	Breadth	3½	3	3	3	3 ?
P_3	Length	8	7½	7½	7	7 ?
	Breadth	4	3½	4	4	4
P_4	Length	4½	4	4	5	5
Series P_2 - P_4		22½	21½	20½	20	21½?
M_1	Length	11	10½	10	10	11
	Breadth	6	6	6	6½	6½
M_2	Length	13½	13	12½	12½	13
	Breadth	6½	6½	7	7½	7
M_3	Length	17	17½	18½	18½	18
	Breadth	6	6	7	6½	7
Series M_1 - M_3		41½	41	41	41	42
Ratio $\frac{P \times 100}{M}$		54	52½	50	49	51
Height of jaw at P_4/M_1		17	17	18	19	18
M^2	Length	14	12½	12½	13	13½
	Breadth	8	8½	9½	10½	9½
M^3	Length	13	13	14½	15	14
	Breadth	7	7½	9	9	9½
	Height	18	17	15	16	18

The closest comparison, both in dimensions and in crown pattern, is with *G. rufifrons* and *G. thomsoni*. Although it is not emphasised by the average figures, comparison of individual dentitions having cheek teeth of similar overall length shows that M_1 in the fossil is consistently larger than in *G. rufifrons* or in *G. thomsoni*. In this respect it approximates to *G. cuvieri* but differs sharply in having broader teeth. It thus seems clear that the fossil cannot be identified specifically with the living African gazelles.

Of the fossil species hitherto described from southern and East Africa whose horns are known, none is comparable with *G. gracilior*. The teeth previously described as *G. wellsi* (Cooke 1949) come close to those in the present collection but identity cannot yet be established. The teeth of *G. wellsi* appear to be somewhat more hypsodont than in *G. gracilior*.

Fig. 22—Phenacotragus vanhoepeni. Holotype frontlet, M 599, facial and left laterial aspects. Two-thirds natural size.

Phenacotragus vanhoepeni sp. nov.

Gazella

Diagnosis: A *Phenacotragus* with horns more massive, rising more vertically from the frontal bone and more compressed laterally than in *P. recki* Schwarz.

Holotype: Frontlet with both horn cores slightly damaged at the tips (M 599; Fig. 22).

Paratypes: (a) Complete brain case with parts of the frontals and lower part of right horn core (M 406).
(b) Damaged skull with palate but lacking roof of brain case (M 598; Fig. 23).

There are a large number of partial skulls and portions of horn cores which belong to an antelope of the gazelle group but differ from the living African species. Many partial upper and lower jaws and teeth belong to a medium sized gazelle and one partial skull furnishes an anatomical link between the upper dentition and the horn cores.

In the holotype frontlet (M 599; Fig. 22) the horn cores rise almost vertically from the brain case and their basal portions diverge slightly. They are sharply recurved backwards, with the terminal portion deflected outwards and upwards. The length of the more complete core, measured along the anterior curve, is 16 cm as preserved and is estimated as 20 - 22 cm when intact. The basal separation between the cores is 18 mm. The cores are compressed laterally, the greatest (antero-posterior) diameter being 42 mm and the least (transverse) diameter 29 mm; 5 cm up from the base the corresponding dimensions are 36 mm and 22 mm; 10 cm from the base they are 28 mm and 17 mm, and at the broken tip are 17½ mm and 12½ mm. The fifty or more other horn cores and fragments confirm that the features shown in the holotype are reasonably typical; the range of variation is small.

As in *Gazella gracilior,* the suture between the frontals runs along a marked ridge and widens into an elevated area at the front of the parietal.

These cores do not compare at all well with those of any of the existing African species of Gazelle, nor with those of the extinct species *G. helmoedi* van Hoepen. They correspond fairly closely with the horn cores of the extinct *Phenacotragus recki,* described by Schwarz (1937) from the Oldoway beds of Tanganyika, and can reasonably be referred to the same genus. The Makapansgat specimens indicate an animal with horns more massive than those of *P. recki* and the horns differ also in rising more steeply from the frontal bone, in having a longer straight lower portion and in being laterally more compressed. These differences are regarded as of specific value.

The paratype brain case (M 406) provides information regarding the back part of the skull, which is a little larger than in *P. recki.* The occipital and basal parts of the brain case are in a good state of preservation but the parietal is very slightly crushed. The nuchal aspect is almost identical with that of the living impala but the

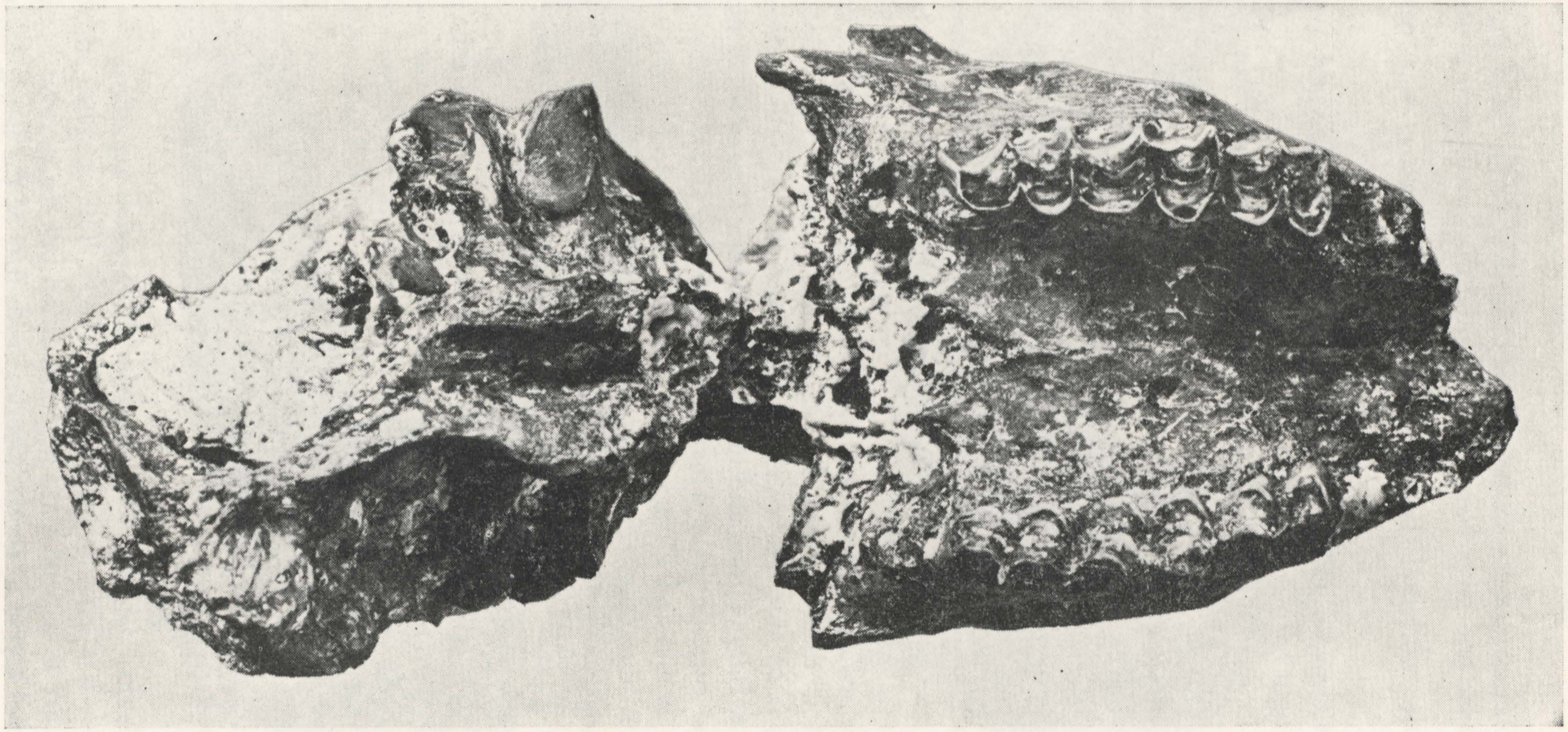

Fig. 23—Phenacotragus vanhoepeni. **Palatal** aspect of paratype skull, M 598. Natural size.

basilar part of the occipital bone in the fossil is stouter and longer with much more strongly developed basilar tubercles. The bulges of the parietal behind the parietal eminence in the impala are lacking in the fossil form, giving a different profile to the brain case. The portion of the occipital bone lying above the occipital crest is wider in the fossil than in the impala.

The paratype skull (M 598) has sufficient of the back of the brain case preserved for it to be virtually certain that it belongs to the same species as the brain case just described. The interest of the specimen attaches primarily to the palate (Fig. 23) which possesses M^1 - M^3 of both sides. The teeth are smaller than those of the impala or the springbok, though similar in general pattern. They agree closely with the palate of *P. recki* figured originally by Schwarz (1937) but in the Makapan specimen the lateral folds are sharper. From this palate it is possible to identify some fourteen partial upper dentitions and a dozen loose upper molars as belonging to the same species. Four of these from the right side have been selected to illustrate different stages of wear; their measurements (in mm) are given below, together with those of the paratype palate, and they are illustrated in Fig. 24.

	Paratype M 598	Eearly wear M 615	Early wear M 611	Moderate wear M 609	Advanced wear M 612	*P. recki*
P^2 Length	—	6½	—	—	—	6½
Breadth	—	6	—	—	—	5½
P^3 Length	—	8	—	10	—	7½
Breadth	—	6	—	6½	—	6½
P^4 Length	—	8	8½	9	7½	8½
Breadth	—	7	7½	7½	9	8
Series P^2 - P^4	—	22½	—	—	—	22½
M^1 Length	14	14	14	13½	11½	13½
Breadth	11	10	9½	10½	11½	11½
M^2 Length	16½	16	16	15	15½	14½
Breadth	11	10	10	10½	11½	10½
M^3 Length	14	—	14	15	17	14½
Breadth	10	—	9	9½	11	10
Series M^1 - M^3	44½	—	44	43½	44	42½
Ratio $\frac{P \times 100}{M}$	—	—	—	—	—	53

It is not possible to associate the lower dentition with the uppers with any great degree of certainty but there are two dozen lower jaws or fragments and a dozen loose lower molars which have the requisite size and form. These may be accepted with some confidence as representing the lower dentition of *P. vanhoepeni.* They are typically gazelline in form, resembling the lower teeth of the springbuck very closely except that the fossil possesses well developed second and third premolars, whereas in the springbuck the second premolar is usually lacking and even the third premolar is vestigial. Six dentitions have been selected to illustrate various stages of wear. Their measurements (in mm) are given below and four are illustrated in Fig. 24.

	M 533 Very Early (R)	M 496 Early (L)	M 502 Moderate (L)	M 42 Moderate (L)	M 38 Moderate (L)	M 35 Advanced (L)
P_2 Length	(DM_2 5?)	4	—	root 6	root 5½	4½
Breadth	3?	3	—	?3	?3½	3½
P_3 Length	(DM_3 9)	8	8½	root 7	root 6½	6½
Breadth	4	4	4½	?4	?4	4
P_4 Length	($DM_4$15½)	10	9	8	9	9
Breadth	6	5	6	5	6	5
Series P_2 - P_4	—	22		21est	21est	20
M_1 Length	14	13	12½	11½	11	11
Breadth	6½	7	7½	7	7½	7
M_2 Length	—	15½	15	15	14	13½
Breadth	—	6½	8	8	7½	8
M_3 Length	—	21	21½	22	23½	22½
Breadth	—	6½	7½	7	7½	8
Series M_1 - M_3	—	49½	49	48½	48½	47
Ratio $\frac{P \times 100}{M}$	—	44½		43	43	42½
Height of jaw at P_4/M_1	20	18	20	20	19	21

The specific name is chosen in honour of Dr E. C. N. van Hoepen, who first recognised the occurence of a true gazelle (*G. helmoedi*) in the Quaternary of South Africa.

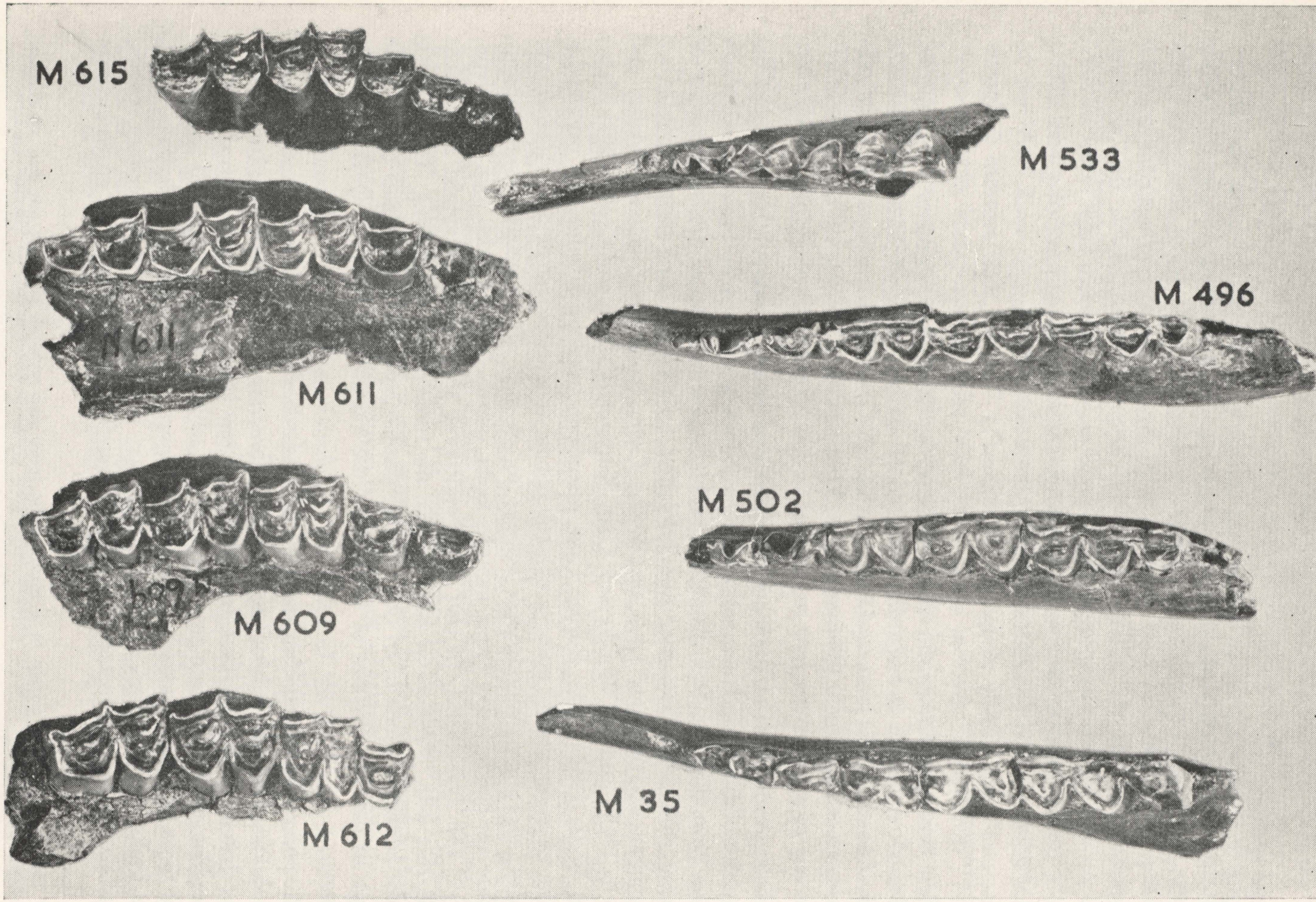

Fig. 24—Phenacotragus vanhoepeni. REFERRED RIGHT UPPER DENTITIONS: M 615: P^2 - M^2 in early wear; M 611: P^4 - M^3 in early wear; M 609: P^3 - M^3 in moderate wear; M 612: P^4 - M^3 in advanced wear. REFERRED LOWER DENTITIONS: M 533: RDM_3 - M_1; M 496: LP_2 - M_3 in early wear; M 502: LP_3 · M_3 in moderate wear; M 35: LP_2 - M_3 in advanced wear. Natural size.

DISCUSSION

Large species

It has been noted that, in several of the species not distinguishable from living forms, the mean size of the fossil remains approaches the upper size limit of the existing type. This is most apparent with the impala and *Tragelaphus,* and is suggested also for the buffalo, kudu and oryx. It seems possible that all these, and perhaps also the klipspringer (*Oreotragus major*), represent large forms ancestral to the smaller existing species. Such a tendency for decrease in size of species during the Quaternary has been observed in other parts of the world.

Environment

The Makapan Limeworks fauna includes no fewer than eighteen bovid species. Of these eight can be regarded as certainly extinct; three of them are identified with forms already known elsewhere while the other five are new. Three species belong to extinct genera (*Phenacotragus, Makapania* and *Pelorocerus* or *Lunatoceras*) and one to a genus not now represented in southern Africa (*Gazella*).

This great wealth of species is clearly related to the physiographic setting of the site in a scrub-covered mountain mass, with extensive open or bush-covered plains at no great distance. It is instructive in this regard to compare the Makapan list of species with those from two sites belonging to a much more recent period (late Gamblian or Makalian*) — the Border Cave, Ingwavuma, (Cooke, Malan and Wells 1945) and the Wonderwerk Cave, Kuruman (Malan and Cooke 1941; Malan and Wells 1943). The Border Cave assemblage represents a broadly comparable range of environments under a climatic regime similar to that of the Makapan site to-day; that from Wonderwerk belongs to an area of appreciably lower rainfall. While the Border Cave fauna includes kudu, impala, and reedbuck, but lacks eland, *Oryx,* and *Damaliscus,* in that of Wonderwerk the three last named are present (together with *"Pelorocerus helmei"*) but the former three are lacking. The presence in the Makapan fauna of an *Oryx* (albeit scantily represented) indicates that at some stage in the accumulation of the deposit the climate was appreciably drier than it is now.

In point of numbers the Makapan fauna is dominated by four species, *Redunca darti, Phenacotragus vanhoepni, Makapania broomi,* and the wildebeest. It is remarkable that three of these four are extinct and two belong to extinct genera. The less abundant species fall into two groups, those which are moderately well represented and those which are notably rare. In the former may be placed the buffalo, eland, and kudu, the supposed nyala, the mountain reedbuck, and three extinct species, *Cephalophu, pricei, Oreotragus major,* and *Gazella gracilior.* The latter group includes

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* Using these terms purely in a stratigraphic sense and without implying any sort of climatic correspondence.

the blue duiker, *Oryx,* impala, the somewhat problematical *Damaliscus,* and the two large extinct species *"Alcelaphus robustus"* and *"Pelorocerus helmei"*.

Although none of these three groupings can be said to consist entirely of species characterising a particular environment, the total impression conveyed by the bovid fauna suggests a moderately well watered, bushy valley opening on to nearby plains which, at no great distance, were decidedly dry.

Age and Affinities

The only pre-Gamblian bovid fauna hitherto described from South Africa is that of the Vaal River deposits (Cooke 1949). This is essentially a plains assemblage, though it includes both "steppe" (*Damaliscus,* springbok, eland) and "savannah" (impala, sable, kudu) species. The Vaal River fauna includes *"Pelorocerus", Alcelaphus robustus,* a *Gazella* seemingly different from the Makapan species, and a giant buffalo (*Homoioceras bainii*), which has not been identified at Makapan. Including the other mammalian groups, the Vaal River assemblage as a whole resembles that of Olduvai in Tanganyika (Leakey 1951) and is probably of Kanjeran age in the main but includes Kamasian elements.

The Makapan Bovidae give the immediate impression of a more archaic character than those of the Vaal River gravels, and the Makapan deposit may confidently be regarded as older than Kanjeran. On the other hand, the large number of species not distinguishable from living forms seems to exclude an age greater than Kageran,* but it must be remembered that more complete knowledge would probably diminish rather than increase this number. As between a Kageran or Kamasian age, the bovid fauna offers little helpful guidance. A more exact assessment of the age of the deposit can therefore be reached only by taking into account the whole of the described fauna. A valuable preliminary attempt in this direction has been made by Ewer (1956). Her arguments in favour of a Kageran age are based on faunal lists for southern Africa in which data for the Bovidae (and some other important elements) were not available. It is not surprising, as she herself anticipated, that her conclusions may need some modification in the light of additional evidence.

Apart from the Bovidae here considered, the fauna of the Makapan Limeworks quarry includes a varied assortment of other mammals. Some of these have been described during the past ten years by different authors but there are still a number of elments in the fauna which have not hitherto been recorded. The following table constitutes as complete a list of the whole fauna as it is possible to present at this stage. In the case of species first named from this site, the author's name and date serves as a reference; in other cases, the reference to the authority for recording the species is given in square brackets after the name of the specific taxonomist. New

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* typified faunally by the deposits at Omo, Kaiso and Kanam.

records are indicated by an asterisk (*) following the item and definitely extinct species are shown by an obelus (†) before it.

INSECTIVORA

Gen. et sp. indet.*

PRIMATES

† *Simopithecus darti* (Broom and Jensen 1946) [Freedman, 1955]
(= *Dinopithecus* sp. (Broom and Hughes 1949); = *Brachygnathopithecus peppercorni* Kitching 1952; = *Gorgopithecus wellsi* Kitching 1953)
† *Parapapio broomi* Jones [Mollet 1946; Freedman 1955] (= *P. makapani* Broom and Hughes 1949)
† *Parapapio jonesi* Broom [Kitching, Wells and Westphal, 1948; Freedman 1955]
† *Cercopithecoides williamsi* Mollet 1946 [Freedman 1955]
† *Australopithecus prometheus* Dart 1948

LAGOMORPHA

Leporidae indet.*

RODENTIA

Muridae indet*
Hystrix cf *africae-australis* Peters [Greenwood 1955]
† *Hystrix major* Greenwood 1955
† *Xenohystrix crassidens* Greenwood 1955
† *Gypsorhychus makapani* Broom 1948

CARNIVORA

Canis sp.*
Vulpes sp. *
Cynictis sp.*
† *Crocuta* cf *brevirostris* Aymard [Toerien 1952]
† *Hyaena makapani* Toerien 1952
Felidae indet*
† *Machaerodus darti* Toerien 1955‡

PROBOSCIDEA

Gen. et sp. indet*

HYRACOIDEA

† *Procavia transvaalensis* Shaw [Churcher 1956]
† *Procavia antiqua* Broom [Churcher 1956]

PERISSODACTYLA

† *Stylohipparion* sp.*
† *Metaschizotherium transvaalensis* George 1950
? *Ceratotherium* sp.*
Diceros cf *bicornis**

---

‡ Equals *Therailurus barlowi* (Broom) according to Ewer (*This Journal* below]

ARTIODACTYLA

† *Potamochoeroides hypsodon* Dale 1948
† *"Pronotochoerus" shawi* Dale 1948
† *Notochoerus* sp.*
Hippopotamus cf *amphibius* Linnaeus [= *H. makapanensis* Kitching 1951]
Giraffa cf *camelopardalis* Linnaeus [Cooke and Wells 1947]
† *Griquatherium* cf *cingulatum* Haughton [Cooke & Wells 1947]
Strepsiceros cf *strepsiceros* (Pallas)*
Strepsiceros (*Tragelaphus*) cf *angasi* (Gray)*
Taurotragus cf *oryx* (Pallas)*
cf *Syncerus caffer* (Sparrman)*
† *Cephalophus pricei* sp.nov.*
cf *Cephalophus* (*Guevei*) *caerulus* (Hamilton Smith)*
† *Redunca darti* sp.nov.*
Redunca cf *fulvorufula* (Afzelius)*
cf *Oryx gazella* (Linnaeus)*
Damaliscus sp. (aff. *albifrons*)*
cf *Gorgon taurinus* (Burchell)*
† cf *Alcelaphus robustus* Cooke*
† cf *Pelorocerus helmei* (Lyle)*
† *Makapania broomi* gen. et sp.nov.*
† *Oreotragus major Wells**
Aepyceros cf *melampus* (Lichtenstein)*
† *Gazella gracilior* sp.nov.*
† *Phenacotragus vanhoepeni* sp.nov.*

In some of the groups listed above (e.g. Lagomorpha) the species have not yet been worked out and it is impossible to indicate whether they are extinct or not. Allowing a minimum of one species in each of these cases, the total faunal list comprises not fewer than forty-eight species. Apart from the Bovidae there are 30 species, of which 19 are certainly extinct and 5 cannot be separated specifically from living forms; the position of the remaining 6 is "doubtful". In the case of the 18 Bovidae, eight are extinct and 9 cannot be distinguished specifically from living species, although in several cases this statement needs to be qualified owing to the fragmentary character of the remains; 1 species (the *Damaliscus*) is probably extinct and may be placed in the "doubtful" category.

Of the 41 adequately determined species 27 are extinct and 14 cannot be separated from living forms. Ewer (1956) gives for the Australopithecine deposits as a whole a figure of 12% for the species "not more than sub-specifically distinct" from the living forms. For the Makapan Limeworks the indicated percentage is now 34%, which affects the conclusions materially. For the percentage of genera which are extinct, Ewer gives 53% for the Australopithecine deposits as a whole; the present Makapan figure is 55% without the Bovidae but only 41% when they are included. This latter figure is comparable with Ewer's 40% each for Omo and Olduvai.

As Ewer's figures for the Transvaal limestone caves did not include any records of Bovidae, her conclusions regarding the probable *relative* ages of the sites are not affected at present. The view that Makapan Limeworks and the Sterkfontein type site are the oldest and are very close to each other in time may later be tested by a study of the Bovidae; the Kromdraai and Swartkrans sites are clearly somewhat younger. One cannot avoid concluding that when the Bovidae at Sterkfontein, Kromdraai and Swartkrans are studied, the apparent percentage of extinct genera will decrease as it has at Makapan and will come more into line with those for Omo and Olduvai, where the Bovidae are already included.

According to Hopwood and to MacInnes (in Leakey 1951), the faunas of Omo, Kanam and Kaiso typify the Kageran stage; those of Olduvai Beds I and II, Laetolil and Rawi characterise the Kamasian stage; and Olduvai Bed IV, Olorgesailie and Kanjera represent the Kanjeran stage. The table below shows the extinct genera represented at Makapan and in one or other of these stages.

MAKAPAN	KAGERAN	KAMASIAN	KANJERAN
Simopithecus	?	x	x
"Machaerodus"	x		
Stylohipparion	x	x	x
Metaschizotherium		x	
Pronotochoerus	x		
Notochoerus	x		
Phenacotragus		x	x

While the statistical value of such a tabulation is slender, it suggests that the Makapan Limeworks deposit may be partly of Kageran age. The best fit would be if it belongs to the latest Kageran or earliest Kamasian. In terms of the European time scale this is most probably Upper Villafranchian. It has been mentioned above that at Makapan a relatively dry climate during at least part of the period represented by this deposit can be inferred. It would probably be rash, however, to equate this too narrowly with the late Kageran dry phase or "Kageran-Kamasian interpluvial" of East Africa (vide du Toit, 1947).

If, as appears to be the case, the Makapan Limeworks fauna is essentially Villafranchian, it is of interest that the Bovidae are mostly referable to genera still living. This feature is also apparent in the assemblage from Omo (which may be a little older). The inference is that the African Bovidae were completely differentiated to the generic level at the beginning of the Pleistocene. Unfortunately their late Tertiary history in this continent is still unknown, but the Villafranchian Bovidae of India are so different from the African forms that a considerable period of separate diversification in Africa must be regarded as highly probable.

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REFERENCES

ALLEN, G. M., 1939. A checklist of African mammals. *Bull. Mus. Comp. Zool. Harvard,* 83: 1-763.

ARAMBOURG, C., 1941. Antilopes nouvelle du Pléistocène ancien de l'Omo (Abyssine). *Bull. Mus. Hist. Nat. Paris* (2) 13: 343.

ARAMBOURG, C., 1947. Contribution à l'étude géologique et paléontologique du bassin du lac Rodolphe et de la basse vallée de l'Omo. Deuxième partie, Paléontologie. *Mission Scient. Omo* 1932-1933 I Géol.-Anthrop.: 418-432.

BARBOUR, G. B., 1949a Ape or man? An incomplete chapter of human ancestry from South Africa. *Ohio J. Sci.* 49: 129-145.

BARBOUR, G. B., 1949b Makapansgat. *Scient. Monthly,* 69: 141-147.

BONÉ, E., 1955. Une clavicule et un nouveau fragment mandibulaire d'Australopithecus prometheus. *Palaeont. Afr.* 3: 87-101.

BOSAZZA, V. L., ADIE, R. J. and BRENNER, S., 1946. Man and the great Kalahari desert. *J. Natal Univ. Coll. Scientific Soc.* 5: 1-9.

BRAIN, C. K., VAN RIET LOWE, C. and DART R. A., 1955. Kafuan stone artefacts in the post-Australopithecine breccia at Makapansgat. *Nature* 175: 16.

BROOM, R., 1937. Notices of a few more new fossil mammals from the caves of the Transvaal. *Ann. Mag. Nat. Hist.* (10) 20: 510-511.

BROOM, R., 1948. The giant rodent mole, Gypsorhychus. *Ann. Transv. Mus.,* 21: 47-49.

BROOM, R. and HUGHES, A. R., 1949. Notes on the fossil baboons of the Makapan Caves. *S. Afr. Sci.* 2: 194-196.

BROOM, R. and JENSEN, J.S., 1946. A new fossil baboon from the caves at Potgietersrust. *Ann. Transv. Mus.* 20: 337-340.

CHURCHER, C. S., 1956. The fossil hyracoidea of the Transvaal and Taungs deposits. *Ann. Transv. Mus.* 22: 477-501.

COOKE, H. B. S., 1949. Fossil mammals of the Vaal River deposits. *Mem. Geol. Surv. S.Afr.,* 35 (3): 117 pp.

COOKE, H. B. S., 1952. Quaternary events in South Africa. *Proc. First Pan-Afr. Congress on Prehistory,* 1947. Oxford: Blackwell: 26-36.

COOKE, H. B. S., MALAN, B. D. and WELLS, L. H., 1945. Fossil Man in the Lebombo Mountains, South Africa: the 'Border Cave', Ingwavuma District, Zululand. *Man* 1945 (3): 6-13.

COOKE, H. B. S. and WELLS, L. H., 1947. Fossil mammals from the Makapan valley, Potgietersrust III Giraffidae. *S. Afr. J. Sci.* 43: 232-235.

DALE, M. M., 1948. New fossil Suidae from the Limeworks Quarry, Makapansgat, Potgietersrust. *S. Afr. Sci.*, 2: 114-116.

DALE, M. M. and TOBIANSKY, D., 1947. Fossil mammals from the Makapan valley, Potgietersrust II Suidae. *S. Afr. J. Sci.* 43: 304.

DART, R. A., 1925. A note on Makapansgat: a site of early human occupation. *S. Afr. J. Sci.*, 22: 454.

DART, R. A., 1948a. An Australopithecus from the Central Transvaal. *S. Afr. Sci.*, 1: 200-201.

DART, R. A. 1948b. An adolescent promethean australopithecine mandible from Makapansgat. *S. Afr. Sci.*, 2: 73-75.

DART, R. A. 1948c. The Makapansgat proto-human *Australopithecus prometheus. Amer. J. phys. Anthrop.* (N.S.) 6: 259-283.

DART, R. A., 1948d. The adolescent mandible of *Australopithecus prometheus. Amer. J. phys. Anthrop.* (N.S.) 6: 391-411.

DART, A. R. 1948e. The first human mandible from the Cave of Hearths, Makapansgat. *S. Afr. archaeol. Bull*, 3: 96-98.

DART, R. A., 1949a. The cranio-facial fragment of *Australopithecus prometheus. Amer. J. phys. Anthrop.* (N.S.) 7: 187-213.

DART, R. A., 1946b. Innominate fragments of *Australopithecus promethus. Amer. J. phys. Anthrop.* (N.S.) 7: 301-333.

DART, R. A., 1949c. A second adult palate of *Australopithecus prometheus. Amer. J. phys. Anthrop.* (N.S.) 7: 335-338.

DART, R. A., 1952. Faunal and climatic fluctuations in the Makapansgat valley: their relation to the geological age and promethean status of Australopithecus. *Proc. First Pan-Afr. Congress on Prehistory*, 1947. Oxford: Blackwell, 96-106.

DART, R. A., 1954. The adult female lower jaw from Makapansgat. *Nature*, 173: 286.

DIETRICH, W. O., 1950. Fossile Antilopen und Rinder Äquatorialafrikas. (Material der Kohl-Larsen'schen Expeditionen). *Palaeontographica* 99, A: 30-32.

DU TOIT, A. L., 1947. Palaeolithic environments in Kenya and the Union — a contrast. *S. Afr. archaeol. Bull.* 2: 28-40.

EWER, R. F., 1956. The dating of the Australopithecinae: faunal evidence. *S. Afr. archaeol. Bull*, 11: 41-45.

FREEDMAN, L., 1955. The fossil Cercopithecoidea of South Africa. *Thesis for the degree of Ph.D., University of Cape Town* (awaiting publication).

GEORGE, M., 1950. A chalicothere from the Limeworks Quarry of the Makapan Valley, Potgietersrust District. *S. Afr. J. Sci.*, 46: 241-242.

GREENWOOD, M., 1955. Fossil hystricoidea from the Makapan Valley, Transvaal. *Palaeont. Afr.* 3: 77-85.

HAUGHTON, S. H., 1947. Notes on the Australopithecine-bearing rocks of the Union of South Africa. *Trans. geol. Soc. S. Afr.* 50: 55-59.

HOFFMAN, A. C., 1953. The fossil alcelaphines of South Africa — genera Peloroceras, Lunatoceras and Alcelaphus. *Nav. Nas. Mus. Bloemfontein* 1 (3): 41-56.

HOPWOOD, A. T., 1934. New fossil mammals from Olduvai, Tanganyika Territory. *Ann. Mag. nat. Hist.* (10) 14: 546-550.

HOPWOOD, A. T. and HOLLYFIELD, J. P., 1954. An annotated bibliography of the fossil mammals of Africa (1742-1950). *Fossil Mammals of Africa,* 8: 194 pp.

KITCHING, J. W., 1951. A new species of Hippopotamus from Potgietersrust. *S. Afr. J. Sci.,* 47: 209.

KITCHING, J. W., 1952. A new type of fossil baboon. *Brachygnathopithecus peppercorni.* gen. et sp.nov. *S. Afr. J. Sci.* 49: 15-17.

KITCHING, J. W., 1953. A new species of fossil baboon from Potgietersrust. *S. Afr. J.Sci.* 50: 66-69.

KITCHING, J. W., WELLS, L. H. and WESTPHAL, E., 1948. Fossil cercopithecid primates from the Limeworks Quarry, Makapansgat, Potgietersrust. *S.Afr.Sci.,* 1: 171-172.

KING, L. C., 1951. The geology of the Makapan and other caves. *Trans. Roy. Soc. S. Afr.,* 33: 121-151.

LEAKEY, L. S. B., 1951. *Olduvai Gorge.* Cambridge: Cambridge University Press. "The Olduvai fauna" by A. T. Hopwood, 20-30 and D. G. MacInnes 31-33.

MALAN, B. D. and COOKE, H. B. S., 1941. A preliminary account of the Wonderwerk Cave, Kuruman District. *S. Afr. J. Sci.* 37: 300-312.

MOLLET, O. D. v. d. S., 1947. Fossil mammals from the Makapan valley, Potgietersrust I. Primates. *S. Afr. J. Sci.,* 43: 295-303.

OAKLEY, K. P., 1954a. The dating of the Australopithecinae of Africa. *Amer. J. phys. Anthrop.* (N.S.) 12: 9-28.

OAKLEY, K. P., 1954b. Study tour of early hominid sites in southern Africa, 1953. *S. Afr. archaeol. Bull.* 9: 75-87.

PILGRIM, G. E., 1939. The fossil Bovidae of India. *Palaeontologia Indica* (N.S.) 26 (1): 356 pp.

ROBINSON, J. T., 1952. The Australopithecine-bearing deposits of the Sterkfontein area. *Ann. Transv. Mus.* 22: 1-19.

SCHLOSSER, M. 1925. in ZITTEL, K. A. von. *Textbook of Palaeontology* London: Macmillan and Co.: 14-20.

SCHWARZ, E. 1937. Die fossilen Antilopen von Oldoway. *Wiss. Ergebn. Oldoway-Exped.* 1913. (N.F.) 4: 8-104.

SIMPSON, G. G., 1945. The principles of classification and a classification of mammals. *Bull. Amer. Mus. nat. Hist.,* 85: 350 pp.

TOERIEN, M. J., 1952. The fossil hyenas of the Makapansgat Valley. *S. Afr. J.Sci.,* 48: 293-300.

TOERIEN, M. J., 1955. A sabre-tooth cat from the Makapansgat Valley. *Palaeont. Afr.* 3: 43-46.

VAN HOEPEN, E. C. N., 1932. Voorlopige beskrywing van Vrystaatse soogdiere. *Palaeont. Navors. nas. Mus. Bloemfontein,* 2: 63-65.

VAN RIET LOWE, C., 1938. The Makapan caves: an archaeological note. *S. Afr. J. Sci.,* 35: 371-381.

VAN RIET LOWE, C., 1943. Further notes on the Makapan caves. *S. Afr. J. Sci.,* 40: 289-295.

VAN RIET LOWE, C., 1948. Cave breccias in the Makapan Valley. *Roy. Soc. S. Afr. Spec. Publ. Robert Broom Comm. Vol.*: 127-131.

WELLS, L. H., 1951. A large fossil klipspringer from Potgietersrust. *S. Afr. J. Sci.* 47: 167-168.

WELLS, L. H. and MALAN, B. D., 1943. A further report on the Wonderwerk Cave, Kuruman District. *S. Afr. J. Sci.* 40: 258-270.