

# Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania. Part II

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References to pages 289 onwards and to the Plates refer to Part I of the present monograph; see footnote on previous page.

## Bovidae from the excavated sites at Olduvai Gorge

In the second part of this paper we deal with the identified bovid material from various sites excavated in the 1950s and 1960s. The accounts of most sites conclude with a table showing the numbers of identified bovid fossils (Tables 1–10). Bracketed numbers in these tables indicate immature bones and milk teeth included in the overall totals immediately to the left. Bones are always counted as adult unless they show some obvious sign of juvenile status, for example a proximal metapodial with strong narrowing of the shaft below the articular surface. No molar teeth have been counted as immature although some would have been in wear contemporaneously with deciduous premolars. Thus the totals for immature fossils and individuals are likely to be underestimates. The limb bone columns embrace only the humerus, radius, ulna and metacarpal of the front leg and the femur, tibia and metatarsal of the back leg. The incidence of identifications for other limb bones was too low for them to be useful, as was also the case for the limb girdles and vertebrae. The minimum numbers of individuals are usually based on mandibular remains coupled with  $M_3$ s, but sometimes limb bones, for example distal humeri, have given the higher total. The minimum number of individuals may be a satisfactory concept when applied to particular levels of excavated sites, but where fossils from a considerable depth of deposit have been taken as a unit, as at the MNK Occupation Site, it is less likely to be close to the real number of individuals from which fossils have been drawn. SHK II is probably the site at which the minimum number of individuals is least reliable, since fossil material has come from the Annexe living floor, the stream channel and the tuff above the channel.

M. D. Leakey (1971b : 258–262) summarizes current knowledge about the excavated sites at Olduvai. She also gives the authoritative geological accounts of the sites, and our short introductory remarks for each site draw upon her information.

The most recent workers on the geology of Olduvai have given measurements in imperial units (miles, yards, feet, inches). When quoting such measurements we have also given the metric equivalents, but these are not the units in which the measurements were originally taken.

### Sites in Bed I

#### DK I

##### Site (22)      Geologic locality 13

DK I is on the north bank of the Main Gorge, about  $1\frac{3}{4}$  miles (2.8 km) upstream of the third fault. It is one of the earliest sites in the Gorge, lying above the Basalt Member and overlain by Tuff IB, for which an age of 1.75 million years has been obtained (Evernden & Curtis 1965 : 354). Excavations were carried out at the site in 1962 and 1963, during the course of which parallel trenches were dug as a succession of grids or strips. Parts of the site dug in 1962 were called DK IA, DK IB and DK IC; strips I–III were dug in 1963. The sequence of deposits, from above downwards, was as follows:

4–5 ft (1.2–1.5 m) of ignimbrite (Tuff IB).

Level 1.  $1\frac{1}{2}$ –2 ft (45–60 cm) of brown bentonitic clay with localized lenses of fine-grained white tuff.



Level 2. 2–2½ ft (60–75 cm) of buff-coloured clayey tuff, merging into level 3.

Level 3. 1–2½ ft (30–75 cm) of grey-buff clayey tuff, less clayey than level 2.

Level 4. Silts, clays and tuffs filling depressions in the basalt.

Cultural and faunal remains were found throughout levels 1, 2 and 3 but especially in the lowest part of level 3. Here the material was concentrated on an old land surface, partly on the eroded surface of the level 4 tuff and partly on the basalt where it rose above the tuff. Levels 1, 2 and 3 amount to a combined depth of only 5–6½ ft (1.5–1.95 m) and there is little evidence of a break in the sequence above the eroded surface at the base of level 3. The period of deposition was probably relatively short and material from the three levels is therefore treated as a single unit. Faunal remains are abundant but very broken (prior to fossilization) and with few associations among the bones. Fossil rhizomes similar to those of papyrus and many crocodile remains found on the hominid occupation surface suggest that standing water was nearby.

Tribe TRAGELAPHINI. This tribe is represented by right mandible 36, left mandible 3001, right M<sup>1</sup>–M<sup>3</sup> 802 and a number of isolated teeth. These are right upper molars 263, 3051A, 3052A, 067/4123; left upper molars 270, 3041, 3049, 067/4123; left lower molars 161, 803, 4152; right M<sub>3</sub> 3049; left M<sub>3</sub> 154; two right upper premolars 154; left upper premolar 230; left P<sub>4</sub> 166; deciduous left P<sup>3</sup> 312; deciduous right upper premolar 067/4085; and deciduous left P<sub>4</sub>s 3049 and 4152. These dentitions and teeth are about the size of the living greater kudu and are presumably referable to *Tragelaphus strepsiceros maryanus*.

The distal end of right humerus 79, distal end of right radius 4088, complete left metacarpal 4141, complete left metatarsal 4429 and proximal end of left metatarsal 71 are assigned to this tribe. They belong to a smaller animal than the reduncine at this site and are rather small for satisfactory assignment to *T. s. maryanus*. A complete left femur 5400 represents a larger kudu-sized tragelaphine. A complete left tibia 876 is possibly tragelaphine but is short and has an upturned edge to its proximal lateral facet.

Tribe BOVINI. An immature left maxilla 4220, incomplete upper molar 067/3473 and deciduous left P<sup>4</sup> 265 probably belong to this tribe. Their occlusal morphology does not differ from that of *Syncerus* teeth in other sites at Olduvai.

Tribe REDUNCINI. Material of this tribe comprises incomplete left mandible 067/4080, immature left mandible 51 and some isolated teeth (right upper molars 54 and 4026; left upper molars 067/3483 and two without numbers; right lower molars 795, 067/3473, 067/3483 and 067/4085; left lower molars 232, 067/4124 and two without numbers; right M<sub>3</sub>s 4060 and 067/4085; left M<sub>3</sub>s 233, 801, 3043 and 5002; right P<sub>3</sub> 067/3483; left P<sub>4</sub> without number; and deciduous right upper premolar 5007). They are too large to fit *Redunca*, and within *Kobus* are of waterbuck rather than kob or lechwe size. Their most likely assignment is to *K. sigmoidalis*.

A right lower molar 797 is too small for *K. sigmoidalis* and is the size of living *Redunca redunca*.

The distal end of right humerus 3230, complete right radius 788, proximal end of right radius 381, distal end of right tibia 4116, distal end of left tibia 119 and proximal end of right metatarsal 3067 are about waterbuck size, but only 788 and 3067 are definitely not tragelaphine.

Tribe HIPPOTRAGINI. An immature cranium with complete horn cores 067/5496 of *Hippotragus gigas* comes from this site. The cranium with left horn core was found *in situ* below Tuff IB in 1961, while the right horn core was found eroding out in 1964. The occipital condyles and most of the basioccipital are missing.

An immature right maxilla 37 + 43 is most probably hippotragine; the sockets for the roots on the inside of the maxilla bone suggest that M<sup>1</sup> was not as large as in the bovine immature left maxilla 4220. This fossil has the same preservation as the immature cranium mentioned above and might be from the same individual. A left maxilla 067/3496 with deciduous P<sup>3</sup> and P<sup>4</sup> could also be hippotragine and possibly also the same individual.

Three single teeth also belong in this tribe. These are right lower molar 168, left lower molar 93 and right M<sub>3</sub> 067/3483. A deciduous left P<sub>4</sub> 067/4149 may belong to this tribe or to the Reduncini.

A complete right femur 3051 shows the anteroposterior elongation of the great trochanter in side view and the shallow hollow between the great trochanter and the articular head in anterior view which are characteristic of this tribe. The pits on the lateral distal condyle for ligament



attachment are not so deep as in alcelaphines. The distal end of right femur 3254 is also hippotragine.

Tribe ALCELAPHINI. *Parmularius altidens* is represented by a complete right horn core with part of the frontal preserved 068/6696, the basal halves of right horn cores 4112 and 4113 and an immature right horn core with part of the frontal and orbit 165.

Incomplete right mandibles 4 and 446, left mandible 161, the associated pair of immature mandibles 578 right and 646 left and immature left maxilla 154 are identified as *P. altidens*. There are also some isolated alcelaphine teeth which are probably this species, as follows; they cannot be seen to have a more primitive morphology than those of *P. altidens* at FLKN I.

Right upper molars 208, 284, 523, 530, 653, 768, 870, 4107, four numbered 4152, 067/3448, 067/3450, 067/3470, 067/3473, 067/3482, 067/4085, 067/4095, 067/4124 and one without number; left upper molars 35, 109, 110, 139, 194, 222, 259, 366, 378, 508, 551, 067/3439, 067/3447, 067/3470, 067/3473, 067/3482 and three without numbers; part of an upper molar 067/3482; right upper premolars 067/3483, 067/4095 and 067/4126; left upper premolars 067/4095 and 067/4126; right lower molars 067/3452, 067/3483 and two without numbers; left lower molars 3353, 4124 and three without numbers; lower molars of indeterminate side 88, 162, 271, 279, 530, 533, 837, 4111, two numbered 067/4085 and four without numbers; right  $M_3$ s 106, 185, 196 and damaged 067/3045; left  $M_3$ s 449, 811, 4106 and 067/3434; right  $P_4$ s 56, 4108, 067/3483 and 067/4149; left  $P_4$  067/3498; and deciduous right  $P_4$  235.

Several isolated teeth are considerably larger than those of *P. altidens*. These are right upper molars 284A, 523, 530, 3305 and 4123; left upper molars 139, 067/3044 and 067/3430; part of an upper molar 067/3431; left upper premolar 067/3483; right lower molar 279; left lower molar and left  $M_3$  161; left lower molars 84, 111, 067/3054 and one without number; parts of lower molars 533 and 067/4091; right  $M_3$ s 165 and 227; and left  $M_3$  4395. They are larger than the teeth associated with the *Connochaetes* cranium at FLKN I, and this would suggest that *Megalotragus kattwinkeli* was present at DK I.

At least two species of alcelaphine are represented by the identified limb bones. These are a more numerous smaller species which presumably goes with the *P. altidens* horn cores, and a less common very large species. Limb bones assigned to the smaller species are as follows; the tibiae differ from those of later *P. altidens* at FLKN I in having a more strongly upturned edge of the lateral facet at the proximal end. There appear to be no other morphological differences.

Distal ends of right humeri 471 and 531, distal end left humerus 3083; proximal ends left radii 5135 and 067/4092, distal end left radius 15; right ulna 3021 and left ulna 3071; complete left metacarpal 76, proximal ends left metacarpals 504 and 3071; distal end right tibia 45, proximal ends left tibiae 78 and 4422A; proximal ends right metatarsals 105 and 067/4081, proximal end left metatarsal 645, distal end metatarsal 3066, immature right metatarsal 185, immature left metatarsal 159; and the associated set of complete left humerus 141, distal end right humerus 168, complete right radius 58, complete left radius with ulna 145 + 57, complete right metacarpal 143, complete left metacarpal 144, and phalanges 53, 85 and 101.

There is quite a size range among the bones of the smaller species, and possibly a still smaller species is represented by the distal end right humerus 67, distal end left humerus 3182, proximal end left radius 5135, complete left tibia 876 and distal end left tibia 45. These are about the size of the small alcelaphine limb bones from levels 1–3 at FLKN I. In Table 1 (opposite) they have been doubtfully referred to Alcelaphini sp. 4.

The size demarcation between *P. altidens* and the larger species is very clear. The limb bones of the latter are proximal end right radius 5190, distal end right radius 414, distal end left radius 067/4093; right ulna 067/4122; complete left metacarpal 85, proximal ends right metacarpals 5 and 521; complete right tibia 4300; distal epiphysis right femur 188; complete right metatarsal 4138A + B, complete left metatarsal 4097, proximal end right metatarsal 316, proximal end left metatarsal 477, distal ends metatarsals 141 and 3073; and associated distal end left humerus 164 and complete left radius 166. The radius and metatarsals of this larger species are very long, whereas those of *Connochaetes* are relatively short. The coronoid fossa on the distal end of humerus 164 is deep, which is unlike *Connochaetes*. These limb bones belong to a very large and long-limbed alcelaphine, most probably *Megalotragus kattwinkeli* or its immediate ancestor.

Tribe ANTILOPINI. *Antidorcas recki* is represented by a complete left mandible 261, incomplete



Table 1 Numbers of bovid bones at DK I

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
<i>Tragelaphus s. maryanus</i>	-	1	2	21 (4)	-	24	3	2
Smaller tragelaphine sp.	-	-	-	-	5	5	2*	-
Larger tragelaphine sp.	-	-	-	-	1	1	1*	-
Tragelaphini total	-	1	2	21 (4)	6	30	-	1
<i>Syncerus aequalis</i>	-	1 (1)	-	2 (1)	-	3	-	1
<i>Kobus sigmodontalis</i>	-	-	2 (1)	22 (1)	2	26	4	1
<i>Redunca</i> sp.	-	-	-	1	-	1	1	-
<i>Hippotragus gigas</i>	1 (1)	1 (1)	-	3	2	7	2	1
<i>Megalotragus ? kottwinkeli</i>	-	-	-	22	17	39	3	-
<i>Parmularius alidensis</i>	4 (1)	1 (1)	5 (2)	83 (1)	27 (2)	120	7	2
<i>Alcelaphini</i> sp. 4?	-	-	-	-	5	5	2	-
<i>Alcelaphini</i> total	4 (1)	1 (1)	5 (2)	105 (1)	49 (2)	164	10	2
<i>Antidorcas recki</i>	-	2 (1)	4	22	16	44	5	1
<i>Antilopini</i> sp. 1	2	-	-	-	-	2	2	-

\* One of the two tragelaphine species represented by limb bones would be *Tragelaphus strepsiceros maryanus*.



left mandibles 272 and 067/4078, right mandible 231, left maxilla 067/4124 and immature left maxilla 191.  $P_2$  is present on mandibles 261 and 272, but its presence or absence on the other mandibles is uncertain. There are also several isolated teeth. These are right upper molars 067/3046, 067/3477, 067/4091, 067/4123 and 067/4124; left upper molars 1475, 067/3451, 067/4123 and 067/4124; upper premolar 067/4085; right lower molars 067/3050, 067/3498, 067/4085 and two numbered 067/3483; left lower molars 4111, 067/3065 and two numbered 067/4085; and right  $M_3$ s 4565 and two numbered 149.

A number of limb bones agree well with those of *A. recki* at other sites. These are distal end right humerus 144, distal end left humerus 4100; complete left radius 4087; proximal ends right metacarpals 194 and 362, distal ends metacarpals 615 and 067/3093; complete left tibia 4366, distal end right tibia 195, distal end left tibia 375; complete left metatarsal 3292, proximal ends left metatarsals 228 and 3129, and distal end metatarsal 639.

Two complete right femora, 3330 and 5385, are about the size of the proximal end of a left femur 1027 at FLKN I and are therefore presumably *A. recki* although rather large. They are smaller than the small alcelaphine limb bones at FLKN I (p. 19).

Two left horn cores, 1962.067/3963 and 3965, from the surface of DK I, could be an antilopine species other than *Antidorcas recki* (see p. 444). This is the species listed as 'Antilopini sp. 1'.

SUMMARY. DK I is interesting for the early records of *Hippotragus gigas* and *Megalotragus ? kattwinkeli*, and for one of the rare reduncine teeth small enough to fit *Redunca*. There is a comparatively high representation of tragelaphines and reduncines, and the normal Bed I partnership of *Antidorcas recki* and *Parmularius altidens* has appeared.

The numbers of bovid bones of each species at DK I is given in Table 1.

### FLK Sites

Three adjacent erosion gullies form a recess in the western wall of the Main Gorge just above its junction with the southern branch. The recess measures some 350 yds (320 m) north-south by about 450 yds (410 m) east-west. There are six sites within the area. These are FLKNN I, FLK I, FLKN I, FLKN II, FLK II, FLK II Maiko Gully and FLKN Ostrich site.

### FLKNN I

#### Site (38) Geologic locality 45

FLKNN I is the most northerly site within these gullies. It consists of a low ridge running approximately east-west and is capped by some 10-12 ft (3.0-3.6 m) of fawn-coloured tuff resembling the Naisiusiu Beds and lying unconformably on the Bed I sediments, the whole of Beds II-IV having been eroded away before its deposition. The site was excavated in 1960-61 and four levels were uncovered, from above downwards:

Level 1. A greenish-grey silty clay with scattered bones and artifacts on its surface and in its upper parts. The top was irregular and friable, indicating weathering. The faunal remains are not weathered but are rather fragmentary. This level can be correlated with level 22 (the occupation or '*Zinjanthropus*' level) of FLK I.

Level 2. A fine-grained buff-white tuff containing some faunal remains but no artifacts. The antelope material was noticeably more complete than in levels 1 and 3 and several partial skeletons were recovered. The remains were mostly found in patches of clay within the tuff.

Level 3. A hominid occupation floor on the surface of a grey silty clay, 6 ins-2 ft (15-60 cm) thick, resting on Tuff IB. The bones were found on the clay surface or in its topmost part which was more friable than the lower part.

Level 4. A clay underlying Tuff IB. This is the equivalent of the upper levels of DK I. There were very few antelope remains.

The many root casts and impressions of reed stalks in Tuff IB and the occurrence of fish, amphibians and waterfowl suggest that the site was near a lake or swamp.

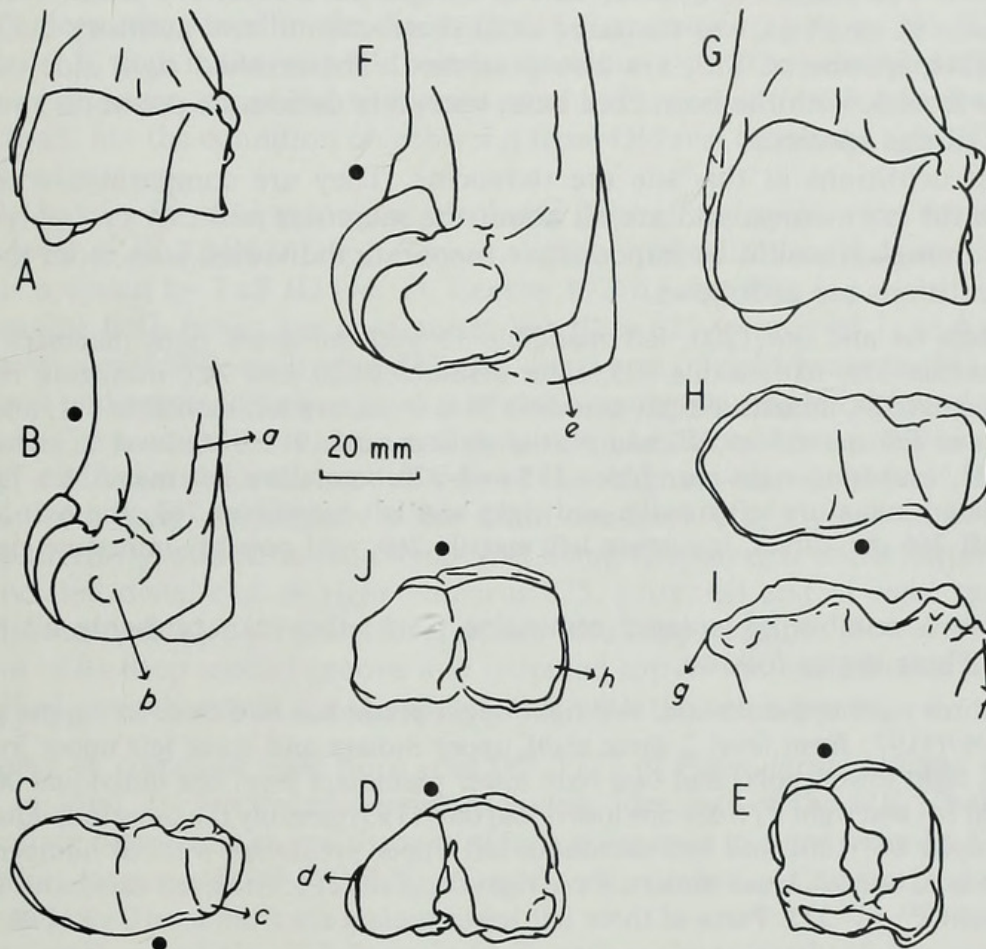
Tribe TRAGELAPHINI. A frontlet with nearly complete horn cores, 60, of *Tragelaphus strepsiceros maryanus* (Leakey 1965 : 40; pl. 42) was found in level 1 at this site. Maxillae (right 557 and left 553) and mandibles of both sides (right 62 and left 66 + 548) and a full set of incisors and



canines, 548, were found with this frontlet. The tooth rows are complete and are the same size and morphology as those of *Tragelaphini* at FLK I and FLKN I. Part of the skeleton of this animal was found beside the skull and dentitions; this consists of most of the pelvic girdle 56, right scapula 549, left patella 544, a crushed radius 541 and several vertebrae (atlas 556, axis 63, three cervicals 63, 64a and 64b, and seven lumbers 539, 540, 550, 551, 552 and 558).

Part of a lower molar 067/1180 from level 2 or 3 is tragelaphine.

Limb bones assigned to this tribe are the associated distal end of right humerus 896, proximal end of right radius 902 and complete right metacarpal 895 from level 2; and the proximal end of left metacarpal 855+883+884 from level 3. They closely resemble limb bones identified as *Tragelaphini* at FLKN I, a site where reduncines are almost unknown, but here at FLKNN I it is apparent that there is very little difference from contemporary reduncines (Fig. 35), and the



**Fig. 35** Limb bones of Olduvai antelopes; A–E *Tragelaphini*, F–J *Reduncini*. Figs A–D and G are of the left side; the remainder have been reversed to appear as if from the left side. Solid dots indicate anterior sides.

A, B. Anterior and lateral views of distal humerus FLKN I 8248.

C. Proximal articular surface of radius FLKN I 8275.

D. Proximal articular surface of metacarpal FLKN I 067/1073.

E. Proximal articular surface of metatarsal FLKN I 7333.

F. Lateral view of distal humerus FLKNN I 368.

G. Anterior view of distal humerus FLK I 235.

H. Proximal articular surface of radius FLKNN I 370.

I. Anterior view of proximal end of same radius.

J. Proximal articular surface of metacarpal FLKNN I 369.

a=strong ridge for extensor carpi radialis origin in tragelaphines, b=shallow hollow for lateral humeroradial ligament in tragelaphines, c=lack of anterior projection in tragelaphines, d=unciform facet not angled in tragelaphines, e=distal end of lateral side low in reduncines, f=small proximal lateral tubercle in reduncines, g=pronounced medial rim in reduncines, h=an infrequent dorsally-directed protuberance on the magnum-trapezoid facet in reduncines.



identifications are correspondingly insecure. It is also odd that the limb bones are much smaller than one would expect for *T. s. maryanus*. The humeri differ from those of living Tragelaphini by having a strong ridge on the lateral side of the distal end for the origin of the extensor carpi radialis. They differ from Reduncini at this site only in having a shallow hollowing for the lateral humeroradial ligament and being slightly smaller. The radii differ from the contemporaneous reduncines in the lack of anteriorly-directed points on the proximal lateral facets (such points are frequent in living tragelaphines, and occasional in living reduncines). The metacarpals are without an angled unciform facet or the upward protuberance of the magnum-trapezoid facet found in reduncines, but again distinction from reduncines is poor.

The associated distal end of left humerus 730, proximal end of left radius 732 and left ulna 731 from level 2 are more doubtfully tragelaphine.

**Tribe REDUNCINI.** The pedicel and lower half of a right horn core, 871 from level 2, belongs to *Kobus sigmoidalis*. A small part of the same skull (basioccipital and auditory bullae) and nearly complete maxillae, numbered 872, are also preserved. The crushed right side of an immature skull, 296 from level 3, with the horn core base, complete deciduous premolar row and first two molars, is also of this species.

Many partial dentitions at this site are reduncine. They are comparable with the maxillae associated with the horn cores, and are all about the same size and can probably be referred to *K. sigmoidalis*, though it would be impossible to separate individual jaws from the living waterbuck. These dentitions are as follows.

Right mandibles 64 and 067/1200, left mandible 13 and immature right mandible 067/1196 from level 1; right maxilla 373, left maxilla 535, right mandibles 629 and 965, immature right maxilla 79, immature left maxilla 374, immature right mandible 516, immature left mandible 591, and the associated immature right and left mandibles 910 and partial right maxilla 911 from level 2; right mandible 351, left mandible 131, immature right mandibles 135 and 920, immature left mandibles 73, 770, 934 and 067/1191, associated immature left maxilla and right and left mandibles 769, and associated immature right 268 and left 266 mandibles, immature left maxilla 269, and possibly immature right maxilla 113 from level 3.

There are also a number of isolated reduncine teeth; they can probably all be assigned to *K. sigmoidalis*. These are as follows.

From level 1 three right upper molars, two right upper premolars and three left upper premolars from one individual 067/1197; from level 2 three right upper molars and three left upper molars from one individual 430, a right lower molar and two right lower premolars from one individual 067/1192, a right lower molar, right  $M_3$  and right  $P_4$  from one individual 067/1195 (possibly the same individual as 067/1192), right upper premolar 067/1201 and two deciduous left upper premolars without numbers; from level 3 two left upper molars, two left lower molars, three right deciduous  $P_4$ s and a left deciduous  $P_4$  all numbered 067/1199, and right  $P^3-M^3$  523. Parts of three left lower molars are from level 2 or level 3.

There are several associations among the limb bones assigned to this tribe, particularly in level 2: distal end right humerus 368, complete right radius 370 and complete right metacarpal 369; distal end right humerus 892, complete right radius 890, right ulna 891 and complete right metacarpal 889; distal end left humerus 500, complete left radius 499, left ulna 499 and complete left metacarpal 498; proximal end left radius 957 and distal end left metacarpal 956; complete right metatarsal 738 and proximal end left metatarsal 736. The above associations are all from level 2. A complete right metacarpal 616 and distal end right humerus 617 are associated in level 2 (field catalogue) or level 3 (written on bones).

There are some other reduncine limb bones. From level 1 these are distal end right humerus 102, proximal end right metacarpal 45, proximal end right metatarsal 818 and proximal end left metatarsal 20. From level 2, distal end left humerus 998, proximal end left radius 1014, distal ends left tibiae 285 and 343, complete right metatarsal 738 and proximal end right metatarsal 579. From level 3, distal end left humerus 067/1253, proximal end right radius 728, nearly complete left radius 936 and ulna 935, proximal ends left radii 364 and 601 (with ulna 604), complete right metacarpal 349 + 350, and proximal ends left metacarpals 168 and 210.

The humeri differ from those of living reduncines in that the distal end of the lateral side descends to a low level behind the insertion for the humeroradial ligament, and in this they



resemble tragelaphines (Fig. 35, p. 7). The radii have a lower and smaller proximal lateral tubercle and a more pronounced medial rim of the proximal medial facet than in living waterbuck. The metacarpals differ from those of living reduncines in the less frequent medial protuberance on the magnum-trapezoid facet. The size of these limb bones is about that of a waterbuck, but a few are smaller and thus nearer the size of contemporaneous tragelaphines. It seems safe to assume that the majority are of *K. sigmoidalis*.

An immature horn core, 067/1174 found at the junction of levels 2 and 3 in 1960, is little compressed and possibly also of *K. sigmoidalis*.

Tribe HIPPOTRAGINI. A *Hippotragus* cranium with horn cores, both mandibles and parts of the maxillae, numbered 608, was found during 1960 in the clay above level 1 at this site, and was thought to be possibly alcelaphine by Leakey (1965 : 66(c)). The braincase has been damaged and distorted behind the horn cores. Several points concerning the anatomy of this interesting find have already been mentioned in the discussion of *Hippotragus gigas*, p. 346. The mandibles have a much smaller  $P_2$  than in the roan and a short diastema. On  $P_4$  the entostylid is set diagonally to the line of the jaw and not parallel to the entoconid. This condition occurs more frequently in sable than in roan, but the condition on other  $P_4$ s from Olduvai cannot be seen. The horizontal ramus of these jaws is deep.

A partial skeleton of a large hippotragine, probably *Hippotragus gigas*, was found at the base of the tripartite level of FLKNN in 1961. This is slightly higher in the sequence than level 1 of FLKNN I and is overlain by Tuff ID (M. D. Leakey 1971b : fig. 19).

Other hippotragine limb bones are a complete left tibia 821 from level 1, and an associated complete right metacarpal 960, right ulna 962 and distal end of right humerus 961 from level 2. The humerus distal end agrees closely with that of the hippotragine skeleton found at the base of the tripartite level. The metacarpal is short and massive and differs from equally-sized reduncines in the absence of a tuberosity on the medial side of the magnum-trapezoid facet, the lack of an angle on the unciform facet, the slightly wider distal condyles, scarcely any hollows at the top of the condyles posteriorly, and from reduncines and living *Hippotragus* in the flatter top articular surface. An associated distal end of right humerus 825, proximal end of right radius 824 and complete right metacarpal 826, all from level 2, are also hippotragine. However, the humerus looks alcelaphine in its deep medial groove and indented top of the medial condyle, and would have been identified as such except for the association with the other bones.

Tribe ALCELAPHINI. A complete right horn core 067/1173 of *Parmularius altidens* was a surface find at this site in 1960. Its backward curvature is very like that of the DK I horn core, or is possibly intermediate between that and the sort of curvature seen in cores from FLK I. The distal half of a *P. altidens* horn core 749 P.P.R.9, referred to as probably Caprini by Leakey (1965 : 68(b)), came from level 3.

An incomplete right mandible, 733 from level 3, with isolated teeth of the same individual (right upper molars 943 and 067/1188; left upper molar 948; left lower molar and left  $M_3$  numbered 067/1188; right  $M_3$  067/1194) agrees in size and morphology with *P. altidens* dentitions at FLKNN I. This mandible shows none of the red coloration present in other FLKNN I dentitions including those from level 3. An alcelaphine right  $M_3$  714 is from level 2 and a right upper molar 067/4676 from level 4.

There are no *in situ* *Parmularius* limb bones at this site; the alcelaphine limb bones are all of one or more species larger than *Parmularius*. As with the reduncines there are associated sets of limb bones in level 2. These are complete right radius 578, right ulna 578 and complete right metacarpal 577; distal end right humerus 344, proximal end right radius 306 + 341, right ulna 342 and complete right metacarpal 305. There is also a complete right alcelaphine humerus 358 from level 2 with no known association, and a complete right metacarpal 405 from level 1. These bones could be of *Connochaetes* or *Megalotragus*. A damaged and very long right tibia 355 and a crushed right femur 354 from level 2 belong more definitely to *Megalotragus* ? *kattwinkeli*. Finally, the distal end of an immature left radius, 347 from level 3, is alcelaphine.

Tribe ANTILOPINI. A left upper molar and upper premolar, 067/4676 from level 4, belong to this tribe. Part of a left metacarpal 067/1280 from level 1, and the fragmentary distal end of a left



tibia 067/1269 and complete right metacarpal 649, both from level 3, may represent *Antidorcas* or *Gazella*. However, the first and second limb bones could belong to the Alcelaphini.

SUMMARY. The main feature of FLKNN I is its many reduncine remains and unusually few alcelaphines. The reduncine predominance must be connected with proximity to water. The associations among limb bones in level 2 are valuable in showing the difficulty of distinguishing tragelaphines from reduncines at a time level of nearly two million years ago. The best Bed I skull of *Hippotragus gigas* and a rare stratigraphically-placed horn core of *Kobus sigmoidalis* occur here. One or more large alcelaphine species are better represented than *Parmularius altidens*, and Antilopini are very poorly represented, a situation in contrast with other Bed I sites.

The species list for the site is:

*Tragelaphus strepsiceros maryanus* (may include the rather small limb bones)

*Kobus sigmoidalis*

*Hippotragus gigas*

*Megalotragus ? kattwinkeli*

? *Connochaetes* sp.

*Parmularius altidens*

Antilopini sp.

The numbers of bovid bones in levels 1, 2 and 3 are shown in Table 2. A large proportion of the reduncines in level 3 are immature.

#### FLK I Site (41) Geologic locality 45

FLK I is almost in the centre of the FLK series of erosion gullies. It was excavated in 1959–60 by means of a trial trench and a succession of trenches designated A, B, C, D, E, F and G. Several levels were uncovered, many of which were barren. From the top downwards the levels with artifacts or fossils were:

Level 7. An irregular seam of clay, between two layers of yellow-grey tuff, about 5–6 ft (1.5–1.8 m) below Tuff IF. A few antelope remains were recovered.

Level 10. A fairly coarse reworked tuff some 9–10 ft (2.7–3.0 m) below Tuff IF. A few antelope bones were found.

Level 11. A hard yellow-buff tuff layer between two layers of clay. There were no antelope remains.

Level 12. A hard, massive buff-yellow tuff about 10–11½ ft (3.0–3.45 m) below Tuff IF. It yielded a crushed antelope skull and skeleton which is impossible to identify.

Level 13. A level some 2 ft (60 cm) thick consisting of irregular and discontinuous bands of clays and tuffs. In some areas the tuffs were well defined but in others they merged into one another.

Level 15. A clayey tuff about 1 ft (30 cm) thick and 15 ft (4.5 m) below Tuff IF.

Levels 16, 17 and 21. Thin tuff layers which were not very fossiliferous.

Level 22. A grey-green silty clay about 1 ft (30 cm) thick and 20 ft (6.0 m) below Tuff IF. This is the level at which the '*Zinjanthropus*' skull was found in 1959. The upper surface of the clay was slightly uneven and the topmost part more friable than the lower part, indicating weathering into a palaeosol. The fossil material, concentrated into a central area a short distance from the skull and an irregular outer margin (M. D. Leakey 1971b : 50, fig. 24), was recovered from the surface of the clay or its uppermost part but was not weathered. There was no vertical diffusion of fossils as in other levels.

At this site the field numbers of fossils and artifacts are preceded by the trench letters.

Tribe TRAGELAPHINI. This tribe is represented by a palate C.067/1083, and associated mandibles right G.067/1100 and left G.067/1095, which are adult, and an associated set of upper (right G.067/1088 and left G.067/1089) and lower (right G.067/1086 and left G.067/1085) immature dentitions. They are all from level 13. The adult lower tooth rows are complete and are comparable in size and morphology with those of the greater kudu. All the dentitions can probably be assigned to *Tragelaphus strepsiceros maryanus*.



Table 2 Numbers of bovid bones at FLKNN I

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
Level 1								
<i>Tragelaphus s. maryanus</i>	1	2	2	-	1	6	1	-
<i>Kobus sigmodontalis</i>	-	-	4 (1)	8	4	16	2	1
<i>Hippotragus gigas</i>	1	2	2	-	1	6	1	-
? <i>Connochaetes</i> sp.	-	-	-	-	1	1	1	-
Level 2								
Smaller tragelaphine sp.?	-	-	-	-	3	3	1	-
<i>Kobus sigmodontalis</i>	1	7 (3)	6 (4)	15 (2)	21	50	3	2
<i>Hippotragus gigas</i>	-	-	-	-	6	6	2	-
<i>Megalotragus ? katiwinkeli</i>	-	-	-	-	2	2	1	-
? <i>Connochaetes</i> sp.	-	-	-	1	8	8	2	-
<i>Parmularius altidens</i>	-	-	-	1	-	1	1	-
Alcelaphini total	-	-	-	1	10	11	4	-
Level 3								
Smaller tragelaphine sp.	-	-	-	-	1	1	1	-
<i>Kobus sigmodontalis</i>	1 (1)	4 (4)	12 (10)	13 (4)	10	40	3	7
Large alcelaphine sp.	-	-	-	-	1 (1)	1	-	1
<i>Parmularius altidens</i>	1	-	1	6	-	8	1	-
Antilopini sp. indet.	-	-	-	-	1	1	1	-



A few isolated teeth also belong in this tribe. These are right upper molar G.067/904, left upper molar C.067/894, right lower molar G.067/896, right  $M_3$  G.067/909 and left  $M_3$  C.067/908 from level 13; left lower molar Balk 067/895 and left  $M_3$  Balk 067/1092 from level 15;  $P^3$  and  $P^4$  in a right maxilla fragment 067/883 of unknown level. These may well also be *T. s. maryanus*.

A number of limb bones are tragelaphine. These are distal end of left humerus G.236 and complete right metatarsal G.067/959 from level 13; complete right metacarpal F.213 from level 21; and complete right metatarsal D.155 from level 22. These are smaller than one would expect limb bones of *T. s. maryanus* to be. The distal half of a left femur G.313 and associated incomplete proximal end of a right metacarpal G.311 from level 22, and a complete left metacarpal G.258 from level 13, are from a larger kudu-sized species, as is the complete femur 5400 from DK I.

Tribe BOVINI. A left mandible with only an unworn  $M_3$  preserved, C.1045 + 1065 + 1186, comes from level 22 of this site. It is presumably conspecific with the bovine at other Bed I sites.

Tribe REDUNCINI. A left maxilla B.46, right mandible D.41, left mandibles B.23 and D.122 and associated right and left mandibles G.388 all come from level 22 of this site. Two incomplete right mandibles, 067/1087 and 067/1091, are of unknown level. These dentitions are of a species of *Kobus* which is probably conspecific with that at FLKNN I, that is, *K. sigmoidalis*. As mentioned in the reduncine discussion, the mandible D.41 has a complete tooth row and may well have a shorter premolar row relative to molar row length than in examples of extant *K. ellipsiprymnus*.

Several isolated reduncine teeth are of *Kobus* rather than *Redunca* size and these can probably also be referred to *K. sigmoidalis*. They are right upper molar G.067/905 and right lower molar G.067/913 from level 13; right F.162, and left lower molars F.156 and G.067/915 from level 15; right lower molars B.566, B.661 and B.067/907, left lower molars B.382 and B.067/906, right  $M_3$ s B.70 and B.067/1082, left  $M_3$  B.449 and right  $P_4$  Balk 134 from level 22. Right and left upper molars numbered 067/4621, deciduous left  $P^2$ – $P^4$  (separate teeth) 067/879, and two right upper molars, two right lower molars, a left lower molar, four right lower premolars, two left lower premolars, a deciduous right  $P^3$ , and two deciduous left  $P^4$ s all numbered 067/921 are of unknown level.

There are some reduncine limb bones at this site, which are about the size of those of the living waterbuck and show the same differences from living reduncines as given in the FLKNN I account. It seems likely that they are all *K. sigmoidalis*. They are as follows.

Proximal end right metacarpal G.197 from level 10; distal ends left humeri G.234 and G.235, proximal end left radius F.220, proximal end left metacarpal G.255 and proximal end right metatarsal C.067/949 from level 13; proximal end right radius F.153, proximal end right metacarpal G.067/964, distal ends left tibiae F.140, D.167 and D.067/970 and proximal ends left metatarsals G.067/932 and D.067/935 from level 15; distal ends right humeri Balk 231 and C.835, distal end left humerus C.1043, proximal end right radius B.59 with right ulna B.60, proximal end right radius B.580 with right ulna B.579, proximal end left metacarpal B.274 + 277, associated distal end left humerus E.95, proximal end left radius E.96 and left ulna E.94, associated complete right humerus C.1092, complete right radius C.1094 and complete right metacarpal C.1095, distal end right tibia B.478, distal end left femur B.20 and proximal ends right metatarsals G.364 and 067/931 from level 22; distal end right tibia K.067/979 from an unknown level above level 22.

The distal end of right humerus B.122, proximal end of right femur B.104 and distal end of right femur A.22, all from level 22, are most probably reduncine and would be of the same species. A complete left metatarsal C.1085 from level 22 is identified as reduncine or hippotragine.

Tribe HIPPOTRAGINI. A species of *Oryx* is represented by a left horn core with part of the frontal and orbital rim, G.390 (Leakey 1965 : 51; pl. 62). The specimen came from level 22 and is only the second record of this genus at Olduvai.

A left mandible G.067/1097 with unworn  $P_4$ – $M_3$  preserved, part of a right lower molar 067/921 and a right  $M_3$  G.067/897 represent a species of *Hippotragus*. The finds are from level 13 and could be from the same individual. The specimens are referred to *H. gigas*.

A deciduous left  $P_4$  067/921 of unknown level is probably hippotragine.

Tribe ALCELAPHINI. *Parmularius altidens* is represented by a right horn core G.233 + 235 P.P.R.3,



part of a left horn core G.252 and part of a right horn core C.067/1078 from level 13, part of a horn core G.067/1080 from level 15, a frontlet with nearly complete horn cores Balk 126+199 (Leakey 1965 : 58; pl. 72) and a left horn core with the orbital rim preserved F.206 P.P.F.7 from level 22. The horn cores of the last two fossils are long, with the lower parts straight and backward curvature limited to the upper parts. There is a fairly large medial swelling at the base, above which the divergence increases. The horn core figured by Leakey (1965 : pl. 74) is not F.206 as stated but left horn core FLKN I 1410 of the same species. The base of a right horn core G.232 from level 13 is probably *P. altidens*.

A number of partial mandibles and isolated teeth are assigned to *P. altidens*. These are as follows.

Part of a left  $M_3$  D.543 from level 7; right mandible G.067/1098 from level 12; right upper molar C.067/920, left upper molar C.067/891 and unworn left  $M_3$  G.067/892 from level 13; right mandibles F.157 and D.067/1094, right upper molars F.163 and F.223, left upper molar D.067/910, right lower molar F.067/916, left lower molars F.159, C.160 and G.067/911 and right  $P_4$  F.124 from level 15; right mandibles D.42, G.361 and C.857, partial left mandibles E.129 and B.347, right upper molars Balk 140, Balk 147, MS 067/912 and 067/917, left upper molars C.1046, B.067/898, MS 067/920 and B.067/4551, right lower molar D.111, left lower molars E.52 and B.067/900, two left lower molars and left  $M_3$  numbered F.247, immature left mandible D.85, and deciduous left  $P_4$  C.932 from level 22. An immature left mandible K.067/1099 is from an unknown level above level 22.

Mandible G.361 would have had a  $P_2$  in life, in mandible G.067/1098 this is uncertain, but in mandibles D.42 and E.129 there is no alveolus in the jaw for a  $P_2$  so that  $P_2$  was missing at the time the animals died. The rounding of the lateral lobes of lower molars may be less developed than in *P. altidens* at later FLKN I, but this is not certain.

Several alcelaphine limb bones at this site are assigned to *P. altidens*. These are as follows.

Proximal and distal ends of a left tibia D.540 and D.541 and distal end left femur D.539 from level 7; distal end right humerus C.067/811, proximal end left metacarpal C.067/965, distal end metacarpal C.067/962, distal end left tibia C.067/972, distal end right femur C.067/817, proximal end left metatarsal C.067/934 and distal ends metatarsals C.067/951 and C.067/952 from level 13; distal end right humerus G.067/807, proximal ends right radii F.152 (with right ulna F.166) and G.067/985, proximal end left radius G.067/990, distal end right radius F.155, complete right metacarpal G.520, proximal end left metacarpal F.149, distal ends metacarpals G.519 and D.067/953, complete right tibia F.138+141, distal end left tibia F.139, complete right metatarsal Balk 067/929 and proximal end left metatarsal F.145 from level 15; distal ends left humeri E.92, E.103 and F.216, proximal end left radius Balk 179, distal ends right radii B.674 and immature MS 067/984, associated distal end left humerus K.3 and proximal end left radius K.1, proximal end right tibia F.193, proximal end left femur C.1001, and proximal end right metatarsal C.067/4547 from level 22. Proximal end right metatarsal K.067/945 is from an unknown level above level 22.

A left maxilla B.067/1093 with  $P^4$ - $M^3$  preserved differs from *P. altidens* dentitions in its larger size and more complicated central cavities. Its less rounded medial lobes may be a feature of being in early wear. A left mandible B.17 with  $P_4$ - $M_3$  is also larger than *P. altidens*. Both pieces are from level 22 and may well represent *Connochaetes* at this site.

A few limb bones are larger than those of *P. altidens* and are possibly conspecific with the larger dentitions. These are proximal end left radius C.067/987 from level 13; distal end right radius G.516 and proximal end left metatarsal F.146 from level 15; distal end right humerus C.895 and distal end left tibia D.106 from level 22; and possibly the associated distal end right humerus D.537 and proximal end right radius D.538 from level 7.

A complete left radius K.067/986 from an unknown level above level 22 is larger and longer than the radii FLKNN I 578 and FLKN I 181+926 and could be conspecific with the very large alcelaphine *Megalotragus ? kattwinkeli* at DK I.

Tribe ANTILOPINI. *Antidorcas recki* is represented by an associated pair of horn cores, right G.229 and left G.230, from level 13 (Leakey 1965 : 65(g); Gentry 1966 : 57). Both have the midfrontal suture, part of the orbit and supraorbital pit preserved.

A number of mandibles and isolated teeth are referred to this species. These are left mandible G.067/1090 and fragmentary right mandible G.515 from level 15; right mandibles B.119, G.154, G.294 and G.323, left mandibles D.35, D.65 and B.492, three right upper molars and two left



upper molars all D.91, two right lower molars Balk 135, right M<sub>3</sub> B.127, left M<sub>3</sub>s B.125 and Balk 180, a right and left upper molar from the Balk without number and an immature left mandible B.188 from level 22. Four right upper molars, a left upper molar and two right lower molars, all numbered 067/899, are from unknown levels. On the M<sub>3</sub>s the talonid is very well developed, as in the similar-sized living *Gazella thomsoni*, and in some it approaches the size of the other two lobes. P<sub>2</sub> is present on mandible B.119 and on G.067/1090 there is an alveolus for a P<sub>2</sub>, but as Gentry (1966 : 61; pl. 2B) has noted, mandibles D.65 and G.154 have very reduced P<sub>2</sub>s and in G.294 P<sub>2</sub> was absent altogether as there is no alveolus in the jaw for it. The presence or absence of P<sub>2</sub> on mandible B.492 is uncertain.

Several limb bones are antilopine and probably all can be assigned to *A. recki*. These are as follows.

Distal end metatarsal D.542 from level 7; proximal end right metacarpal D.545 and proximal end right femur G.188 from level 10; distal end metacarpal C.067/937, proximal end right tibia C.067/971, distal ends right tibiae G.25, C.067/967 and C.067/977 and distal ends metatarsals F.219, G.253 and F.067/944 from level 13; proximal end right radius F.154, right ulna G.523, proximal end right metacarpal G.509, distal ends metacarpals G.517 and G.067/961, distal ends left tibiae G.510 and Balk 067/967, distal end left femur F.150 and proximal end left metatarsal F.147 from level 15; proximal end right humerus D.81, proximal end left humerus D.56, distal ends right humeri B.75 and Balk 120, distal end left humerus 499, associated distal end right humerus B.135 and proximal end right radius (with ulna) B.136, associated distal end left humerus C.1181, proximal end left radius C.1177 and left ulna C.1176, proximal ends left radii D.100 (with ulna) and Balk 119, part of a right ulna B.40, complete left metacarpal D.133, proximal ends left metacarpals B.166 and one without number, distal ends metacarpals B.387 and MS 067/954, complete right tibia K.9, complete left tibia F.161, part of shaft at proximal end right tibia D.104, proximal ends left tibiae D.36, D.69 and E.115, distal ends right tibiae B.364, B.380 and B.067/978, almost complete left femur F.220, distal end right femur MS 067/818, complete right metatarsal K.10, complete left metatarsal F.219, proximal ends right metatarsals B.140, G.358 and C.1054, proximal end left metatarsal C.067/942 and distal end metatarsal D.26+124 from level 22. Proximal end left femur K.067/814, proximal end right metatarsal K.067/930, and distal end metatarsal K.067/950 are from an unknown level above level 22.

A left M<sub>3</sub> C.067/901, proximal end left humerus B.139, distal end metacarpal D.129 and complete right metatarsal D.129, all from level 22, are rather larger than the other antilopine remains.

SUMMARY. At FLK I the association between *Parmularius altidens* and *Antidorcas recki* reappears, but tragelaphine and reduncine fossils are still numerous. The oryx horn core is a notable occurrence. The species list for the site is:

*Tragelaphus strepsiceros maryanus*

*Tragelaphus* sp.

*Syncerus acoelotus*

*Kobus sigmoidalis*

*Oryx* sp.

*Hippotragus gigas*

*Megalotragus* ? *kattwinkeli*

? *Connochaetes* sp.

*Parmularius altidens*

*Antidorcas recki*

(Also large teeth and limb bones perhaps of a second antilopine species)

The numbers of bovid bones in levels 13, 15 and 22 are shown in Table 3.

#### FLKN I

Site (40) Geologic number 45

FLKN is situated on the far side of the ridge which lies to the north of FLK. There are more than 20 ft (6.0 m) of deposit in lower and middle Bed II and the upper part of Bed I. As at FLKNN I, erosion has removed Beds III and IV and the upper part of Bed II so that later deposits rest



Table 3 Numbers of bovid bones at FLK I

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
Level 13								
<i>Tragelaphus s. maryanus</i>	-	3 (2)	4 (2)	5	-	12	2	1
Smaller tragelaphine sp.	-	-	-	-	2	2	1*	-
Larger tragelaphine sp.	-	-	-	-	1	1	1*	-
<i>Kobus sigmodontalis</i>	-	-	-	2	5	7	2	-
<i>Hippotragus gigas</i>	-	-	1	2	-	3	1	-
? <i>Connochaetes</i> sp.	-	-	-	-	1	1	1	-
<i>Parmularius altidens</i>	3	-	-	3	8	14	2	-
<i>Antidorcas recki</i>	2	-	-	-	8	10	3	-
Level 15								
<i>Tragelaphus s. maryanus</i>	-	-	-	2	-	2	1	-
<i>Kobus sigmodontalis</i>	-	-	-	3	7	10	3	-
? <i>Connochaetes</i> sp.	-	-	-	-	2	2	1	-
<i>Parmularius altidens</i>	1	-	2	8	14	25	3	-
<i>Antidorcas recki</i>	-	-	2	-	9	11	2	-
Level 22								
Smaller tragelaphine sp.	-	-	-	-	1	1	1*	-
Larger tragelaphine sp.	-	-	-	-	2	2	1*	-
Tragelaphini total	-	-	-	-	3	3	-	-
<i>Syncerus aequalis</i>	-	-	1	-	-	1	1	-
<i>Kobus sigmodontalis</i>	-	1	5	9	18	29	4	-
<i>Oryx</i> sp.	1	-	-	-	-	1	1	-
? <i>Connochaetes</i> sp.	-	1	-	-	2	4	1	-
<i>Parmularius altidens</i>	2	-	6 (1)	15 (1)	11 (1)	34	4	2
Alcelaphini total	2	1	7 (1)	15 (1)	13 (1)	38	5	2
<i>Antidorcas recki</i>	-	-	8 (1)	12	38	58	5	1
Larger antelope sp.	-	-	-	1	3	4	1	-
Antilopini total	-	-	8 (1)	13	41	62	6	1

\* One of the two tragelaphine species represented by limb bones would be *Tragelaphus strepsiceros maryanus*.



unconformably on the eroded surface of Bed II within 13 ft (3.9 m) of the I-II contact. The sequence of deposits, from those of Bed II downwards, is as follows.

Bed II. (a) A grey-brown silty clay of maximum depth of  $6\frac{1}{2}$  ft (1.95 m), without remains.

(b) A sandy conglomerate 10 ft (3.0 m) above the base of Bed II. The horizon can be traced through other deposits west to the fourth fault. At HWK East II the deposit (there forming level 4) is 2 ft (60 cm) thick; here at FLKN II it is only 1 ft (30 cm) thick. It yielded a number of artifacts, many of which are made from chert, and some bones.

(c) Six levels of clay and limestone of varying thicknesses down to the underlying Tuff IF. The lowest level from which artifacts and faunal remains were recovered from Bed II at FLKN was a clay horizon which contained many root casts,  $4\frac{1}{2}$  ft (1.35 m) thick. Artifacts and bones were sparsely scattered through the deposit. This level can be correlated with level 2 at HWK East II.

Bed I. (a) Tuff IF.

(b) Levels 1+2+3, the top levels of FLKN I. A single horizon, 2-3 ft (60-90 cm) thick, of grey-brown silty clay, arbitrarily subdivided into levels during excavation. Remains were especially concentrated in levels 1 and 3, indicating two periods of hominid occupation. A small amount of material was found in level 2 but was probably derived from level 1. Material from the upper occupation level is therefore given as from levels 1-2, that from the lower as from level 3, and that of unknown origin (excavated before 1961) as levels 1-3.

(c) Level 4. A dark brown silty clay, 3 or 4 ins (7.5 or 10.25 cm) to  $1\frac{1}{2}$  ft (45 cm) thick. In some places it lensed out entirely so that level 3 rested directly on level 5.

(d) Level 5. A green-yellow clay with one or more ferruginous bands and several thin horizontal seams of fine-grained white tuff near the base. Artifacts and bones were more plentiful at the top of the deposit than in the lower part, though the surface did not seem so weathered as on the occupation floors of FLKNN I and FLK I.

(e) Level 6. A dark grey-brown silty clay with white streaks,  $1\frac{1}{2}$  ft (45 cm) thick. The deposit is mostly overlain by a massive layer of limestone, several feet thick, so only a part has been excavated. An elephant had been butchered at this level.

All the levels of FLKN I were contorted and faulted on a local scale, with displacements of a few inches, and all yielded cultural and faunal remains. The site was excavated by a series of trenches; a trial trench and trenches I and II were dug in 1960, trench III in 1961 and trenches IV and V in 1962. The lowest part of the site was 5 ft (1.5 m) below Tuff IF and thus 15 ft (4.5 m) above level 22 (the occupation or '*Zinjanthropus*' level) of FLK I.

Tribe TRAGELAPHINI. This tribe is represented by a right mandible 7634 from levels 1-2; associated incomplete maxillae right 6061 and left 6060, left upper molar 067/21, right lower molar 6170 and right and left upper premolars 067/368 from level 3; left mandible 882 from levels 1-3; right mandible 1182, right upper molar 067/182 and left upper molar 6225 from level 4; immature left mandible 7846 from level 5. The teeth are close to the size of the greater kudu and these dentitions are presumably *Tragelaphus strepsiceros maryanus*. The mandible 7634 is fairly complete and has a tooth row and horizontal ramus the same size as in mandibles DK I 3001 and FLK I 067/1100. An unworn left  $P_3$  from level 1-3, and an unworn left upper molar 067/170, right upper premolar 067/238, left upper premolar 067/228, right lower premolar 067/237 and deciduous right upper premolar 067/4774, all from level 6, are more doubtfully assigned to this tribe.

The proximal end of right radius with ulna 7686 and proximal end left radius 8379 from levels 1-2; proximal end left metacarpal 825 from levels 1-3; complete left metacarpal 9269 from level 4; distal end left humerus 9292, complete left radius 9290, proximal end left radius with ulna 10199, complete left metacarpal 067/1073 and complete right metatarsal 7333 from level 5; and associated complete left humerus 8248, complete left radius 8275, left ulna 8249 and proximal end left metacarpal 8250 from level 6 are all assigned to the Tragelaphini but are rather small to be *T. s. maryanus*. The proximal ends of radii 7686 and 8379 have projecting anterior points on the lateral



facets, unlike the other tragelaphine radii. The distal end of a right femur 10227 from level 5 is relatively smaller than the other bones.

**Tribe BOVINI.** Ten isolated teeth belong in this tribe. These are associated left  $P_3$ ,  $P_4$ ,  $M_1$  and four incisors 1567, and left lower molar 171 from levels 1–2; left  $P^2$  067/226 and right  $P^3$  067/227 from level 6. Their occlusal morphology is about as simple as that of *Pelorovis oldowayensis* but they are smaller than *P. oldowayensis* or buffalo species. On the  $P_4$  1567 the paraconid and metaconid are growing towards one another, but there is no actual fusion to form a complete medial wall anteriorly. In this respect the tooth is less advanced than in *P. oldowayensis* or living *Syncerus caffer*.

By its size and low distal condyles the distal end of a metacarpal 437 from levels 1–2 is bovine and probably belongs to the same species as the teeth.

**Tribe REDUNCINI.** Deciduous left  $P^3$  and  $P^4$  067/336 from level 3 are reduncine and of a size appropriate for *Kobus sigmoidalis*, although attribution to *K. ellipsiprymnus* is possible for such pieces as noted above (p. 327). A right lower molar 067/185 from level 4 is smaller and probably of *Redunca*.

**Tribe HIPPOTRAGINI.** On the evidence of left lower molar 067/4778 from level 6 and complete right metacarpal 5152 from level 4 a member of this tribe is present. A right  $M_3$  and part of another lower molar 7122 from level 4, complete left tibia 7207 from levels 1–2, proximal end left tibia 7797 and proximal end right metatarsal 7097 from level 3, and immature left radius 1800 and complete left tibia 1450 + 1459 from level 5 are possibly also hippotragine. The proximal end of left femur 896 from levels 1–3 is identified as belonging in this tribe or possibly in the Bovini.

**Tribe ALCELAPHINI.** This tribe is represented by 39 horn cores and skull pieces, 31 adult and 14 immature partial dentitions and many teeth and limb bones. Thirty four of the horn cores and skull pieces are of *Parmularius altidens* and the majority of the alcelaphine remains can confidently be referred to this species. The cranial pieces of *P. altidens* are as follows.

An associated pair of complete horn cores with most of a crushed cranium and the parietal boss 8065, part of a cranium consisting of the parietals with parietal boss, the occipitals and basioccipital 7465, an immature frontlet with the basal halves of both horn cores 1315 P.P.F.15 (Leakey 1965 : 58; pl. 73), a parietal boss 067/9 and a possibly immature horn core 637 from levels 1–2; the base of a right horn core with the midfrontal suture and part of the orbital rim 1166 P.P.R.8, an incomplete frontlet with partial horn cores 1392, complete left horn core 1410 P.P.R.6 (Leakey 1965 : pl. 74 which is not FLK I 206), complete right horn 5123, parietal boss 6174, frontlet with both horn core bases and the parietal boss 10130, and a frontlet with the parietal boss, complete left horn core and base of the right 10160 from level 3; a partial cranium consisting of the parietal with parietal boss and bases of both horn cores, the occipital, occipital condyles and paraoccipital processes 178 + 979 P.P.R.11 (Leakey 1965 : 59(e)), left horn core 067/267, and parietal bosses 858 and 067/244 from levels 1–3; the basal half of a right horn core with part of the orbital rim 1775, base of a left horn core 1777, a partial frontlet with the right horn core 8129, and parietal bosses 067/245 and 067/247 from level 4; a frontlet with complete horn cores 9401, a frontlet with horn core bases and parietal boss 10220, base of a right horn core 10279, base of a horn core 7814, part of a horn core 067/268, and parietal bosses 7869 and 067/253 from level 5.

The horn cores at this site differ from the complete specimens known from FLK I in having a smaller basal swelling and the tips still less backwardly curved. There is a certain amount of variability among the horn cores; 1410 P.P.R.6 and 9401 are rather long, while 1410 P.P.R.6, 5123 and 10160 show little backward curvature in side view. Parts of horn cores 485 and 9108 from levels 1–2, 7516 from level 3, 695 and 990 from levels 1–3, and 7329 and 9371 from level 5 probably belong to *P. altidens*.

The more complete dentitions assigned to *P. altidens* are as follows.

Left maxillae 1037 and 1604, right mandibles 208, 1109, and 8045 and left mandible 1099 from levels 1–2; left maxilla 1155 and associated right and left maxillae 1136, right mandibles 1406, 1728, 5167, 8115 and 10144 from level 3; right mandibles 208, 211, 340 and 824 + 841, and left mandibles 21, 38 and 265 from levels 1–3; right mandible 5175, left mandibles 1179 and 067/184 and associated right and left mandibles 1198 from level 4; right maxillae 9383 and 067/79 and left maxilla 10209 from level 5. The above dentitions are all adult. There are also a number that are immature. These are right mandible



7685 and left mandible 1589 from levels 1–2; right maxilla 5008, left maxilla 1138, and right mandibles 6111, 7733 and 7775 from level 3; left maxilla 430, right mandible 706 and left mandible 405 from levels 1–3; right mandible 1746 from level 4; right mandibles 6269 and 10212 from level 5; left mandible 9476 from level 6.

These dentitions are all of *P. altidens* size and are slightly smaller than the living hartebeest. Mandible 1109 lacks an alveolus in the jaw for a  $P_2$  so that  $P_2$  was missing in life, and  $P_2$  was probably also missing in mandible 265. The presence or absence of  $P_2$  in mandible 1406 is uncertain, but in mandibles 38, 208, 1198 (right) and probably 1728  $P_2$  or its alveolus is still present. Deciduous  $P_2$  is present on the immature mandibles 1746, 7775, 9476 and 10212. A number of isolated alcelaphine teeth also belong to *P. altidens*.

Only the complete limb bones of *P. altidens* are listed here although there are many other, more fragmentary, remains at this site.

The limb bones are right humeri 7070 and 067/515, left humerus 260, right radii 2 + 57, 688 and 067/4741, left radius 1046, right metacarpals 51, 404, 1291 and 8836, left metacarpals 1053 and 8044, left tibiae 7074 and 7084 and right metatarsals 88, 99 + 100, 1265, 1266 and 1347 from levels 1–2; left radius 7779 + 7780, right metatarsals 5002 + 5019 and 6191 and left metatarsals 1120, 6201 and 10168 from level 3; right metacarpal 749, left metacarpals 639, 965 and 973, right metatarsal 067/1076 and left metatarsals 657 and 811 from levels 1–3; right metacarpals 1776 and 5107 and left metatarsals 8128 and 8141 from level 4; right metacarpals 7853 and 8157, left metacarpals 5195 and 8196, right metatarsal 5135 and left metatarsals 7867 and 9342 from level 5; and left radius 8247 and left metacarpal 10440 from level 6.

A cranium of *Connochaetes* sp. with complete horn cores 7154 comes from level 5. The horn cores are dorsoventrally compressed but less so than in living male wildebeests, and there is less tendency for a keel to be developed along the anterior edge. The horn core insertions are wide apart and lie between the orbits and the occipital top instead of at the occipital top. As the horn cores pass outwards they bend less downwards and slightly backwards, and the tips turn upwards but less inwards than in most *C. taurinus*. There are transverse ridges on the middle part of the top surface of the horn cores. The basioccipital is as found in the living species. A few teeth were found in association with the cranium. These are two left upper molars, a right upper molar and right upper premolar, a damaged upper premolar and an incisor or incisiform canine. They correspond in size with the smaller teeth of the Bed II size group (i), which are supposedly of *Connochaetes*, and are smaller than the very large teeth from DK I which are taken to belong to *Megalotragus*.

A partial left maxilla 9382 and immature left maxilla 067/240 from level 5, and an incomplete left mandible 1431 from level 4, are larger than dentitions of *Parmularius altidens* and are possibly of *Connochaetes*.

A right metacarpal 5107 from level 4 is alcelaphine but not of *Parmularius altidens* since it is shorter and the distal condyles are too low and wide in anterior view; its shortness contrasts with the very long radius and metapodials of *Megalotragus ? kattwinkeli* at DK I, and it could well belong to *Connochaetes*.

A complete left horn core, 5123 from level 3, is of *Beatragus antiquus*. It is longer and thicker than horn cores on a Recent skull of *B. hunteri* with a sheath length of 600 mm and a horn core length of 480 mm. It has marks made by the grubs of a moth allied to or identical with *Ceratophaga vastella*. The basal half of a right horn core of *B. antiquus* 7132 comes from the surface of level 5.

A few alcelaphine limb bones are larger than those of *P. altidens*. These are the distal end of immature right radius 393 + 345, incomplete proximal end left femur 9058, distal end right femur 8704 and proximal end right metatarsal 7042 from levels 1–2; distal end right humerus 5036 and distal ends right tibiae 7101 and 9180 from level 3; associated distal end right humerus 927 and complete right radius 181 + 926 from levels 1–3; complete left metatarsal 8127 and proximal end right metatarsal 5087 from level 4; proximal end right radius 7844 and proximal end left radius 1225 from level 5. Probably none of these limb bones are from a species so large as the largest alcelaphine at DK I. It seems likely that they belong to *Connochaetes* sp. and *Beatragus antiquus*.

A horn core 7884 from level 6 and a horn core with a crushed braincase 5196 P.P.R.10 from level 5 could be of a small alcelaphine. The horn cores are very compressed, long and spiralled and have not been found at any other site. They are described more fully on p. 418 as Alcelaphini



sp. 4. Two mandibles with complete horizontal and vertical rami but both lacking teeth, right 1293 from levels 1–2 and left 137 from levels 1–3, could perhaps be conspecific although there is no association with the horn cores. They agree well with two other Olduvai mandibles, left 1941 F.109 from the surface of Bed I and left 1941 F.102 from the surface of Bed II, which have more complete tooth rows.

Some small limb bones from levels 1–2 are probably small Alcelaphini rather than large Antilopini. These are proximal end right radius with ulna 84, distal end left radius 8778, proximal end right femur 8809 and proximal end left femur 233. Perhaps they are conspecific with the horn cores 7884 and 5196.

Tribe NEOTRAGINI. A pair of horn cores 10229 from level 5, with a small part of the frontal preserved, are tentatively placed in this tribe.

Tribe ANTILOPINI. *Antidorcas recki* is represented by a number of skull pieces. These are a frontlet with the bases of both horn cores 1039 (figured as Reduncini by Leakey 1965 : 47; pl. 53), frontlet with complete right horn core and base of the left 1307 (Leakey 1965 : 65(h)), base of right horn core with the frontal 1650, left horn core 7266 with associated maxillae and mandibles, right horn core with the midfrontal suture and supraorbital pit 8659 and base of a horn core 10008 from levels 1–2; left horn core with the midfrontal suture, top of the orbital rim and an unusually large supraorbital pit 1139 (Leakey 1965 : 65(g); Gentry 1966 : 104(g)) from level 3; the occipital and basioccipital region of a skull 067/257 from levels 1–3; crushed skull with both horn cores and maxillae 6334 (Leakey 1965 : 65(i); Gentry 1966 : 58; pl. 1B), left horn core with the midfrontal suture, top of the orbital rim and supraorbital pit 8194 with several associated limb bones, crushed skull with maxillae 067/466, complete right horn core 067/250 (Gentry 1966 : 78; pl. 7A) and parts of horn cores 6173 and 10284 from level 5.

Several dentitions, mostly incomplete, belong to this species. They are as follows.

Right maxilla 9055, left maxillae 7426 and one without number, right mandibles 7015 and 8532, left mandibles 8711, 067/400, 067/434, 067/453 and 067/462, and associated right 1045 and left 1044 mandibles from levels 1–2; right maxilla 618, left maxilla 1152, and right mandibles 6010 and 6044 from level 3; right maxilla 871, left maxillae 627 and 067/463, right mandibles 681, 935 and 067/26, and left mandibles 503, 914, 976 and 067/465 from levels 1–3; right mandible 5148 and left mandible 8136 from level 4; palate 7555, left maxillae 7564 and 10286, right mandibles 7332, 7554 and 9377, and left mandibles 1211 and 7873 from level 5. A left maxilla 067/464 is known only to be from levels 1–5. These are all adult dentitions. There are also a few immature dentitions. These are right maxilla 1281, left maxillae 1327 and 1511 and an associated pair of mandibles 1310 from levels 1–2; left mandible 9196 from level 3; left mandible 231 from levels 1–3; and left maxilla 6176 and right mandibles 7828 and 067/74 from level 5.

A  $P_2$  is present on mandible 9377, and on 6010, 7015, 7873 and 067/453 there is an alveolus for a  $P_2$  although the tooth itself is now missing. Mandible 976 has a very reduced  $P_2$  (Gentry 1966 : 61). The presence or absence of  $P_2$  on 8532 is uncertain. Deciduous  $P_2$ s are present on the immature mandibles 231, 1310 (right and left) and 7828, and there is an alveolus in the jaw for deciduous  $P_2$  on 067/74.

The pair of maxillae 7266, together with right 7284 and left 7266 mandibles of the same individual, which belong with the left horn core 7266 from levels 1–2 listed above, are of interest because the right maxilla provides the first nearly complete facial region of *A. recki* to occur in Bed I. From this specimen it can be seen that the face is larger than in males of living *Gazella thomsoni*. The preorbital fossa has an upper rim and more marked lower rim as in all Antilopini, and is as small in area as in *G. dorcas*. It is, however, less deep, and is also less deep than in the *A. recki* holotype skull. The fossa is probably larger than in the living springbok, but the face larger in size than in gazelles coupled with a small fossa are definitely resemblances to springbok. The mandibles would have had a  $P_2$  in life, but in both cases the tooth is now missing.

There are a number of isolated antilopine teeth which are assigned to *A. recki*, but they will not be listed here.

A complete right maxilla 1662 from levels 1–2 (Pl. 40, fig. 6; Gentry 1966 : 59; pl. 1C) and some isolated teeth are possibly large enough to represent a larger species of Antilopini in Bed I. The isolated teeth are a right upper molar 8594, a left upper molar without number, right lower



Table 4 Numbers of bovid bones at FLKN I

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
Levels 1 + 2 + 3								
<i>Tragelaphus s. malyanus</i>	-	2	2	4	-	8	2	-
Smaller tragelaphine sp.	-	-	-	-	4	4	-	-
<i>Syncerus acoelotus</i>	-	-	-	8	1	9	1	-
<i>Kobus sigm./ellipsiprymnus</i>	-	-	-	2 (2)	-	2	-	1
<i>Beatragus antiquus</i>	1	-	-	-	-	1	1	-
Larger alcelaphine sp.	-	-	-	-	9 (1)	9	2	1
<i>Parmularius altidens</i>	20 (2)	8 (3)	20 (6)	100 (5)	266 (9)	414	22	5
Alcelaphini sp. 4?	-	-	2	-	4	6	1	-
Alcelaphini total	21 (2)	8 (3)	22 (6)	100 (5)	279 (9)	430	25*	6
<i>Antidorcas recki</i>	8	13 (3)	24 (4)	57 (2)	191 (4)	293	18	5
Larger antilopine sp.	-	1	-	10	-	11	2	-
Antilopini total	8	14 (3)	24 (4)	67 (2)	191 (4)	304	18	5
? Caprinae sp.	-	-	-	-	3	3	1	-
Level 4								
<i>Tragelaphus s. malyanus</i>	-	-	1	2	-	3	1	-
Smaller tragelaphine sp.	-	-	-	-	1	1	-	-
<i>Kobus sigm./ellipsiprymnus</i>	-	-	-	2	-	2	1	-
<i>Redunca</i> sp.	-	-	-	1	-	1	1	-
Hippotragini sp.	-	-	-	-	1	1	1	-
<i>Connochaetes</i> sp.	-	-	1	-	1	2	1	-
Larger alcelaphine sp.	-	-	-	-	2	2	1	-
<i>Parmularius altidens</i>	5	-	6 (1)	17 (3)	37	65	5	1
Alcelaphini total	5	-	7 (1)	17 (3)	40	69	6†	1
<i>Antidorcas recki</i>	-	-	2	19	10 (1)	31	2	1

\* One of the two adult individuals represented by the larger alcelaphine limb bones could be the *Beatragus antiquus* and has been omitted.† The individual represented by the larger alcelaphine limb bones could be the same as the *Connochaetes* sp. and has therefore been omitted.



TABLE 4 (cont.)

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
Level 5								
<i>Tragelaphus s. meryanus</i>	-	-	1 (1)	-	-	1	-	1
Smaller tragelaphine sp.	-	-	-	-	7	7	2	-
<i>Connochaetes</i> sp.	1	2 (1)	-	6	-	9	2	1
<i>Beatragus antiquus</i>	1	-	-	-	-	1	1	-
Larger alcelaphine sp.	-	-	-	-	2	2	1	-
<i>Parmularius altidens</i>	9	3	2 (2)	15	27	56	5	1
Alcelaphini sp. 4	1	-	-	-	-	1	1	-
Alcelaphini total	12	5 (1)	2 (2)	21	29	69	7†	2
? Neotragini sp.	2	-	-	-	-	2	1	-
<i>Antidorcas recki</i>	6	8 (1)	7 (2)	80 (1)	69 (2)	170	14	2
? Caprinae sp.	-	-	-	-	1	1	1	-
Level 6								
Smaller tragelaphine sp.	-	-	-	-	4	4	1	-
<i>Syncerus acoelotus</i>	-	-	-	2	-	2	1	-
Hippotragini sp.	-	-	-	1	-	1	1	-
<i>Parmularius altidens</i>	-	-	1 (1)	10	12 (1)	23	3	1
Alcelaphini sp. 4	1	-	-	-	-	1	1	-
<i>Antidorcas recki</i>	-	-	-	12	11 (1)	23	2	1

† The individual represented by the larger alcelaphine limb bones could be the same as the *Connochaetes* sp. or *Beatragus antiquus* and has been omitted from this total.



molar 8712 and right M<sub>3</sub> 067/427 from levels 1–2; right upper molars 121 and 067/34, left upper molars 122 and 067/24 and right P<sup>3</sup> and P<sup>4</sup> 183 from levels 1–3.

Several small limb bones found in level 5 were associated with the horn core 8194. These are complete left humerus 8191, distal end left humerus 8186A, complete right radius 8179, proximal half left radius with ulna 8188, complete left metacarpal 8192, distal half metacarpal 8193, complete right tibia 8180, head of left femur 8186, complete right metatarsal 8178, complete left metatarsal 8183, right scapula 8181, left scapula 8184, right astragalus 8187 and some other foot bones. Since there are parts of two left humeri more than one individual is represented.

Apart from the associated collection, only the complete antilopine limb bones at this site are listed, as follows.

Right humerus 7276, left humerus 7213, associated right 1010 + 1041 and left 1300 radii, left radius 1605 with some associated footbones, right metacarpals 7029, 7368, 7448 and 10034, left metacarpals 1273, 1306, 7064, 7406 and 7671, associated right 1246 and left 1284 tibiae, and right metatarsals 7017, 7371 and 8737 from levels 1–2; left radius with ulna 6049, right metacarpals 7781 and 067/1168, left metacarpals 6050, 7782 and 7784, right metatarsal 6198, and left metatarsal 5000 from level 3; associated right 50 and left 70 radii with ulnae, left radii 666 (with ulna), 682 and 730, left metacarpals 655, 762 and 764, left tibia 157, right metatarsal 464 and left metatarsals 3, 179 and 530 from levels 1–3; right humerus 10263, left humerus 8191, right radii 8179 and 067/4787, right metacarpals 1450 and 7540, left metacarpal 8192, right tibia 8180, right metatarsals 1454, 1758, 5194, 8178, 9369, 10230 and 10232, and left metatarsals 8183, 9372, 10288 and 10289A from level 5; right femur 8256, and associated left tibia 8264 and right 8263 and left 8259 metatarsals from level 6.

These bones are presumably all of *A. recki*, and show considerable variation in size (Pl. 39, fig. 3). The largest limb bones referred to the Antilopini, for example the proximal end of left femur 1027 from levels 1–2, are still slightly smaller than the small alcelaphine limb bones (p. 19) found at this site.

The proximal ends of two radii from levels 1–2, right 7725 and left 7066, are of normal antilopine size but possibly belong to a very small alcelaphine because the rear part of the lateral facet is far forwards.

Subfamily ? CAPRINAE. A right metatarsal 067/1009 from level 3, a left metatarsal 068/6665 from levels 1–3, and a left metacarpal 9394 from level 5 are complete and very short. We can only suggest that they may represent some species of caprine. The distal end of a left tibia 7243 from levels 1–2 may belong with the metapodials.

SUMMARY. Site FLKN I is all but overwhelmed by *Parmularius altidens* and *Antidorcas recki*, the first being more abundant in levels 1–4 and the second in levels 5 and 6. There is also evidence of *Connochaetes* sp. and *Beatragus antiquus*, but *Megalotragus* has not been found. A few tragelaphine fossils are present, but reduncines and hippotragines are almost absent. A *Redunca*-sized tooth occurs.

The species list for the site is:

*Tragelaphus strepsiceros maryanus* (may include the rather small limb bones)

*Syncerus acoelotus*

*Kobus sigmoidalis/ellipsiprymnus*

*Redunca* sp.

Hippotragini sp.

*Connochaetes* sp.

*Beatragus antiquus*

*Parmularius altidens*

Alcelaphini sp. 4

? Neotragini sp.

*Antidorcas recki*

(Also large teeth perhaps of a second antilopine species)

? Caprinae sp.

The numbers of bovid bones in levels 1–6 are shown in Table 4.



HWK I  
Site (46)      Geologic locality 44

Tribe ALCELAPHINI. A well-preserved left side of a braincase with almost complete left horn core 068/6650 was found at this site in 1962 (Pl. 20, fig. 1). It is marked 'In situ top of Bed I near *Deinotherium* skeleton'. It belongs to *Parmularius altidens*. The mid-dorsal part of the braincase is unfortunately not preserved to show the condition of the parietal boss. The horn core is obliquely inserted and bends very slightly backwards as in advanced *P. altidens* and in *P. angusticornis*.

Other HWK sites are discussed below (p. 24).

Other remains from Bed I

Apart from material collected before the Second World War and mostly housed in London, some bovid remains from Bed I have been found later as isolated occurrences or at archaeological sites with little fauna.

Tribe HIPOTRAGINI. The female paratype cranium of *Hippotragus gigas*, 1957.56 P.P.T.3, came from VEK at the top of Bed I.

Tribe ALCELAPHINI. Part of a right horn core of *Beatragus antiquus* was found at MJTK in 1963. The base of a left horn core 1959.129 of *Aepyceros* was found at THC at a horizon equivalent to DK I. The horn core is marked 'MTK I'. Impala horn cores from BK II and the surface of SHK II have been identified as *A. melampus*, and the THC horn core cannot be separated from them at species level. However, it has yet to be established whether the impala at this level is the same as the living species.

Tribe ANTILOPINI. A right horn core THC I 068/6656 of *Antidorcas recki* was a surface find in 1962. The midfrontal suture, supraorbital pit and part of the orbital rim are preserved.

**Sites of uncertain stratigraphic position within Beds I and II**

FLKN Ostrich Site  
Site (39)

This site is of uncertain stratigraphic position. At present it is thought to be a Bed II deposit which has slumped into Bed I, or possibly it was originally Bed I. It has yielded some artifacts, ostrich and crocodile remains and fragmentary bovids.

Tribe TRAGELAPHINI. An immature left mandible with deciduous P<sub>4</sub>, M<sub>1</sub> and M<sub>2</sub> 342, part of a right upper molar 288, left lower molar 350, part of a lower molar 287, right P<sub>4</sub> 312, left P<sub>4</sub> 311 and right P<sub>3</sub> 346 belong in this tribe.

Tribe HIPOTRAGINI. A right upper molar 355 and a right M<sub>3</sub> 354 are both hippotragine.

Tribe REDUNCINI. A right upper molar 290 probably belongs in this tribe and is of the size of the *Kobus sigmoidalis/ellipsiprymnus* lineage.

Tribe ALCELAPHINI. A mandible 067/243 with M<sub>1</sub> to erupting M<sub>3</sub> and erupting P<sub>3</sub> and P<sub>4</sub> lacks an alveolus in the jaw for a P<sub>2</sub>. Some isolated teeth also belong in this tribe. These are right upper molars 291 and 292, left upper molars 356 and 067/175, part of upper molar 289, parts of lower molars 351 and one without number, parts of right M<sub>3</sub>s 294 and 298, left M<sub>3</sub>s 248 and 297, part of left M<sub>3</sub> 290 and right lower premolar 309. They are all of medium, not large, size.

A complete left metacarpal 275 and proximal end of a right radius are the size of *Connochaetes* or *Megalotragus*. The distal end of a left tibia 219 is rather small for *Parmularius altidens*.

Tribe ANTILOPINI. A right lower molar 306 and left lower molars 352 and 369 belong in this tribe. A complete right metacarpal 276, distal end of a metacarpal 365, damaged distal end of a metacarpal 366, distal end of a metatarsal 277 and distal end of a left radius 304 are also antilopine.

KK  
Site (49)      Geologic locality 42

A number of fossils were recovered from KK in 1959. They came from Beds I and II, but it was



difficult to determine the levels in relation to the stratigraphic sequence elsewhere in the Gorge. M. D. Leakey (1971b : 287) concludes that the Bed II fossils originate from middle Bed II.

Tribe TRAGELAPHINI. A cranium 068/5813 of *Tragelaphus strepsiceros maryanus* is the most interesting bovid at KK, supposedly from Bed II. If it were from middle Bed II it would supplement the evidence of a tooth at HWK EE II that *T. s. maryanus* survived the end of lower Bed II. However, Leakey (1965 : 42) stated that it came from Bed I. It has been omitted from Table 12 (pp. 56-7).

Tribe BOVINI. A right astragalus, 211 from Bed II, is large enough to belong to *Pelorovis oldowayensis*.

Tribe ANTILOPINI. A horn core of *Antidorcas recki*, 309 from Bed I, has strong mediolateral compression, and agrees closely with two horn cores from HWK II and HWK EE II. *Gazella* sp. is represented by 310 from Bed I and 224 from Bed II. The former is a female horn core and the latter a horn core tip. Proximal and distal metatarsal pieces 248 and 249 from Bed I belong to a gazelle-sized species, but the proximal end shows some non-antilopine characters (Gentry 1966 : 73).

## Sites in Lower Bed II

### HWK Sites

The HWK gullies lie to the south of the confluence of the Main and Side Gorges and were first located in 1931. They originate from a saddle connecting two pinnacles capped with Beds III and IV which are known as the 'Castle' and the 'Tower'. HWK Main or Castle is a long, narrow gully running northwards from the saddle down to the floor of the Gorge; excavations in lower Bed II took place in 1959-60. HWK East is a gully beginning at the saddle and running mainly eastwards for  $\frac{1}{4}$  mile (0.4 km), then northwards to drain into the Main Gorge; excavations in lower Bed II and the lower part of middle Bed II were carried out in 1962-63. In the whole of the HWK area the Upper Member of Bed I is represented only by the upper series of deposits since the underlying basalt rises in irregular hummocks to within 20 ft (6.0 m) of Tuff IF. (For HWK I see above, p. 23.)

### HWK II

#### Site (46) Geologic locality 44

Tribe REDUNCINI. An almost complete right mandible 451 and a right  $M_3$  455 are of *Kobus sigmoidalis* size. The distal end of a reduncine left radius 414 is also comparable in size with the Bed I reduncine. Presumably they belong to the *K. sigmoidalis/ellipsiprymnus* lineage.

Tribe ALCELAPHINI. Three horn cores from this site belong to a species which may be related to *Parmularius rugosus*. These are a complete right horn core 067/5523, a complete left horn core 58 and the distal half of a right horn core 54.

A right mandible 477, right upper molar 454, left upper molars 452 and 551, right lower molar 456 and left lower molar 453 are alcelaphine. They are the size of Bed I *Parmularius altidens*.

A few limb bones are alcelaphine. The proximal ends of right radii 413 and 415, distal end right radius 411, distal end left radius 418, proximal end left metacarpal 426 and distal ends left tibiae 402, 403 and 405 are probably all *Parmularius*. The proximal end of right radius 412 and distal ends of right radii 409 and 410 are larger and probably *Megalotragus kattwinkeli* or *Connochaetes*.

Tribe ANTILOPINI. Four horn cores are of *Antidorcas recki*. These are a right horn core without the base 473, a complete left horn core with the frontal suture, orbital rim and supraorbital pit 568, the base of a left horn core with the frontal and supraorbital pit 471 and a complete right horn core 472 which is small, transversely compressed and possibly female (Gentry 1966 : 57, 64). 473 and 568 resemble Bed I *A. recki* horn cores.

A few limb bones are antilopine and probably belong to *A. recki*. These are distal end right humerus 408, proximal end right radius 417, distal end left radius 416 and distal end metatarsal 423.



HWK East II  
Site (48)      Geologic locality 43

Three parallel trenches were cut into the northern side of the HWK East gully and the sequence of deposits, from above downwards, was as follows.

- (a) A thick deposit of red-brown and grey tuffs with some minor clay horizons. The top was some 30 ft (9.0 m) above the base of Bed II.
- (b) Level 5. A reworked tuff, 1–2 ft (30–60 cm) thick, with lenses of unconsolidated coarse grey sand in hollows in the surface of the underlying sandy conglomerate. It yielded fragmentary faunal remains, including two teeth of *Pelorovis oldowayensis*.
- (c) Level 4. The sandy conglomerate, a chert-bearing horizon about 2 ft (60 cm) thick and its lower surface some 8 ft (2.4 m) above the base of Bed II. The same horizon occurs at FLKN II. It yielded a few rolled animal bones.
- (d) Level 3. A buff-grey reworked tuff, 9 ins–2 ft (23–60 cm) thick, with sparse animal remains. Antelope material from levels 3, 4 and 5 is treated as a single unit.
- (e) Tuff IIA, the Lemuta Member. The tuff is aeolian and very thin in this area, occurring in depressions on the surface of level 2.
- (f) Level 2. About 5½ ft (1.65 m) of light brown clay containing many root casts and a horizontal band of limestone nodules some 2 ft (60 cm) from the base. This level corresponds to the clay with root casts at FLKN II. Artifacts and faunal remains were scattered throughout the clay but were more concentrated near the base and midway. The bones were more plentiful and better preserved than in any other level at this site. The horizon was subdivided at the time of excavation but is now treated as a single unit.
- (g) A coarse-grained grey tuff with rootlets sometimes occurred between levels 1 and 2. It occurred also at FLKN I and elsewhere in the HWK gullies.
- (h) Level 1. A palaeosol on the surface of an irregular horizon of brown silty clay filling depressions in the surface of Tuff IF. This appeared to be a hominid occupation floor. Faunal remains were scarce and fragmentary. Tuff IF had undergone erosion in this area before the deposition of the clay.

HWK East II Levels 1 and 2

Tribe TRAGELAPHINI. The holotype of *Tragelaphus strepsiceros maryanus* was found in level 2 (M. D. Leakey, personal communication) of this site in 1959 (Leakey 1965 : 40; pls 40–41). This cranium is now in the National Museum of Tanzania in Dar es Salaam. A small piece of horn core, 4038 found in level 1 in 1963, has the keel and open spiral of the kudus and may also be *T. s. maryanus*. The spiral is anticlockwise, so the piece is probably from the right side.

A few teeth and limb bones are identified as tragelaphine. These are right upper molar 990, part of an upper molar 767, left lower molars 251b and 976, a  $P_3$  probably of the right side 067/1792, left  $P_3$  766, deciduous left  $P_3$  3819, deciduous left  $P_4$  3819b, distal end of a metacarpal 230 and distal end of a left femur 3778. These are all from level 2. The metacarpal distal end is of a size appropriate for *T. s. maryanus*, but the femur distal end may be too small.

Tribe BOVINI. Half a right upper molar 067/1812 from level 1, and a left upper premolar 067/1855 from level 2, are probably bovine and could belong to *Syncerus acoelotus*. They are too small for *Pelorovis oldowayensis*. The proximal end of a right metatarsal 2083 from level 1 is probably bovine.

Tribe REDUNCINI. Four isolated teeth from level 1 are reduncine and the size of *Kobus sigmoidalis*. These are left upper molar 4088, right lower molar 79, left lower molar 142 and part of right  $M_3$  136. Similar teeth in level 2 are a left upper molar 703 and a damaged deciduous left  $P_4$  3819. Presumably they are from the *K. sigmoidalis/ellipsiprymnus* lineage.

Tribe HIPOTRAGINI. Right upper molar 835, right lower molars 251c and 705 and a well worn left  $P_4$  3819a belong in this tribe and are presumably *Hippotragus gigas*. They are all from level 2.

Tribe ALCELAPHINI. A horn core, 131 found in level 1 in 1962, is most likely to be a female of *Beatragus antiquus*. It is shown to be of the right side by a small part of the orbit and a shallow postcornual groove. Its upright insertion and course agree closely with other specimens from



Olduvai. A well-preserved frontlet S.217 of the same species was found in 1971 *in situ* in the rootlet clay of level 2.

A horn core tip 891 from level 2 is very like the type A horn cores from BK II tentatively assigned to *Damaliscus niro*, but is less mediolaterally compressed. A horn core tip 980 also from level 2 could possibly be the same undetermined species.

There are a number of alcelaphine dentitions. These are incomplete right maxillae 520, 2193 and 3942, right mandible 128, left mandibles 168 and 3983 and immature left mandible 25 from level 1; left mandible 2895, immature right maxilla 711, immature right mandible 1059 and immature left mandibles 455 and 1050 from level 2. These dentitions have the size and morphology of *Parmularius altidens*. Mandibles 25, 168 and 455 have the horizontal ramus almost entirely preserved, and in 128 and 3938 enough is present for it to be clear that in all five mandibles the ramus is deep under the teeth (Pl. 37, fig. 6), and in this respect they resemble *Connochaetes*. The teeth, however, are too small relative to this jaw size for *Connochaetes*. It is probable that the dentitions belong to some species of *Parmularius*. Somewhat smaller mandibles with deep horizontal rami are known from size group (ii) dentitions at BK II. Mandibles 168 and 3938 have  $P_3$ - $M_3$  preserved and no alveolus in the jaw for a  $P_2$ , while enough of the jaw of 128 is preserved to show that there is again no alveolus for a  $P_2$ . Immature mandible 25 has no alveolus for a deciduous  $P_2$  and at this early stage  $P_2$  is already missing. Maxilla 3942 has a very reduced  $P^2$ .

Several isolated teeth are alcelaphine. These are as follows; the teeth are mostly the same size as those of the more complete dentitions, and no attempt will be made to assign them to species.

Right upper molars 513, 2121, 3914, 4059 and 4072, left upper molars 78, 141, 514, 2154, 4065, 067/1795, 067/1796, 067/1798 and 067/1800, part of an upper molar 4036, right lower molars 4090 and 067/1803, left lower molars 4073, 067/1804 and 067/1806, right  $M_3$  26, parts of two molars numbered 067/1809, left  $P^4$  4089, left  $P_4$ s 564 and 067/1799, and deciduous left  $P^4$  067/1802 from level 1; right upper molars 251a, 587, 590, 888, 920a, 920b, 981, 067/1853 and 067/1857, left upper molars 576, 577, 586, 589, 787, 945, 965 and 067/1778, right lower molars 692 and 974, left lower molar 067/1775, two lower molars numbered 920, part of a lower molar 920b, right  $M_4$  251a, left  $M_3$ s 251, 579 and 920b, left upper premolar 251a, and left  $P_4$ s 712 and 2328 from level 2. A right upper molar 067/1765, left upper molar 067/1781, left lower molar 067/1771, right upper premolar 067/1786, left upper premolar 067/1774, and deciduous left  $P^4$  067/1777 are either from level 1 or level 2.

Nearly all the alcelaphine limb bones are the size of Bed I *Parmularius altidens* or possibly a little larger. They could belong to *P. altidens*, or *P. altidens* at a stage transitional to *P. angusticornis*, or more probably to the species from various levels in the HWK area which has resemblances to *P. rugosus*.

The limb bones from level 1 are complete left humerus 82, distal ends right humeri 17, 63, 1097 and 3894, distal end left humerus 72, complete right radii 14 and 58, proximal ends right radii 124, 214 and 4052, proximal ends left radii 59 and 87, distal end left radius 2201, right ulnae 175 and 3867, left ulna 19, associated complete left humerus 1098, complete left radius 1099 and left ulna 2173, complete right metacarpal 1093, complete left metacarpals 66 and 67, immature right metacarpal 2038, distal end metacarpal 2020, complete right tibia 2002, almost complete left tibia 2162, distal ends right tibiae 2170, 4002 and 4008, distal ends left tibiae 68 and 2208, proximal end right femur 2132, proximal end left femur 532, almost complete right metatarsal 3974, proximal ends right metatarsals 61, 71, 2175, 3969, 4034 and 4110, shaft of right metatarsal 4009, proximal end left metatarsal 2035 and distal ends metatarsals 2096, 3863 and 3966. From level 2 there are distal end left humerus 3782, proximal end right radius 958, proximal end left radius 1054, associated complete right humerus 935 and complete right radius 936, immature left metacarpals 62+83 and 1063+1067, proximal end right metacarpal 930, distal ends metacarpals 452, 1019 and 1045, distal end left tibia 1076, proximal end right metatarsal 1056, proximal end left metatarsal 1088, and distal end metatarsal 1047.

A few limb bones belong to a larger species, perhaps *Megalotragus kattwinkeli*. The bones are less common than at some sites, DK I for instance, and the only pieces are a complete right radius 3886, distal end metacarpal 2081, distal end left tibia 4020, complete left metatarsal 2053 and proximal end right metatarsal 2026 from level 1, and a complete right metatarsal 067/4691 from level 2. The radius is the size of the large radius 166 at DK I, and the complete metatarsals are unlike *Connochaetes* in their great length.

The distal end of a left radius 2100 from level 1 is intermediate in size between the smaller



limb bones and those of the larger species. A complete left metacarpal 2176 from level 1 is of a species smaller than *P. altidens*. To it may belong the proximal end of left metacarpal 3910 and distal end of metacarpal 3857 from level 1, and distal end of metacarpal 236 from level 2. These are about the size of the small alcelaphine limb bones at FLKN I, and in Table 5 (p. 28) they have been doubtfully referred to Alcelaphini sp. 4. The distal ends of alcelaphine tibiae at this site are less indented at the back of the articular facets in ventral view than those of the living species.

Tribe ANTILOPINI. *Antidorcas recki* is represented by three horn cores from level 2. These are a complete right horn core 278, a right horn core without the base 979 and part of a horn core 972. The horn cores are short, with a flattened lateral surface, strong transverse ridges and no greatly increased divergence of their distal parts. They agree well with Bed I horn cores. The base of a horn core 1962.068/6653 is of unknown level.

A few dentitions and isolated teeth are assigned to *A. recki*.

These are left maxilla 2041, left mandible 2103, right upper molars 11, 563 and 067/1810, left upper molars 563, 067/1805 and two numbered 562, right lower molar 067/1811, left lower molar 4091, parts of two molars numbered 067/1809, and a right lower molar and right and left lower premolars without numbers from level 1; right maxilla 301, left maxilla 907, left mandible 067/1854, right upper molars 067/1838 and 067/1842, left upper molars 977, 067/1773, 067/1793, 067/1859 and two numbered 920c, two upper molars numbered 920, two right lower molars numbered 920c, left lower molar 920c, right M<sub>3</sub> 067/1852 and left M<sub>3</sub> 790 from level 2. A right lower molar 067/1785, left lower molar 067/1766, left M<sub>3</sub> 067/1768 and deciduous right P<sup>4</sup> 067/1787 are either from level 1 or level 2.

Limb bones assigned to *A. recki* are distal end right humerus 37, distal end left humerus 067/1895, distal end right radius 43, complete left tibia 2010, distal end right tibia 3984, distal end right femur 067/1881, complete left metatarsal 4026, proximal end left metatarsal 2003 and distal ends metatarsals 51 and 4049. These are all from level 1. The distal end of right tibia 3790 and distal end of metatarsal 3791 are from level 2.

SUMMARY. Levels 1 and 2 of HWK East II have scanty remains of reduncines and hippotragines, and for almost the last time until Bed III deposits there appear reduncine teeth of a size appropriate for the *Kobus sigmoidalis/ellipsiprymnus* lineage. *Antidorcas recki* is common and is found in association with an alcelaphine as in Bed I sites, but here the alcelaphine is not known to be *Parmularius altidens*; more probably it is *P. rugosus* or its ancestor.

The species list for levels 1 and 2 together is:

*Tragelaphus strepsiceros maryanus*  
*Syncerus acoelotus*  
*Kobus sigmoidalis/ellipsiprymnus*  
*Hippotragus gigas*  
*Megalotragus ? kattwinkeli*  
*Beatragus antiquus*  
*? Parmularius sp.*  
*Alcelaphini sp. 4 ?*  
*Antidorcas recki*

The numbers of bovid bones in levels 1 and 2 are shown in Table 5.

#### FLKN II (Clay with root casts)

This level can be correlated with level 2 at HWK East II.

Tribe TRAGELAPHINI. The proximal end of a right metatarsal 067/4958 belongs in this tribe, and probably also the distal end of a right tibia 067/4886. These are the size of most of the tragelaphine limb bones in Bed I.

Tribe REDUNCINI. A right upper molar 067/5013 and a left P<sub>4</sub> 067/5025 are definitely reduncine, while the proximal end of a right radius 067/4985 and distal end of a right tibia 067/4953 are probably reduncine. They are the size of the *Kobus sigmoidalis/ellipsiprymnus* lineage.

Tribe ALCELAPHINI. The proximal half of a left horn core 067/4998 is of *Beatragus antiquus*.



Table 5 Numbers of bovid bones at HWK East II, levels 1 and 2

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
Level 1								
<i>Tragelaphus s. meryan</i>	1	-	-	-	-	1	1	-
<i>Syncerus acoelotus</i>	-	-	-	1	-	1	1	-
<i>Kobus sigm./ellipsiprymnus</i>	-	-	-	4	-	4	1	-
<i>Megalotragus ? katiwinkeli</i>	-	-	-	-	2	2	1	-
<i>Beatragus antiquus</i>	1	-	-	-	-	1	1	-
Large alcelaphine sp.	-	-	-	-	3	3	1	-
Large/medium alcelaphine	-	-	-	-	1	1	1	-
? <i>Parmularius</i> sp.	-	3	4 (1)	27 (1)	46 (1)	80	6	1
Alcelaphini sp. 4?	-	-	-	-	3	3	2	-
Alcelaphini total	1	3	4 (1)	27 (1)	55 (1)	90	10*	1
<i>Antidorcas recki</i>	-	1	1	14	10	26	2	-
Level 2								
<i>Tragelaphus s. meryan</i>	1	-	-	8 (2)	2	11	1	1
<i>Syncerus acoelotus</i>	-	-	-	1	-	1	1	-
<i>Kobus sigm./ellipsiprymnus</i>	-	-	-	2 (1)	-	2	1	1
<i>Hippotragus gigas</i>	-	-	-	4	-	4	1	-
<i>Megalotragus ? katiwinkeli</i>	-	-	-	-	1	1	1	-
<i>Beatragus antiquus</i>	1	-	-	-	-	1	1	-
? <i>Parmularius</i> sp.	-	1 (1)	4 (3)	30	15 (2)	50	3	2
Alcelaphini sp. 4?	-	-	-	-	1	1	1	-
Alcelaphini total	1	1 (1)	4 (3)	30	17 (2)	53	6	2
<i>Antidorcas recki</i>	3	2	1	15	2	23	3	-

\* Omitting the individuals represented by the large and large/medium limb bones.



It is rather robust and has the usual transverse ridges. A cranium 1960.067/4951 with pieces of both horn cores 067/4946+4948 and 4949 is a possible intermediate stage between *Parmularius altidens* and *P. angusticornis*.

Four single teeth belong in this tribe. These are part of a right upper molar 067/5012, right lower molar 067/5018, right M<sub>3</sub> 8820 and deciduous right P<sup>3</sup> 067/4942. They are all medium-sized.

There are no very large limb bones at this site and those present are all of smaller size (size group (ii) of later Bed II sites). These are distal end left humerus 067/4952, proximal end right radius 067/4947, proximal end left radius 067/4986, left ulna 067/4880, proximal end left metacarpal 067/4990+067/5002, distal end metacarpal 067/4914, proximal end left metatarsal 067/4963 and distal end metatarsal 8817. The proximal lateral tubercle on the radius 067/4947 is high as in alcelaphines, but the lateral facet is not very indented posteriorly.

Tribe ANTILOPINI. Five teeth belong in this tribe. These are right upper molar 067/4937 and left upper molars 067/4909, 067/4910, 067/4928 and 067/4969.

The proximal end of left tibia 067/4869, distal end metatarsal 067/4925 and distal end metacarpal 067/4855 are the size of *Antidorcas recki* limb bones, but a right femur (proximal end 067/4859, distal end 067/4885, part of the shaft missing) is larger than femora of *A. recki* though smaller than the proximal ends of femora 233 and 8809 of very small Alcelaphini at FLKN I.

#### Other remains from Lower Bed II

Tribe ALCELAPHINI. A crushed cranium and parts of a skeleton, apparently of *Damaliscus agelaius*, FLK West 1969.82a, were found above Tuff IF in greenish clays below the sandy conglomerate. Some antilopine limb bones were found with the skeleton.

An alcelaphine cranium S.208 was collected in 1970 from the Lemuta Tuff Member. It has some resemblance to *Rabaticeras arambourgi*, but in this paper we have referred it to Alcelaphini species 2.

### Sites in Middle Bed II

#### HWK EE II

In 1972 Mrs M. D. Leakey excavated at this site near the base of middle Bed II at a level equivalent to level 4 of HWK East II. An account is to be published later. Meanwhile we have seen some bovid material from the site.

Tribe TRAGELAPHINI. Part of a right maxilla 3916 with M<sup>2</sup> and M<sup>3</sup> would best fit *Tragelaphus strepsiceros maryanus* by the size of the teeth. A right deciduous P<sup>2</sup> from I/12 is also probably tragelaphine.

Tribe REDUNCINI. A left M<sub>3</sub> 1123 is large enough to belong to the *Kobus sigmoidalis/ellipsiprymnus* lineage. It is too large to belong to a kob.

Tribe ALCELAPHINI. A right horn core 2315 from the sandy conglomerate belongs to the primitive *Connochaetes* sp. likely to be ancestral to *C. taurinus* and otherwise confined to Beds I and lower II. We saw a cast of the horn core.

Three pieces of *Parmularius angusticornis* are a frontlet with complete horn cores 172, a frontlet with complete right horn core and virtually complete left horn core 635 and a complete right horn core 2180.

Three more fossils belong to a smaller alcelaphine tentatively associated with the *Parmularius rugosus* lineage. These are frontlets 2061 and 2181 and right horn core 954. The last-mentioned piece may be of a female. We have also seen a cast of frontlet 285 belonging to this species.

A very small alcelaphine is also present, represented by two left mandibles, 1156 with P<sub>3</sub> to erupting M<sub>3</sub> and 4302 with P<sub>3</sub> to M<sub>2</sub>. Neither has an alveolus for P<sub>2</sub>, nor are paraconid and metaconid fused on P<sub>4</sub>. A complete right metatarsal 1168 is likely to be conspecific. It has a strong longitudinal groove on its anterior side and is therefore unlike Antilopini despite its small size. Its length and least thickness are 161 and 11.4 mm.

There are other dentitions and isolated teeth from this site belonging to the Alcelaphini.

Tribe ANTILOPINI. Two horn cores of *Antidorcas recki*, 2780 and 3108, agree with HWK II



1959.472, KK I 1959.309 and BM(NH) M 14512 from Bed I in being very strongly compressed mediolaterally. Part of a left mandible with deciduous  $P_3$ - $M_1$  and erupting  $M_2$  and  $M_3$  and with an alveolus for deciduous  $P_2$  is probably *A. recki* by the great ramus depth below  $M_2$ .

*Gazella* sp. is represented by a complete right horn core 2396.

There are also a few antilopine teeth at this site.

SUMMARY. HWK EE II will be a very interesting site when a complete account can be given. It has three categories of bovids:

(i) The last survivors of species otherwise known only from Beds I and lower II: *Tragelaphus strepsiceros maryanus* (provisional), *Kobus sigmoidalis/ellipsiprymnus* and *Connochaetes* sp.

(ii) Species which appear temporarily in the Olduvai region at this period: *Parmularius* ? *rugosus* and the narrow-horned variety of *Antidorcas recki*.

(iii) One species confined to middle and upper Bed II: *Parmularius angusticornis*.

#### HWK East II Levels 3-5

Tribe BOVINI. A right upper molar 2687 and a right  $M_3$  2688, both slightly worn, are large with a simple occlusal pattern and are definitely *Pelorovis oldowayensis*. This is the earliest record of known horizon at Olduvai.

Tribe HIPOTRAGINI. A left lower molar 067/1839 is the only possible evidence of this tribe in these levels. It may be *Hippotragus gigas* by the signs of a well-developed goat fold anteriorly.

Tribe ALCELAPHINI. An immature frontlet 068/6649 with complete right horn core and basal half of the left was found in clay above the sandy conglomerate above these levels. The specimen is smaller than three adult horn cores of a species like *Parmularius rugosus* from HWK II and the midfrontal suture is still open. It is best taken as belonging to this species.

An immature left mandible 2917 is alcelaphine. It has a very small deciduous  $P_2$ . A number of single teeth also belong to this tribe; they agree with *Parmularius altidens* but could belong to the species like *P. rugosus*.

These are right upper molars 2890, 3482, 3487, 067/1813, 067/1820, 067/1822, 067/1847, 067/1848 and 067/1850, left upper molars 2918 and 067/1844, right lower molars 690, 068/1815, 067/1824, 067/1860 and damaged 067/1828, left lower molars 2220 and 067/1860, parts of lower molars 067/1824, 067/1834 and 067/1849, right  $M_3$  695, right upper premolar 067/1836, left upper premolars 3485 and 067/1824, right  $P_4$ s 2223, 2225 and 067/1829, left  $P_2$  067/1824, left  $P_4$  067/1831, deciduous right  $P^3$  067/1817, deciduous left  $P^3$  067/1823, deciduous right  $P^4$  067/1845, and deciduous right  $P_4$ s 3495, 067/1830 and damaged 067/1835.

A number of alcelaphine limb bones are the size of *P. altidens* or possibly a little larger. These are distal ends left humeri 3218 and 067/1899, proximal ends left metacarpals 3337 and 067/1908, distal end metacarpal 2948, proximal end right femur 067/1955, distal left femur 067/1917, complete left tibia 067/1906, distal end right tibia 693, proximal end left metatarsal 067/1904 and distal end metatarsal 067/1907.

The proximal ends of right metacarpals 2976A and incomplete 3154 are larger and perhaps belong to *Megalotragus kattwinkeli*. The proximal end of right radius 067/1900 is the size of the distal end of left radius 2100 from level 1 of this site and is intermediate between the larger and smaller limb bones.

Tribe ANTILOPINI. A few antilopine remains were found in these levels and are presumably *Antidorcas recki*. These are partial right maxilla 067/1788, right upper molar 067/1816, left upper molars 2221, 067/1769 and 067/1818, right lower molars 067/1814 and 067/1819, left lower molars 067/1826 and 067/1827, right  $M_3$ s 2219, 067/1782, 067/1843 and 067/1846, left  $M_3$  067/1833, right lower premolar 067/1824, left  $P_3$  067/1789 and proximal end right radius 067/1903.

SUMMARY. The numbers of bovid bones of each species at HWK East II levels 3-5 are given in Table 6, p. 33.

#### MNK II

Site (71)      Geologic locality 88

The MNK gully is on the south bank of the Side Gorge, opposite FC, and about 0.8 mile (1.3 km)



upstream from the confluence with the Main Gorge. Much of Beds II, III and IV is visible, the exposures extending down to Tuff IF at the top of Bed I. MNK Skull Site is in the lower half of the gully in the lower part of middle Bed II, 24 ft (7.2 m) above the base of Bed II, while the Main Occupation Site is some 17 ft (5.1 m) higher, in the upper part of middle Bed II, the two sites being about 60 ft (18.0 m) from one another. The sequence of deposits, from above downwards, is as follows:

- (a) A fine-grained reworked tuff, exposed to a depth of 10 ft (3.0 m), with patches of clay and grey sand at the base and often reddened in the upper part. The Main Occupation Site occurs within the lower 4½ ft (1.35 m) of this tuff.
- (b) About 3 ft (90 cm) of hard grey tuff with pumice particles in the lower part and an irregular, eroded upper surface.
- (c) 3 ft (90 cm) of clay.
- (d) 4 ft (1.2 m) of reworked tuffs containing thin gravel seams, usually partly reddened.
- (e) An irregular layer of limestone, 9 ins (23 cm) thick.
- (f) About 13 ft (3.9 m) of reworked tuffs and clays. The Skull Site occurs in the upper part of these deposits.
- (g) Several levels of tuffs and clays with layers of chert down to Tuff IF.

#### MNK II Skull Site

Artifacts and a few faunal remains were scattered throughout the 4½ ft (1.35 m) of grey, sandy reworked tuff in which three hominid teeth were found, and in the underlying 6 ft (1.8 m) of clay in which two fragments of a hominid skull occurred.

Tribe TRAGELAPHINI. Part of a lower molar 067/1460 belongs in this tribe.

Tribe ALCELAPHINI. A right maxilla with M<sup>1</sup>–M<sup>3</sup> preserved 89, right upper molars 47, 067/1436 and 067/1445, left upper molar 067/1406, part of upper molar 067/1431, right lower molar 067/1453, part of lower molar 067/1397, part of right M<sub>3</sub> 067/1389, right P<sup>3</sup> or P<sup>4</sup> 067/1429, deciduous right P<sup>3</sup> 067/1458 and deciduous right P<sup>4</sup> 067/1391 are alcelaphine. They belong in size group (ii) of later Bed II sites, although the maxilla is clearly small even for this size group.

Tribe ANTILOPINI. Part of a right upper molar 067/1448 represents this tribe.

#### MNK II Main Occupation Site

The Occupation Site was excavated in 1963 by means of four trenches. Remains were found scattered throughout the 4½ ft (1.35 m) of deposit. Except for material on the eroded surface of the underlying hard grey tuff, the remains were not on any recognizable 'surfaces', so the site may have been reoccupied on successive occasions, at sufficient intervals for soil and vegetation to have accumulated over previous occupation surfaces. At the time of excavation the deposit was subdivided into six levels, and the fossils marked accordingly, but the material is now treated as a single unit.

Tribe TRAGELAPHINI. An incomplete pair of horn cores and four associated skull pieces (the occipital, basioccipital, part of the roof and side of the braincase, and an unidentified fragment), 067/2054, are of a large tragelaphine. The horn cores have the open spiral and prominent keel of kudu species. The spiralling is anticlockwise in one horn core which is therefore from the right side, and clockwise in the other, left, horn core. Both pieces are the upper halves of horn cores and are comparable in size with those of the living greater kudu. On the basis of its very large size as indicated by the occipital fragment and its horn cores having a definite triangular cross-section, the specimen is referred to *Tragelaphus strepsiceros grandis*. There is more of an approach to a posterolateral keel than in living greater kudus. The fragment of skull roof and side of the braincase has a deep groove at the top of the braincase side, below the back of the horn core insertion, as is present on the holotype skull of *T. s. grandis* and to a lesser extent in living greater and lesser kudus; this is a feature connected with horn core size, angle of insertion and shape of the braincase.

A left upper molar 067/1407 of greater kudu size is referred to *T. s. grandis* and two unworn left lower premolars 067/1417 are possibly also of this species.



Tribe BOVINI. *Pelorovis oldowayensis* is now known to be present at this site and this, together with the HWK East II record, extends its temporal range back from SHK II to much earlier in middle Bed II. There are eight single teeth. These are right upper molar 3264, left upper molar 3269, right lower molar 2321, left lower molars 480 and 067/1410, right M<sub>3</sub> 2380, right P<sub>3</sub> 2336 and right P<sub>4</sub> 3113. They agree in size and morphology with later *P. oldowayensis* teeth.

A right upper molar 1130 and possibly a deciduous right upper premolar 1338 belong in this tribe and would be from a bovine smaller than *P. oldowayensis*. These teeth could be of *Syncerus acoelotus* as at other Bed II sites.

A number of limb bones are bovine. These are complete right radius 2411, proximal end left radius 2861, left ulna 067/1372, distal end metacarpal 2825, distal ends right tibiae 1277 and 1591 and distal end left tibia 3423. The complete radius can be seen to be rather small for *P. oldowayensis* but it is not certain to which species any of the limb bones would belong.

Tribe REDUNCINI. The skull, dentitions and partial skeleton of a small kob-sized reduncine were found at this site. The skull 104+106 is crushed and incomplete. The mandibles, right 107 and left 108, and the right maxilla 103 retain only their molars and the P<sub>4</sub>s. The postcranial skeleton consists of the atlas vertebra 110, right metacarpal 105, right ulna 109, right femur 101, right tibia 102 and right metatarsal 100.

The proximal end of a right metatarsal 715 is damaged and doubtfully reduncine. It is of waterbuck size and is certainly not alcelaphine. A deciduous right P<sub>4</sub> 067/1435 is definitely reduncine and is of kob size.

Tribe HIPPOTRAGINI. A single right lower molar 1087 is the only evidence for this tribe.

Tribe ALCELAPHINI. A complete left horn core with the frontal and part of the orbital rim 3258 is of *Megalotragus kattwinkeli*. It is rather shorter than the horn core on the neotype skull BM(NH) M 21447. The horn core insertions would be close together and the horn cores backwardly directed with little divergence at the base and not very downwardly directed (the frontal between the horn cores being regarded as dorsal and not anterior so that the tooth rows would be horizontal if present). The horn core is close to the orbit and there is no temporal fossa. A large, moderately deep but not greatly elongated postcornual fossa is present, and there is transverse ribbing across the front surface of the horn core.

A left horn core 2716 is of *Connochaetes*. It is either *Connochaetes* sp. or *C. taurinus olduvaiensis*, being too incomplete basally for certain assignment. The very little dorsoventral flattening at the base suggests that it is a female.

There are two sizes among the alcelaphine dentitions at this site, corresponding with the size groups at SHK II and BK II.

(i) A left mandible 2070 has a molar row of the same large size and simple occlusal pattern as teeth of *Megalotragus kattwinkeli* as seen on the neotype skull (Leakey 1965 : pl. 82). Eight upper and nine lower isolated alcelaphine teeth of large size are also assigned to this group.

(ii) A partial maxilla 2259 and left mandibles 136, 976 and 2403 belong in this size group. 136 and 976 are the only mandibles at this site which would be complete enough for any presence of P<sub>2</sub> to be seen, and in both cases it is seen to be absent. A rather small right mandible 1725 also belongs in this size group but is likely to be a different species from the other specimens, perhaps *Damaliscus agelaius*. There are 28 upper and 35 lower alcelaphine teeth in this size category.

The alcelaphine limb bones are also divisible into two sizes, which again correspond with the size groups at SHK II and BK II. The group of 'large' limb bones consists of part of the distal end of left humerus 1870, proximal ends left radii 718 and 3050, distal end right radius 3472, distal end left radius 2190, complete left metacarpal 2704, proximal end right femur 1831, complete right tibia 167, complete left metatarsals 169 and 2718 and proximal end left metatarsal 067/1365. The metapodials are relatively longer than in living *Connochaetes* and some pieces, radius 3050 for instance, reach the size of the very large DK I and HWK East II alcelaphine limb bones. They belong with the size group (i) alcelaphine dentitions and most of them are probably of *Megalotragus kattwinkeli*. A complete left metatarsal 752 is of a large-sized alcelaphine, and has proportions and length appropriate for *Connochaetes* rather than *M. kattwinkeli*.

Limb bones of the 'small' category are the distal end of right humerus 3177, distal end left



Table 6 Numbers of bovid bones at HWK East II, levels 3-5

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
<i>Pelorovis oldowayensis</i>	-	-	-	2	-	2	1	-
<i>Hippotragus gigas</i> ?	-	-	-	1	-	1	1	-
Large alcelaphine sp.	-	-	-	-	2	2	2	-
Large/medium alcelaphine	-	-	-	-	1	1	1	-
<i>Parmularius</i> aff. <i>rugosus</i>	1 (1)	-	1 (1)	36 (6)	11	49	3	3
Alcelaphini total	1 (1)	-	1 (1)	36 (6)	14	52	6	3
<i>Antidorcas recki</i>	-	1	-	15	1	17	4	-

Table 7 Numbers of bovid bones at MNK II

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
<i>Tragelaphus s. grandis</i>	1	-	-	3	-	4	1	-
<i>Pelorovis oldowayensis</i>	-	-	-	8	-	8	1	-
<i>Syncerus acoelotus</i>	-	-	-	2 (1)	-	2	1	1
Bovini	-	-	-	-	7	7	2	-
Bovini total	-	-	-	10 (1)	7	17	2*	1
<i>Kobus kob</i>	1	1	2	1 (1)	5	10	1	1
<i>Hippotragus gigas</i>	-	-	-	1	-	1	1	-
<i>Megalotragus kottwinkeli</i>	1	-	1	-	-	2	1	-
<i>Connochaetes ? taurinus</i>	1	-	-	-	1	2	1	-
Alcelaphini size group (i)	-	-	-	17	11	28	-	-
Alcelaphini size group (ii)	-	1	3	63 (5)	11	78	-	-
Smaller Alcelaphini, group (ii)	-	-	1	-	1	2	-	-
Alcelaphini total	2	1	5	80 (5)	24	112	-	-
Antilopini sp. indet.	-	-	-	1	-	1	-	-
Antilopini sp. 1	1	-	-	-	-	1	1	-

\* Omitting the two individuals represented by limb bones.



humerus 1495, part of proximal end right radius 067/1486, proximal end left radius 1296, distal end right radius 1286, distal end left radius 2953, right ulna 1391, proximal ends left metacarpals 2670 and 3320 and proximal ends right metatarsals 775 and 067/1484. These limb bones are rather larger than those of *Parmularius altidens* of Bed I. They would belong with the alcelaphine dentitions of size group (ii). The proximal end of a rather small right metatarsal 3385 is of similar size to the very small alcelaphine limb bones from FLKN I. It could perhaps be conspecific with the mandible 1725 rather than with the FLKN species.

Tribe ANTILOPINI. A single left upper molar 067/1426 belongs in this tribe. It is not possible to say whether it is *Antidorcas recki* or *Gazella*.

The base of a left horn core 2818 appears to be of an unknown antilopine species with some resemblances to *Gazella*. The specimen is small but adult and has the supraorbital pit preserved. Similar horn cores have been found at BK II and from the surface of DK I, and have been listed as 'Antilopini sp. 1'.

SUMMARY. At MNK II *Tragelaphus strepsiceros maryanus* has been replaced by *T. s. grandis*, and the *Kobus sigmoidalis/ellipsiprymnus* lineage by *K. kob*. The middle and upper Bed II co-existence of *Pelorovis oldowayensis* with *Syncerus acoelotus* has emerged. MNK II is also the first site at which bovines are clearly commoner than tragelaphines, and this is a pattern which continues into Bed III. Another feature in common with other middle and upper Bed II sites is the heavy representation of alcelaphines and a drop in the proportion of antilopines. Except at the highly unusual site of FLKNN I the antilopines have hitherto been present in numbers equal to at least a third of the alcelaphines.

The numbers of bovid bones of each species at the site are shown in Table 7, p. 33. Here the alcelaphine size group (i) includes material likely to belong to *Megalotragus kattwinkeli* and *Connochaetes*, while size group (ii) would contain *Parmularius angusticornis* and *Damaliscus niro* if those species are found here as at later Bed II sites.

## FC West II

Site (62)      Geologic locality 89

The site lies on the north bank of the Side Gorge, 1 mile (1.6 km) above the confluence with the Main Gorge. A trench was cut into the deposits of Bed II in 1963 and the following sequence, from above downwards, was exposed:

- (a) Tuff IID.
- (b) About 25 ft (7.5 m) of a buff-white tuff, a clayey tuff, a sandy tuff and a consolidated fine sand. A few implements and bones occurred in these levels.
- (c) 1½–3 ft (45–90 cm) of a reworked tuff with scattered cultural and faunal material.
- (d) A rich hominid occupation floor on the surface of a clay.
- (e) 14 ft (4.2 m) of barren tuffs and clays, starting with Tuff IIB at the top.
- (f) The chert-containing bed, as at other Bed II sites.

Tribe REDUNCINI. A complete right metatarsal 1 is possibly reduncine and is *Kobus*-sized with a length and least thickness of 209 and 25.4 mm.

Tribe ALCELAPHINI. A number of single teeth are alcelaphine. These are right upper molars 64, 317 and 067/5252, left upper molars 067/5416 and 067/5265, right lower molars 69, 254 and 067/5265, left lower molars 253, 722 and 067/5265, lower molars 067/5416 and two numbered 067/5252, parts of lower molars 204, 067/5252 and 067/5253, part of a molar 067/5265, right P<sub>4</sub> 067/5265, left P<sub>4</sub> 067/5277 and deciduous left P<sup>4</sup> 067/5252. An unworn right upper molar 1206 is larger than the other teeth.

The distal end of a left radius 452 is alcelaphine and large-sized. It would belong to *Megalotragus kattwinkeli* or *Connochaetes*. The distal end of a left humerus 387 is medium-sized. The distal end of a metacarpal 287 and the distal end of a metatarsal 268 probably belong in this tribe and are medium-sized.

Tribe NEOTRAGINI. An incomplete right mandible 167 with deciduous P<sub>2</sub>–P<sub>4</sub> is extremely small and probably belongs in this tribe.



Tribe ANTILOPINI. An incomplete right horn core 201, with the top of the orbital rim, supraorbital pit and postcornual fossa, is *Gazella* (p. 438). It appears to be somewhat more transversely compressed than *Gazella* horn cores from SHK II and BK II, and has a less deep postcornual fossa, but it is probably the same species.

A left M<sub>3</sub> 067/5252 and the distal end of a right tibia 85 are antilopine. They could be *Gazella* sp. or *Antidorcas recki*.

## SHK II

Site (68)      Geologic locality 92

SHK is situated in a long, narrow gully cutting into the south bank of the Side Gorge, about 1½ miles (2.4 km) from the confluence of the Main and Side Gorges. The site is on the west side of the gully where the exposures are from the upper part of middle Bed II to Bed III. On the east side of the gully the exposures extend from the top of Bed II down to Tuff IF at the top of Bed I, including a horizon with chert nodules as at other Bed II sites. Tuff IID is visible at about 62 ft (18.6 m) above the base of Bed II. Excavations in Bed II were carried out in 1953, 1955 and 1957. The sequence of exposures, from above downwards, was as follows.

- (a) 8 ft (2.4 m) of tuffs and clayey tuffs, some coarse and others fine-grained. The fossil remains were not concentrated at a particular level. There was some evidence of water rolling. The herd of *Antidorcas recki* now in the British Museum (Natural History) was found in these deposits in 1935.
- (b) A conglomerate filling a channel 2½ ft (75 cm) deep and 5–6 ft (1.5–1.8 m) wide, cutting through the lower part of (a) down to the surface of the underlying brown clay, and containing artifacts and bones. The material recovered was mainly fresh but some large artifacts were water-rolled.
- (c) A chestnut brown clay whose top was 32 ft (9.6 m) above the base of Bed II, its base not exposed.

Faunal remains from the three horizons have been treated as a single unit. At a subsidiary site, SHK Annexe, about 100 yds (91.4 m) from the Main Site, an occupation level on the surface of the underlying brown clay occurred at the level of the channel conglomerate.

Tribe TRAGELAPHINI. The base of a horn core with an open spiral 1953.286 is of greater kudu size, or still larger, and is presumably of *Tragelaphus strepsiceros grandis*. The spiralling is clockwise so the piece is from the left side, and the sharp keel is anteriorly inserted at the base.

An immature partial right mandible 1953.270 and right M<sub>3</sub>s 1957.125 and 1957.227 are tragelaphines of large size and are assigned to this species.

The distal end of a left tibia 1957.474 is from a bushbuck-sized tragelaphine and this must represent another, much smaller, species.

Tribe BOVINI. Three teeth of *Pelorovis oldowayensis* can now be added to the crushed horn core and dental material already known from this site (Gentry 1967 : 253, 257). These are right upper molar 1957.1181, left lower molar 1957.422 and a lower molar 1957.1130.

Four teeth appear to be of *Syncerus acoelotus*, and have a more complicated occlusal pattern than is found in most *P. oldowayensis*. These are right upper molars 1953.259, 1957.148 and 1957.290 and left upper molar from the surface 1953.197.

Tribe REDUNCINI. The basal half of a horn core 1957.579 with a small part of the braincase preserved was a surface find at this site. It is of *Kobus* rather than *Redunca* size (Leakey 1965 : 47, *Kobus* species B, said to be a right horn core but in fact a left), and looks more like a rather large kob than a waterbuck in its small divergence and lack of a flattened lateral surface.

A left M<sub>3</sub> 1957.396 is reduncine and the size of a kob.

Tribe HIPPOTRAGINI. The base of a left horn core with the frontal suture, orbital rim and a small part of the braincase 1953.281 is of *Hippotragus gigas* (Leakey 1965 : 50).

An immature right mandible 1957.618, right lower molar 1957.506 and left lower molar 1957.219 are assigned to *H. gigas*. 1957.618 has two molars in place behind the deciduous P<sub>4</sub> and both have goat folds passing down the entire exposed height of the tooth; the M<sub>2</sub> in particular is too small for the jaw to belong to a bovine.

The distal end of a left tibia 1955.32 is probably hippotragine.



Tribe ALCELAPHINI. A number of horn cores of *Parmularius angusticornis* are known from this site, the best preserved being the left one with part of the braincase 1957.1284 assigned by Leakey to *Damaliscus antiquus* (1965 : 56). It shows a massive cross-section near the base followed by a gradual thinning, a slight backwards curvature, no transverse ridges on the front and a rather weak alcelaphine groove without a marked anterior edge. More of the horn core is preserved than in specimens illustrated by Leakey, and its divergence in anterior view exceeds that seen in illustrated specimens. Other horn cores of this species from SHK II are a left 1952.598, base of a right 1955.424 and left 1957.945.

A horn core without number found at this site in 1952 is a *Parmularius* doubtfully referred to the *P. rugosus* lineage.

*Damaliscus niro* is represented by two fairly large horn cores, right 1953.282 and left 1957.1184 (Leakey 1965 : pl. 55 centre and right specimens), both showing such good identifying features as the overall mediolateral compression, flattened lateral surface towards the distal end, pronounced transverse ridges on the front surface, backwards curvature in side view and the front part of any section of the horn core being wider than the back. 1953.282 has parts of the frontal and braincase preserved and in side view shows the oblique insertion of the horn cores of this species, which is none the less more upright than in the living topi *Damaliscus lunatus*. Enough of the frontal is preserved to show the sharp descent of the braincase roof behind the horn core.

*Connochaetes* is represented by part of a left horn core 1953.283. The distal part of a horn core 1957.946 (Pl. 16, fig. 2) is probably also of wildebeest, although the curvature is less developed than in other horn cores; the alternative of considering it a *Beatragus* with more curvature than normal is less satisfactory because of the absence of transverse ridges and a cross-section which is too little compressed.

A left horn core with part of the frontals 1953.280, and parts of two other horn cores 1957.92 (a surface specimen) and 1953.234, are thought to be possibly related to *Rabaticeras arambourgi* or to the north African Villafranchian *Numidocapra crassicornis* (p. 418).

The alcelaphine dentitions and isolated teeth at this site can be divided into two size groups as at other Bed II sites.

(i) A left mandible 1957.256 belongs in this size group. In its large size and the simple occlusal morphology of its molar row it is probably *Megalotragus kattwinkeli*. Fifteen upper and five lower isolated alcelaphine teeth are assigned to this category.

(ii) An immature left maxilla 1957.760 and left mandibles 1953.272, 1957.268 and 1957.455 have teeth of smaller size and are probably the dentitions of *Parmularius angusticornis* and *Damaliscus niro*. Twenty upper and 35 lower isolated teeth are assigned to this size group. Left upper molars 1957.457 and 1957.617, right lower molars 1955.15 and 1957.116, left lower molar 1957.309, right M<sub>3</sub> 1957.392 and left M<sub>3</sub> 1957.228 are rather smaller than other teeth included here.

There are two size categories among the alcelaphine limb bones. Limb bones of the 'large' group are about the size of the MNK II bones, although the metapodials seem a little smaller. They are presumably of *Megalotragus* or possibly some are *Connochaetes*. They are the associated complete right radius 1957.282 and complete left radius 1957.283, proximal ends right radii 1953.270 and 1957.929, right ulna 1957.352, complete right metacarpals 1957.558 and 1957.1350, proximal end right metacarpal 1957.89 (surface), distal ends metacarpals 1957.578 (surface) and 1957.469, proximal end right tibia 1957.729, immature left tibia 1957.762 + 764, distal end right femur 1957.328, complete right metatarsal 1957.839, complete left metatarsal 1957.231 and immature complete left metatarsal 1957.731. These limb bones would belong with the size group (i) teeth.

The limb bones of the 'small' category, as follows, are more numerous and are an appropriate size to go with the size group (ii) teeth.

Distal end right humerus 1957.1181, distal ends left humeri 1957.23, 1957.581 (surface), 1957.761 and 1957.944, complete right radius with ulna 1957.209, proximal ends right radii 1955.41, 1957.88 (surface), 1957.130 and 1957.1307, distal end right radius 1957.1423, distal ends left radii 1957.470 and 1957.732, part of left ulna 1957.825, complete right metacarpal 1957.330, immature complete right metacarpal 1957.208, immature complete left metacarpal 1957.285, proximal end right metacarpal 1953.274,



proximal ends left metacarpals 1955.40, 1957.204, 1957.237 and 1957.805, distal ends metacarpals 1953.271, 1953.272a, 1957.273a, 1957.423 (surface) and 1957.725, distal ends right tibiae 1953.271a, 1957.86 (surface), 1957.87 (surface) and 1957.824, distal end left tibia 1957.556, distal ends left femora 1957.415 and 1957.1180, complete left metatarsal 1957.933, and distal end metatarsal 1957.90 (surface).

There are also a few rather smaller limb bones. These are distal end left humerus 1957.765, proximal end left metacarpal 1955.213 and proximal end right metatarsal 1957.763. These are about the size of the very small alcelaphine limb bones from FLKN I but are not necessarily conspecific with them.

Tribe ANTILOPINI. The herd of *Antidorcas recki*, consisting of some nine or ten mostly immature individuals, was found at this site in 1935. This material is in the British Museum (Natural History) and has already been described (Gentry 1966 : 77). Included in the herd is the young adult cranium M 21464 and older frontlet M 21462 (Gentry 1966 : pl. 5) which both have complete horn cores (see p. 429). A right mandible M 22379 was found with the herd but differs in some morphological details from other mandibles in *A. recki* (Gentry 1966 : 66; pl. 3A).

An incomplete immature right mandible in Nairobi, 1957.75 from the surface of SHK II, is assigned to *A. recki*.

A complete right horn core 1953.285, with the top of the orbital rim, supraorbital pit and the frontal suture preserved, differs from horn cores of *A. recki* in lacking the sharp bending back near the base, the transverse ridges and the outward divergence in the upper part. This horn core curves only slightly back at the base and slightly forwards near the tip. It has a flattened lateral side, a rounded medial side and almost no transverse compression. The level of the frontals between the horn core bases would be about the same as that of the orbital rims. The supra-orbital pit is large, and there is a rather large and deep postcornual fossa. This specimen is *Gazella* (Gentry 1966 : 65; pl. 2C).

A left mandible 1957.793, lacking only P<sub>2</sub> which has broken off, has a shallower ramus under the teeth and a relatively longer premolar row than in *A. recki*, the total tooth row length being about the same. This is probably also *Gazella* (Gentry 1966 : 66; pl. 3A) and the same species as the horn core.

A lower molar 1957.756 and the distal end of a left radius 1957.99 (surface) are both antilopine but it is not possible to assign them to *A. recki* or to *Gazella*.

SUMMARY. At SHK II the coexistence of *Pelorovis oldowayensis* and *Syncerus acoelotus* continues as at MNK II. The numbers of bovid bones of each species at SHK II are shown in Table 8. The alcelaphine teeth and limb bones of size group (i) are likely to be *Megalotragus kattwinkeli* and *Connochaetes*, and those of size group (ii) to include mostly *Parmularius angusticornis* and *Damaliscus niro*. Apart from the 1935 herd of *Antidorcas recki*, included in Table 8, only one juvenile mandible of *A. recki* and four other antilopine bones are known from SHK II. Gentry (1966 : 84) gave the minimum number of individuals in the herd as 9 or 10, based on metatarsals. However, it has proved possible to make use of an almost adult individual for which there was an association between mandible and metatarsal, and this produces the new minimum numbers shown here.

#### Other remains from Middle Bed II

Tribe BOVINI. A bovine distal metacarpal of the size of *Pelorovis oldowayensis* 1957.367 was a surface find at FC II.

A frontlet of a small *Syncerus acoelotus* with very short horn cores was found in 1973 in Elephant K in a conglomerate 5 ft (1.5 m) above the Lemuta Member.

Tribe HIPPOTRAGINI. A complete left horn core with part of the braincase 068/6663 of *Hippotragus gigas* was found at FLK II in 1961.

Tribe ALCELAPHINI. A damaged frontlet 1962.068/6648 of *Parmularius angusticornis* was found in aeolian grey ash at Long K East II. The basal halves of both horn cores and part of the braincase with a flat-topped parietal boss are preserved. The horn cores taper abruptly just above the base and are inclined slightly backwards.

A large alcelaphine basioccipital 068/6651 was also found at Long K East in 1962.



**Table 8** Numbers of bovid bones at SHK II

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
<i>Tragelaphus strepsiceros grandis</i>	1	-	1 (1)	2	-	4	2	1
<i>Tragelaphus cf. scriptus</i>	-	-	-	-	1	1	1	-
<i>Pelorovis oldowayensis</i>	1	1	-	7	2 (1)	11	2	1
<i>Syncerus acoelotus</i>	-	-	-	4	-	4	1	-
Bovini total	1	1	-	11	2	15	3	1
<i>Kobus kob</i>	1	-	-	1	-	2	1	-
<i>Hippotragus gigas</i>	1	-	1 (1)	2	1	5	1	1
<i>Megalotragus kattrinkeli</i>	-	-	1	-	-	1	1	-
<i>Connochaetes ? taurinus</i>	1	-	-	-	-	1	1	-
<i>Parmularius angusticornis</i>	4	-	-	-	-	4	3	-
<i>Parmularius ? rugosus</i>	1	-	-	-	-	1	1	-
<i>Damaliscus niro</i>	2	-	-	-	-	2	1	-
Alcelaphini sp. 3	3	-	-	-	-	3	2	-
Alcelaphini size group (i)	-	-	-	20	16 (2)	36	-	-
Alcelaphini size group (ii)	-	1 (1)	3	48	37 (2)	89	-	-
Smaller Alcelaphini, group (ii)	-	-	-	7	3	10	-	-
Alcelaphini total	11	1 (1)	4	75	56 (2)	146	-	-
<i>Antidorcas recki</i>	4 (2)	4 (4)	14 (7)	15	82 (60)	119 (73)	4	7
<i>Gazella</i> sp.	1	-	1	-	-	2	1	-
Antilopini sp. indet.	-	-	-	1	1	2	-	-
Antilopini total	5 (2)	4 (4)	15 (7)	16	83 (60)	123 (73)	5	7



Two complete horn cores of *Damaliscus niro* were found at Elephant K II in 1963. Right horn core 068/5919 came from *in situ* gravel, while left horn core 068/5920 was a surface find. 068/5920 is rather longer and more robust than 068/5919, and somewhat larger than the two SHK II examples and BK II 1955.159. Both horn cores have slight transverse ridges on the anterior surfaces, and have part of the braincase and orbital region attached.

An incomplete cranium with horn cores 068/5975 came from black sand above the sandy conglomerate at HWK EE II in 1965. It has been tentatively linked with the *Parmularius rugosus* lineage.

A male cranium with incomplete horn cores, S.38 found in 1968 at geologic locality 54, probably came from middle or upper Bed II. It belongs to *Damaliscus agelaius*.

Tribe ANTILOPINI. A complete right horn core of *Antidorcas recki* was found at Long K West II in 1962 (Pl. 39, fig. 1). It is numbered 068/6657 and is marked 'Grey ash *in situ*'. It has preserved the frontal, top of the orbital rim and midfrontal suture. It bends backwards and has transverse ridges on the anterior surface. It is a little more upright at the base and a little more deflected outwards than Bed I horn cores, but the divergence in its upper parts is less than in later SHK II horn cores.

The base of a right *Gazella* horn core 199 with the frontal, supraorbital pit, midfrontal suture and damaged orbital rim came from EF-HR in 1963. It lacks the internally hollowed frontals of *Antidorcas recki* so that the level of the frontal medial to the horn core base is no higher than the orbital rim.

An almost complete right horn core 068/6695 belongs to *Gazella* and probably came from middle or upper Bed II or possibly from Bed I.

## Sites in Upper Bed II

	TK II
Site (19)	Geologic locality 16

TK is a large gully on the north side of the Main Gorge. Beds II, III and IV are exposed over considerable areas. Excavations in the upper part of Bed II were carried out in 1963. Two trenches were cut and the following sequence, from above downwards, was exposed:

- (a) The basal part of Bed III.
- (b) 4 ft (1.2 m) of tuffs and clays interbedded with limestone, as normally occurs below the base of Bed III.
- (c) 2½ ft (75 cm) of tuff with scattered artifacts and a few fragments of bone.
- (d) A hominid occupation floor on the weathered surface of a clay at the line of contact with the overlying tuff. There were many artifacts and a number of mammalian remains.
- (e) A tuff, 1–2 ft (30–60 cm) thick, with scattered artifacts.
- (f) A second hominid occupation floor, also on a weathered clay surface, about 10 ft (3.0 m) below the base of Bed III. The horizon was excavated in one trench only and artifacts and faunal remains were concentrated at one end of this trench.
- (g) A channel 3 ft (90 cm) deep cut into the underlying Tuff IID. Artifacts and bone fragments occurred in the lower part of the filling.

The site appears to have been a camping ground which was occupied on two occasions and perhaps visited temporarily at the times when the tuffs between the lower and upper occupation floors and above the upper occupation floor were being deposited. The antelope material from this site has been considered as a single unit.

Tribe BOVINI. Left upper molars 1647, 1684a and two numbered 067/5331a, and right lower molar 1268 are smaller than molars of *Pelorovis oldowayensis* and probably belong to *Syncerus acoelotus*.

The distal end of a right humerus 067/5333 is probably *P. oldowayensis*, but the distal end of a right radius 2627 may well be the *Syncerus*. Part of the proximal end of a left radius 2623 is probably bovine.

Tribe HIPOTRAGINI. The back of a large skull 067/5310 consisting of the occipital surface, occipital condyles, bases of the paraoccipital processes, basioccipital and the right auditory bulla, is of *Hippotragus gigas*. The lack of a central longitudinal groove in the basioccipital, the small



bullae, the short basioccipital and the outline of the occipital surface are typically hippotragine. The nuchal crest is strong, as on the *H. gigas* holotype, but the shallow hollowings on either side of the median vertical line at the top of the occipital surface, which are present on the holotype and DK I skulls, are here absent. The basioccipital of this specimen is shorter than in the living roan or sable. Left M<sub>3</sub> 537 is identified as *H. gigas*.

Tribe ALCELAPHINI. There are a number of alcelaphine dentitions and single teeth and these can be divided into the same size groups as at other Bed II sites.

(i) A partial right mandible 067/5329, right upper molar 61 and left lower molar 2269 are of large size and belong in this size group.

(ii) Right upper molars 2192 and 067/5306, left upper molars 918, 1285, 1598, 067/5308, 067/5318 and 067/5332, left lower molars 1164, 1261 and 067/5308, right M<sub>3</sub> 067/5332, part of an unworn right M<sub>3</sub> 1786 and two right upper premolars numbered 067/5308 belong in this size group. An incomplete right mandible 2395, left upper molars 067/5314 and 067/5331b and left M<sub>3</sub> 2519 are smaller than the other teeth. Mandible 2395 has an alveolus in the jaw for a P<sub>2</sub>.

The distal end of a left radius 1870 and part of the proximal end of a right ulna 067/5299 are alcelaphine and large-sized, and would belong with the size group (i) teeth.

Tribe ANTILOPINI. A left upper molar 067/5308, right lower molar 067/5332 and left lower molar 067/5307 belong in this tribe. It is not possible to say whether they are *Antidorcas recki* or *Gazella*.

## BK II

Site (66) Geologic locality 94

BK lies on the south bank of the Side Gorge about 2 miles (3.2 km) above the confluence with the Main Gorge. Discovered in 1935, the site consists of two erosion gullies, west and east, linked by a short cliff which runs parallel to the river course. Beds II, III and IV are exposed in the gullies and the cliff, although Bed IV has been largely denuded. Excavations in Bed II were carried out from 1952 to 1957 and in 1963, at a level approximately 25 ft (7.6 m) above SHK II. A series of clays, tuffs, silts, sands and gravels in which artifacts and bones occurred represents the filling of an old river channel which cuts out Tuff IID in places. Cross-bedding suggests the river flowed in a north-east or south-west direction, with a maximum depth in the excavated area of 8½ ft (2.6 m). A sequence of deposits within the channel could not be established because of the cross-bedding, so the whole deposit is considered as a unit. A few of the remains from the coarser horizons of sand and gravel are rolled, but most of the material has not been transported far enough for it to become abraded. Much material of *Pelorovis oldowayensis* was found at this site and the more complete remains were found in a clay which seems to represent a swamp or quiet backwater adjoining the main river.

Former subdivisions of the site into a main area, BK II East and BK II Extension have been disregarded, except for the recording of these designations when they occur as parts of specimen field-numbers.

Tribe TRAGELAPHINI. Four isolated teeth belong in this tribe. These are right upper molar 1963.157, left upper molar 1963.3015, right lower molar 1957.695 and unworn right lower molar 1963.1615. These are of greater kudu size and are presumably of *Tragelaphus strepsiceros grandis*.

A large left tragelaphine femur 1963.802 is presumably also *T. s. grandis*.

Tribe BOVINI. A herd of *Pelorovis oldowayensis* was found at BK II and discussed by Gentry (1967). Additional material is now known. A nearly complete left horn core 1957.1509 is from a young individual. A horn core base 1952.356 and a damaged and weathered horn core piece 1963.067/1648 are also of *P. oldowayensis*. Additional isolated teeth are the right upper molars 1963.3251 and two numbered 068/5865, left upper molars 1955.37 and 1963.2127, parts of upper molars 1963.485, 1963.491, 1963.662, 1963.664 and 1963.2552, right lower molar 1963.1972, left lower molars 1955.38 and 1963.1609, right M<sub>3</sub> 1963.2486, right upper premolars 298, 067/5201 and 1963.2058, left upper premolars 1963.1447 and 1963.067/2449, upper premolar 1963.2228, right P<sub>2</sub> 1953 BK II Ext 150, left P<sub>2</sub> 1957.067/2457, left P<sub>3</sub> 1955.286 and right P<sub>4</sub> 1957.1500.

A few limb bones of *P. oldowayensis* have also subsequently been found in the National Museum of Kenya, Nairobi. These are distal end right humerus 1953 BK II Ext 8, complete left radius



1963.2201, proximal ends right metacarpals 1963.1940 and 1963.3069, proximal end right tibia 1963.2763, and distal ends right tibiae 1953 BK II Ext 178 and 1953 BK II Ext 318.

There is a considerable amount of material of *Syncerus acoelotus* at this site, as at MNK II and SHK II, the teeth being smaller than those of *P. oldowayensis* while the occlusal morphology is more complicated than in many *P. oldowayensis*. The specimens are incomplete left maxilla 1963.2757, incomplete right mandibles 1953.067/5229, 1953.067/5230, 1963.2717, 1963.2765 and 1963.2818, incomplete left mandible 1955.76, immature right mandible 1953 BK II Ext 77 (Pl. 11, fig. 2), immature left mandible 1963.3182, right upper molars 1952.133, 1953 BK II Ext 354, 1955.59, 1955.126 and 1957.858, left upper molars 1953 BK II Ext 83, 1953 BK II Ext 181 and 068/8787, right lower molar 1952.161, part of lower molar 1955.308, right  $M_3$ s 1952.128, 1953.85, 1953 BK II Ext 357 and 1957.512, left  $M_3$  1955.31, left upper premolar 1952.135, left  $P_3$ s 1963.710 and 1963.067/2479 and right lower premolar 1955.326.

There can be little doubt that nearly all the upper teeth are bovine, matching the large number of definitely identified lower jaws and single teeth. The immature mandible 1953.77 was thought to be bovine rather than hippotragine. Its  $M_1$  has a goat fold, a situation often paralleled in living *Syncerus*. The goat fold does not persist lower down, and does not appear at all on  $M_2$  or  $M_3$ . The upward curvature of the lower edge of the horizontal ramus posteriorly also suggests Bovini rather than Hippotragini. The other immature mandible 1963.3182 appears to be bovine by the large size of  $M_1$ . The occlusal morphology of these teeth is about as advanced as in the living buffalo *Syncerus caffer*. They are generally smaller than bovine teeth from the Beds III–IV junction.

Two left upper molars, 1953 BK II Ext 84 and 1957.532, are larger than the other teeth of *S. acoelotus*. However, they differ from *P. oldowayensis* by their small size, localized ribs on their lateral walls and complicated outlines of their central cavities (Gentry 1967 : 295). A left upper molar 1963.3362 is either *S. acoelotus* or *P. oldowayensis*, and a left lower molar 1952.163 and deciduous right  $P_4$  1963.1454 are either *S. acoelotus* or a hippotragine.

Some bovine limb bones smaller than *P. oldowayensis* are presumably conspecific with the smaller bovine teeth. They are proximal end right radius 1963.1628, complete right metacarpal 1952.218, distal end metacarpal 1963.824, proximal end left metatarsal 1952.226, distal ends metatarsals 1955.212, 1963.2547 and doubtfully 1952.221.

The distal end of a right humerus 1953.067/5217 from BK II East is probably bovine. The well-marked distal condyles suggest Alcelaphini, but the low level of the distal lateral end behind the hollow, the shallowness of the distal lateral hollow and the prominent extensor carpi radialis ridge on the distal lateral side are unlike alcelaphine humeri. The coronoid fossa is markedly deep and therefore unlike *Connochaetes*. The size eliminates Reduncini, and the presence of a coronoid fossa rules out Hippotragini.

Tribe REDUNCINI. A frontlet with incomplete horn cores 1953 P.P.R.1 from BK II East (Leakey 1965 : 47, *Kobus* species A) is assigned to *Kobus kob*. The distal end of a *Kobus* horn core 1953.9 was a surface find at BK II. A reduncine left  $M_3$  1957.1362 is the size of a living kob and agrees well with the  $M_3$  1957.396 from SHK II. A nearly complete left humerus BK II East 1953.442 and the distal end of a left humerus 1957.42 are very likely to be of kob by their combination of slanted distal condyles and a deep hollow on the distal end of the lateral side.

Tribe HIPOTRAGINI. *Hippotragus gigas* is represented by a left horn core, possibly female, with the orbital rim and a small part of the braincase 1953 P.P.R.5 from BK II East (Leakey 1965 : 50); a complete horn core 1963.3042 unattached to any skull part but which, by comparison with the horn cores on the *H. gigas* holotype, is from the left side; and a frontal with part of the parietal 067/5345. The horn core 1963.3042 resembles the FLK II horn core of *H. gigas* in being curved back as much as horn cores of the living roan and sable.

A partial left maxilla 1963.2226 and a right mandible with worn  $P_3$ – $M_1$  1952.149 are hippotragine. The short premolar row evident on the mandible resembles that of the *H. gigas* mandible FLKNN I 608. A few single teeth are hippotragine. These are right lower molars 1963.2713 and 1963.067/2437, left lower molar 1955.172, right  $M_3$  1953.067/5224 and deciduous right  $P_4$  1952.167. The last tooth shows an advanced complicated occlusal morphology. The proximal end of a right metatarsal 1953 BK II Ext 137 is probably hippotragine.



Tribe ALCELAPHINI. *Megalotragus kattwinkeli* is represented by the base of a right horn core 1963.2718, labelled '*Alcelaphus howardi*', and differing from the MNK II horn core of *M. kattwinkeli* only in its greater dorsoventral compression. It shows the insertion close to the mid-line, little divergence at the base and indications of horizontal ribbing on the anterior surface. The pronounced and irregular longitudinal grooving at the base of a complete right horn core 1963.3383 matches that on the holotype of *A. howardi* and suggests that this horn core is not *Connochaetes*. The specimen is narrower transversely at the base than other conspecific horn cores in Nairobi. The base of a left horn core with the frontal 1963.459 is also *M. kattwinkeli*.

*Connochaetes taurinus olduvaiensis* is represented by a complete right horn core 1963.1353, an incomplete right horn core 1957.18 and a complete left horn core 1955 P.P.F.1. The first shows quite extensive rugosity of the frontals at the horn core base, but less than in the *Connochaetes* specimens from Elandsfontein. 1955 P.P.F.1 was figured by Leakey (1965 : pl. 52 lower picture, which is not BM(NH) M 21452 as stated in the caption), shown in rear view which does not display the full extent of the curvature. The distal half of a left horn core 1963.1278, and the tip of a left horn core 1963.176 showing damage by larvae of *Ceratophaga vastella* or an allied moth, are also of this species. The distal part of a horn core 1957.1505 is extremely similar to 1957.946 from SHK II and may also be from *Connochaetes*.

*Parmularius angusticornis* is represented by a cranium with the proximal halves of both horn cores 1955 P.P.T.1 which was the holotype of *Damaliscus antiquus* Leakey (1965 : 55; pl. 67), a partial horn core 1963.14, the basal half of a left horn core 1963.2813, a partial frontlet with complete right horn core 1963.2499, a frontlet with both horn cores preserved nearly to the tips 1963.2499, a left horn core 1963.067/1650 and a complete right horn core 1961.068/6660 from BK II East.

A right horn core of *Damaliscus niro*, 1955.159, is very similar to the horn cores already described from SHK II and figured by Leakey (1965 : pl. 55). Its large basal mediolateral diameter diminishes rather rapidly. Other BK II horn cores tentatively assigned to *D. niro* have a different morphology, and have already been listed as types A and B in the species account of *D. niro*; one of them, right 1957.365, had been identified by Leakey (1965 : 51) as *Hippotragus* cf. *equinus*. A fragment of a larger horn core 1953.067/5235 P.P.R.2 (assigned to *Hippotragus* cf. *niger* by Leakey 1965 : 50) has extensive grooving from the activities of a moth larva allied to or the same as the living *Ceratophaga vastella*. A partial skull roof showing the positions of the horn core bases 1963.478 is most likely to be of *D. niro*.

A frontlet without horn cores 1953.067/5460 from BK II East can be assigned to the same species as the horn cores 1941 F.3000 and SHK II 1953.280 by its braincase (see p. 417). The braincase roof bends quite strongly downwards a little way behind the level of the horn core bases. The right frontal is preserved and an internal frontal sinus is present. It is a smaller individual than the other specimens and is the only record of the species at this site.

An incomplete left horn core with the midfrontal suture 1957.662 is of *Aepyceros melampus* (Leakey 1965 : 65; Gentry 1966 : 104); it is one of the few records of the genus at Olduvai.

There is a more complete series of alcelaphine dentitions at BK II than at other Bed II sites, consisting of some 30 partial mandibles and six incomplete maxillae which can be divided into two size groups. None of the dentitions in either size group shows an occlusal morphology as complicated (advanced) as teeth of living *Alcelaphus* or *Damaliscus*.

(i) According to the size and morphology of the teeth on the neotype skull of *Megalotragus kattwinkeli*, the largest dentitions belong to this species. These are left maxilla 1963.2980, immature left maxilla 1963.458, right mandibles 1952.120, 1953 BK II Ext 78, 1955.75, 1957.15, 1957.713 and 1963.2255 and left mandibles 1952.122, 1957.699, 1957.712, 1957.979 and 1957.39 from BK II East. A right mandible 068/5536 is either from this site or SHK II. The mandible 1957.979 has  $M_1$ – $M_3$  preserved and the remains of  $P_3$  and  $P_4$  which have broken off, but no alveolus in the jaw for a  $P_2$ . The mandible 1952.122 has a basal pillar on the  $M_3$ . A number of dentitions are slightly smaller, but still large, and these presumably belong to *Connochaetes*. They are left maxilla 1963.670, and left mandibles 1952.148, 1952.622 and 1963.3177. The mandible 1952.148 has  $P_4$ – $M_2$  preserved and the remains of  $P_3$ , while 1952.622 has  $P_3$ – $M_1$  preserved; neither of these jaws has an alveolus for a  $P_2$ . To this size group are assigned 47 upper and 15



lower isolated teeth of large size. The group would have limb bones in the alcelaphine category 'large'.

(ii) Several smaller dentitions are about the size of the living hartebeest and slightly larger than Bed I *Parmularius altidens*. These presumably belong to *P. angusticornis* and *Damaliscus niro*. They are associated right and left maxillae 1952.067/6647 and 067/6646, immature maxilla 1953.067/5219, right mandibles 1957.34, 1963.24, 1963.1065 and 1963.1442, left mandibles 1952.150, 1952.151, 1953 BK II Ext 76, 1957.21, 1963.935, 1963.941, 1963.2444 and 1963.3139, immature right mandibles 1963.291 and 1963.067/1625, and immature left mandible 1963.2550. The adult mandibles 1953 BK II Ext 76, 1963.24, 1963.935, 1963.1065 and 1963.3139 all lack an alveolus in the jaw for a  $P_2$ . In the immature mandibles 1963.291 and 1963.2550 deciduous  $P_2$  or its alveolus is present, but in 1963.067/1635 there is no alveolus for a deciduous  $P_2$  and at this early stage  $P_2$  is already missing. Some of the mandibles in this size group, 1963.1065 and 1963.2444 for example, have enough of the mandibular ramus preserved to show that this is deeper under the teeth than in the living hartebeest, and in this respect they resemble the wildebeest. However, the size of the tooth row relative to this depth is too small for *Connochaetes*. These mandibles resemble those with deep rami at HWK East II but are slightly smaller. A left mandible 1957.1452 with  $P_3$ - $M_3$  is smaller than the living hartebeest and is probably a different species from the other specimens, perhaps *Damaliscus agelaius*. It lacks an alveolus for a  $P_2$ . In this size group are included 60 upper and 55 lower isolated teeth, although some may belong in size group (i); the difficulty is because we do not know whether an isolated molar is  $M_1$ ,  $M_2$  or  $M_3$ , coupled with the size variations occurring within any one species.

As at other Bed II sites, the alcelaphine limb bones can be divided into two sizes but, among specimens from the 1963 excavation at least, the large size grouping has become more variable. This is unlike SHK II but recalls the earlier sites DK I, FLKNN I, HWK East II and MNK II. The proportion of large limb bones is greater here than at SHK II. The 'large' limb bones are as follows.

Distal ends right humeri 1953 BK II Ext 126 and 1963.378, distal ends left humeri 1957.519, 1963.2440 and 1963.2762, complete left radii 1953 BK II Ext 426+428 and 1963.854+863, proximal ends right radii 1953 BK II Ext 189 and incomplete 1963.644, proximal ends left radii 1953 BK II Ext 50 and incomplete 1963.195, distal ends right radii 1953 BK II Ext 427 and immature 1953 BK II Ext 430, distal ends left radii 1953.067/5234 and 1957.717, complete right metacarpals 1952.219 and 1963.2609, proximal ends right metacarpals 1952.227 and 1963.3378, proximal ends left metacarpals 1953.067/5474 and 1957.541, distal ends metacarpals 1953 BK II Ext 412, 1957.1038, 1963.401 and 1963.3231, incomplete proximal end right femur 1963.403, proximal ends left femora 1953 BK II Ext 8, 1953 BK II Ext 119 and 1955.7, distal ends right femora 1952.83 and 1963.2626, distal ends left femora 1952.81, 1952.82, 1952.211, 1953 BK II Ext 068/6697, 1955.067/5395, 1963.3039 and immature 1952.346, complete right tibiae 1953 BK II Ext 417, 1957.1379, 1963.3036 and immature 1963.801, complete left tibia 1963.2680, proximal ends left tibiae 1952.212 and 1955.316, distal ends right tibiae 1952.215, 1952.229, 1953 BK II Ext 420, 1957.067/5393, 1963.16, 1963.769, 1963.934 and 1963.1934A, distal ends left tibiae 1953 BK II Ext 419, 1955.107B, 1955.283, 1963.1276 and 1963.3232, complete left metatarsals 1953 BK II Ext 416, 1953.067/5508 and 1953.067/5509, proximal ends right metatarsals 1953 BK II Ext 137, 1955.175 and 1963.2434, and distal ends metatarsals 1952.222, 1952.223 and 1953 BK II Ext 411.

The distal ends of tibiae 1955.107B and 1963.769 have some characters resembling Tragelaphini, such as the rear of the back fibula facet being forward from the edge of the bone and the short medial malleolus, but the fairly marked tuberosity on the anterior surface suggests that they are alcelaphine. The metatarsal 1953.067/5509 is short and has an anterior groove, a deep foramen at the top of the posterior surface and deep hollows on the lateral and medial sides of the distal condyles. It has poor flanges on the anterior surface distally and lacks deep hollows above the distal condyles posteriorly. It most probably belongs to *Connochaetes*.

Limb bones of the 'small' category are as follows.

Proximal end right humerus 1953.067/5215, distal ends right humeri 1963.2492 and 1963.2716, distal ends left humeri 1955.263 and 1963.2639, complete left radii 1957.26 and 1957.1466, proximal ends right radii 1953 BK II Ext 173 and immature 1957.1193, proximal ends left radii 1953 BK II Ext 429, 1953.067/5386, 1957.882, 1957.1185 and 1963.2599, distal ends right radii 1952.067/5388, 1953 BK II Ext 067/5209 and 1957.517, distal ends left radii 1953.067/5214, 1955.215 and 1957.1194, right ulna



1963.449, left ulnae 1963.30, 1963.2624 and incomplete 1963.1941, complete right metacarpal 1957.1381, complete left metacarpals 1963.2311 and 1963.3229, proximal ends right metacarpals 1957.15 and 1963.860, proximal end left metacarpal 1957.1469, distal end metacarpal 1957.919, proximal ends left femora 1952.308, 1963.2245 and damaged 1963.2516, distal ends right femora 1953 BK II Ext 30, 1953 BK II Ext 067/5390 and 1955.068/6698, distal ends left femora 1953 BK II Ext 322 and 1953.068/6701, proximal end right tibia 1953 BK II Ext 422, proximal ends left tibiae 1952.217, 1952.632 and 1955.068/6700, distal ends right tibiae 1953 BK II Ext 320, 1953 BK II Ext 321, 1955.36, 1955.107A, 1955.253 and 1957.40 from BK II East, distal ends left tibiae 1952.216, 1953 BK II Ext 177, 1955.319, 1957.57 and immature 1963.067/1633, immature right metatarsal 1957.1192, proximal ends right metatarsals 1955.067/5467 and 1963.2445, distal end metatarsal 1953.207 from BK II East, and the associated complete right femur 1953 BK II Ext 067/5364, complete right tibia 1953 BK II Ext 067/5363 and complete right metatarsal 1953 BK II Ext 067/5506.

A few limb bones are smaller than the others of this category. These are distal ends right humeri 1963.397 and 1963.1642, complete right metacarpal 1953 BK II Ext 337, complete right tibia 1957.1261, proximal end left metatarsal 1953.068/6699 and distal ends metatarsals 1952.224 and 1957.1265.

Tribe ANTILOPINI. An almost complete right horn core 1955.71 is of *Antidorcas recki* (Gentry 1966 : 79).

A nearly complete left horn core 1955.218+226 is most probably *Gazella* (Gentry 1966 : 65). Although a little longer and set slightly further from the midfrontal suture, it would be conspecific with the right horn core 1953.285 from SHK II. Despite the very deep postcornual fossa, these horn cores could not be considered as reduncine as they lack forward curvature in their upper parts and are not inserted sufficiently obliquely in side view. An incomplete mandible 1952.152 would probably have a ramus too shallow under the tooth row for *A. recki* and, like the mandible SHK II 1957.793, may well belong to *Gazella* (Gentry 1966 : 66).

A few single teeth and parts of limb bones belong in this tribe. These are right upper molar 1963.2740, left upper molars 1957.1084 and 1963.067/2466, distal end right humerus 1963.3253, distal end left humerus 1957.1039, complete right radius 1963.3037, distal end right radius 1953 BK II Ext 42, proximal end left metacarpal 1957.1264 and distal end left tibia 1963.1365. It is not possible to say whether these would belong to *A. recki* or *Gazella*.

Two horn core bases from this site, right 1957.991 and left 1955.63, appear to be of an antilopine like *Gazella* but with no flattened lateral surface and with considerable divergence (see p. 445). Both specimens have the frontal suture, supraorbital pit and part of the braincase preserved. The same species occurs at MNK II and two horn cores were found on the surface of DK I. It has been listed as 'Antilopini sp. 1'.

SUMMARY. The large size of later Bed II bovids is well shown at BK II by the herd of *Pelorovis oldowayensis*, a number of large *Hippotragus gigas* and the dentitions of *Megalotragus kattwinkeli*. *M. kattwinkeli* and *Connochaetes taurinus*, the largest alcelaphines, are relatively commoner than at earlier Bed II sites. *Damaliscus niro* is common. Antilopini are poorly represented by only one *Antidorcas* horn core and one horn core of *Gazella*. The numbers of bovid bones of each species are shown in Table 9.

#### Other remains from Upper Bed II

Tribe TRAGELAPHINI. A right upper molar 720 and left upper molar 1220 are from GRC II and are assigned to *Tragelaphus strepsiceros grandis*.

Tribe BOVINI. A right lower molar 640 of *Pelorovis oldowayensis* was found at GRC II in 1952. A left mandibular fragment and a distal metatarsal of *P. oldowayensis*, both unnumbered, are known from MRC II.

The holotype cranium of *Syncerus acoelotus* 068/5811 was recovered from basal gravels at Kar K in 1962. Other pieces of the same species are a cranium collected from FK West in 1962 (National Museum of Tanzania OF 67.48), part of a right mandible 068/5795 which may be associated with the last cranium, a right maxilla 068/6655 from the surface of Rhino K in 1962 and a left metatarsal 068/6662 from SC in 1962.



Table 9 Numbers of bovid bones at BK II

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
<i>Tragelaphus strepsiceros grandis</i>	—	—	—	4	1	5	1	—
<i>Pelorovis oldowayensis</i>	28 (1)	—	11	71	76	186	13	1
<i>Syncerus acoelotus</i>	—	1	8 (2)	19	8	36	6	1
Bovini total	28	1	19 (2)	90	84	222	19	2
<i>Kobus kob</i>	2	—	—	1	2	5	2	—
<i>Hippotragus gigas</i>	3	1	1	5 (1)	—	10	2	1
<i>Megalotragus kottwinkeli</i>	3	2 (1)	11	—	—	16	5	1
<i>Connochaetes t. olduvaiensis</i>	5	1	3	—	1	10	3	—
<i>Parmularius angusticornis</i>	7	—	—	—	—	7	5	—
<i>Damaliscus niro</i>	26	—	—	—	—	26	10	—
Alcelaphini sp. 3	1	—	—	—	—	1	1	—
Alcelaphini size group (i)	—	—	—	62 (1)	67 (3)	129	—	—
Alcelaphini size group (ii)	—	3 (1)	15 (3)	115 (3)	61 (3)	194	—	—
Smaller Alcelaphini, group (ii)	—	—	1	—	7	8	—	—
<i>Aepyceros melampus</i>	1	—	—	—	—	1	1	—
Alcelaphini total	43	6 (2)	30 (3)	177 (4)	136 (6)	392	—	—
<i>Antidorcas recki</i>	1	—	—	—	—	1	1	—
<i>Gazella</i> sp.	1	—	1	—	—	2	1	—
Antilopini sp. 1	2	—	—	—	—	2	1	—
Antilopini sp. indet.	—	—	—	—	3	6	9	—
Antilopini total	4	—	1	3	6	14	3	—



Tribe REDUNCINI. A kob frontlet with complete horn cores 068/6659 was found at ? MRC II in 1962, and is smaller than the large kob frontlet and horn core from JK2 GP8 III.

Tribe ALCELAPHINI. A horn core of *Damaliscus niro* 068/5692 and a few alcelaphine teeth were recovered from GRC II in 1963.

A complete right horn core 068/6654 of *Beatragus antiquus* came from Kit K II at the first fault in 1962.

A left horn core F.3001 P.P.F.5 is probably a male of *Parmularius angusticornis* (p. 388). The fossil is marked 'Bed II *in situ*' and came from upper Bed II in 1941 (Leakey 1965 : 60).

### Sites in Bed III and above

#### JK2 sites

Sites (20, 21)      Geologic locality 14

The JK2 sites lie on the north side of the Main Gorge between the third and fourth faults. Beds II–IV are present, except that in this area the separate Beds III and IV give way in a westward direction to Beds III–IV as an indivisible unit. However, the excavated occupation sites are known to be in Bed III.

From the base of Bed IV downwards the following levels are found (R. L. Hay, personal communication, September 1973):

- (a) A grey clay.
- (b) A prominent horizon of markedly red clay.
- (c) A grey clay, this being the level for the occupation site of trench 8, referred to below as the GP8 excavation.
- (d) A siltstone, the so-called pit bed.
- (e) A sandstone horizon which in its lower parts becomes a conglomeratic sand. The artifacts and fossils excavated in trenches A and B (= JK2 A and JK2 B in the following pages) came from this level, about 1.5 m below trench 8 and 2.7 m above the base of Bed III. These two trenches were formerly believed to have been dug in a channel cutting and therefore to be higher in the section than trench 8, but it is now known that this is not so.
- (f) Clay horizons, again giving way below to a conglomeratic sand.
- (g) A clay horizon, the base of which rests on Bed II 39 ft (11.8 m) below the top of Bed III.

#### JK2 III

Tribe TRAGELAPHINI. Four single teeth belong in this tribe. These are right upper molar A.3220 J3, part of a lower molar A.325, right upper premolar JK2 b and deciduous right upper premolar A.1530 J.

The proximal end of a left femur, labelled 'JK2 Top', is tragelaphine. It is rather small compared with the femur 1963.802 from BK II assigned to *Tragelaphus strepsiceros grandis*.

Tribe BOVINI. A number of partial dentitions and isolated teeth are bovine. These are right maxilla A.1021, right mandible A.2833, left mandible JK2 b, right upper molars A.975, A.2859, B.FL2, B.FL2-19, B.FL3-16, B.FO3-40 and one from the scree in trench B, left upper molars A.188, A.1091, incomplete A.2101 and one from the scree in trench B, part of an upper molar JK2 b, right lower molars A.1913 I and A.3210, left M<sub>3</sub> B.FFM5-6, parts of lower molars A.370, A.2533, A.N30, B.FO8-5, B.S/F II 43 and two found in 1961, left P<sub>2</sub> A.3270 F3a, and left lower premolars A.3270 G3, B.FL3-79 and JK2 Top. These are presumably of *Syncerus acoelotus* although the larger ones, mandible JK2 b and upper molar A.188 for example, might be of sufficient size for *Pelorovis antiquus*, were this species to occur at so early an horizon.

A few limb bones belong in this tribe. They are distal end right humerus JK2 B, distal end left humerus B.FFL5-6, proximal ends left radii A.1951 and B.FIF N4-14, distal epiphysis of right radius JK2 b, distal end metacarpal A.1830, part of the distal end of left tibia A.1515 and part of the proximal end of right metatarsal A.2879. The bones are of large size and proximal end radius A.1951, distal end metacarpal A.1830 and distal end tibia A.1515 are as large as Bed II *P. oldowayensis*. The medial malleolus on distal end tibia A.1515 is short as in the *Syncerus* and *Pelorovis* group of African bovines (see Gentry 1967 : 282).



Tribe REDUNCINI. A left upper molar A.1438 N is only just larger than upper molars of living *R. redunca* and is probably *Redunca*. A right lower molar JK2 b and deciduous left P<sub>4</sub> A.3271 M8 are probably of a kob-sized reduncine, as at JK2 GP8 III. A larger reduncine left lower molar B.FFM4-9 is from a waterbuck-sized reduncine.

The distal end of a right tibia JK2 b is reduncine and of *Kobus* rather than *Redunca* size.

Tribe HIPPOTRAGINI. The base of a large left horn core A.2677 is probably *Hippotragus gigas*. Three single teeth are of *Hippotragus* and presumably *H. gigas*. They are right lower molar A.3028, left lower molar A.2838 and part of a right lower molar found in 1961.

Tribe ALCELAPHINI. *Megalotragus kattwinkeli* is represented by a complete right horn core, A.72 found in 1961, with the frontal, orbital rim and a series of supraorbital pits preserved. It agrees well with other specimens in the close, posterior horn core insertions, divergence at the base decreasing higher up and strong transverse ridges. The base of the horn core is swollen anteriorly. The horn core is smaller than some other specimens of the species, MNK II 3258 for example, and is therefore possibly a female. It is not dorsoventrally compressed. Part of the right side of the braincase of this fossil is preserved, numbered A.78, but is separated from the horn core. The basal half of a left horn core with the frontal preserved, A.2426, is also *M. kattwinkeli* and demonstrates the extreme bending down of the braincase on the facial axis in this species. It too has a swollen base anteriorly.

*Damaliscus niro* is represented by a horn core complete to the tip but without a base, marked '1963 JK2 Bed IV basal gravel *in situ*', and the proximal half of a horn core also marked '1963 JK2 Bed IV *in situ*'. They show the characteristic features of this species, being very compressed, with a flattened lateral surface, transverse ridges on the front surface, wider at the front than behind and backwardly curved in side view. They are as large as the horn cores from SHK II and BK II 1955.159. The basal part of a left horn core of *D. niro* A.1130 has the orbital rim and part of the frontal preserved; it lacks transverse ridges, but there is a postcornual groove and the frontal behind the horn core descends too steeply for *Hippotragus*. The base of a right horn core A.118 is also of *D. niro*. Parts of a horn core A.976 and a right horn core A.2348 are like the type A horn cores from BK II tentatively assigned to *D. niro*.

A fairly small right horn core, A.03 220 recovered in 1961, is referred to *Parmularius rugosus* (p. 392). It is clearly alcelaphine by its internal frontal sinuses, postcornual groove and fairly complex curvature.

A frontlet A.1129 with the proximal half of the right horn core and both orbital rims, and an almost complete left horn core B.E/S K7-1 with the frontal, parietal, complete orbital rim and the supraorbital pit, are of *Rabaticeras arambourgi* (p. 408). Both specimens were recovered in 1962. A fragmentary left horn core A.346 found in 1961 is also of this species.

Two horn cores agree well with those of the herd of *Damaliscus agelaius* excavated from Fifth Fault Korongo (site VFK) III-IV. These are a left horn core A.1446 found in 1962 and a partial horn core marked '1961 B.T.T.F. Floor'. The distal part of a horn core A.345 is probably *D. agelaius*.

The alcelaphine dentitions and single teeth can be divided into two size groups as at the Bed II sites.

(i) An incomplete right mandible A.2828 and left mandible A.3261 are of *Connochaetes* or a rather small *Megalotragus kattwinkeli*. The molars have a somewhat simple occlusal pattern as in *M. kattwinkeli*. A number of large isolated teeth belong in this size group. These are right upper molars A.594 KG, A.1213, A.1914, A.2011, A.2271, A.2334 H, A.2257, A.2573, A.2808, B.FL3, B.F3-29, B.FO4-25, B.FP4-21, one from the scree in trench B, two labelled JK2 b and two labelled JK2 Top, left upper molars A.2931, A.3273, B.FP6-42, one from the scree in trench B, and one labelled JK2 Top, right lower molars A.1424, A.2810, B.FP7-1, JK2 b and one from the scree in trench B, left lower molar A.2000, right M<sub>3s</sub> A.1739, A.1955, A.2584 M8, A.2718 and B.FP4-2, and left M<sub>3s</sub> A.1099, A.1821, A.2078 and A.3020. A left upper molar A.990 is larger than the others.

(ii) Two partial right maxillae labelled JK2 and a right maxilla labelled JK2 Top belong in this size group. There are also the right mandibles A.1444, A.2060, A.2091, A.2780, A.2934,



A.3012, B.FQB-1 and B.FQ4-10, left mandible B.FL2-21 and immature right mandible A.2157. The mandibles A.2060, A.2091, B.FQB-1 and B.FQ4-10 all lack an alveolus in the jaw for a P<sub>2</sub>. Both upper and lower molars have more complicated central cavities, with a greater development of indentation, than teeth of this size group in Bed II. A few mandibles are smaller and agree in size and morphology with dentitions of the VFK III–IV herd of *Damaliscus agelaius* with which they are presumably conspecific. They are the left mandibles A.384, A.1372, B.FFM3-14 and 1963.068/6692. Both A.384 and 1963.068/6692 lack an alveolus in the jaw for a P<sub>2</sub>. 149 upper and 187 lower isolated alcelaphine teeth belong in this size group.

The alcelaphine limb bones can also be divided into two size groups as at the Bed II sites. The category of 'large' limb bones consists of distal ends right humeri A.556, A.2444 and B.S/F II 39, distal end left humerus A.817, proximal end left radius A.1322, distal end right radius JK2 IV gravel, distal end left radius A.758, complete left metacarpal A.1272, distal ends metacarpals A.719, A.1201, A.1455, A.1859 and B.FQ2-2, distal end left tibia JK2 Top and distal end metatarsal B.FFN5-12. These would belong with the teeth of size group (i). The bones are presumably at least partly of *Megalotragus kattwinkeli*.

Most of the limb bones are 'small' sized. They would belong with the teeth of size group (ii). They are distal end right humerus B.II 10, complete right radius A.1305 + 1491, proximal end left radius B.II, distal ends right radii A.3218, B.FFM3-2 and JK2 b, distal ends left radii A.1454 and B.S/F II 33, left ulna A.1048, complete right metacarpal A.1592, proximal end right metacarpal B.FM5-8, proximal end left metacarpal A.1402, distal ends metacarpals A.646, A.1517 and B.II 36, proximal end right tibia A.1565, proximal end left tibia A.1627, distal ends left tibiae A.L6 135 and JK2 b, proximal ends right femora A.708 and A.926, proximal ends left femora A.142 and A.2198, distal end left femur A.343, complete left metatarsal A.1671, proximal end immature left metatarsal A.2122 and distal ends metatarsals A.376, A.871, A.1872 and B.3. Some of the bones are transitional to the 'large' category. A few limb bones are smaller than the others in this category. These are distal end right humerus A.1219, proximal end right radius A.2077, proximal ends left radii A.1701, JK2 and JK2 Top, right ulna A.1882, proximal end left tibia A.433, distal end right tibia B.34, distal end left tibia B.FFM11-5 and distal end metatarsal A.1478.

Tribe ANTILOPINI. This tribe is represented by two mandibles, a right B.FM4-7 and a left from the scree in trench B. On the left one it can be seen that there is an alveolus for a P<sub>2</sub>. There are also a number of isolated teeth. These are right upper molars A.1595 M9, A.1696 J, A.4524 J and JK2 B, left upper molars A.725, A.1696 L and JK2 b, right lower molars A.1643 and A.3271 MO, left lower molars A.963 and one from the scree in trench B, left M<sub>3s</sub> A.1696 L and one from the scree in trench B, left P<sub>3</sub> and P<sub>4</sub> JK2 b and a lower premolar A.1643. They are likely to be of *Antidorcas recki*.

SUMMARY. By JK2 III times a different representation of bovids from that at the Bed II sites has appeared. There is no definite *Pelorovis*, and the bovine remains are of *Syncerus acoelotus*. *Megalotragus kattwinkeli* and *Damaliscus niro* are still present, as in Bed II, but the sparsely represented *Parmularius* is *P. rugosus* and not the common Bed II *P. angusticornis*. *Rabaticeras arambourgi* is a new arrival among the fossils. Antilopine remains are few.

The numbers of bovid bones of each species at JK2 III are shown in Table 10. Alcelaphine teeth and limb bones of size group (i) are likely to be of *Megalotragus kattwinkeli*, and those of size group (ii) would include *Damaliscus niro* and *Rabaticeras arambourgi*. The most likely identity for the smaller alcelaphines of size group (ii) is *Damaliscus agelaius*.

#### JK2 GP8 III

Tribe BOVINI. Right mandibles GN 24 and Sec 6, right upper molars GN 5 and GN 21, parts of two lower molars Sec 4 1334 and 1335 and a left P<sup>4</sup> labelled 'GP8 Sec 8' are likely to be of *Syncerus acoelotus*. The teeth are smaller than in *Pelorovis oldowayensis* and have a more complicated occlusal pattern. The P<sub>4</sub> on mandible GN 24 has a closed metaconid–paraconid wall which is unlike *S. acoelotus* teeth, but this could be because the tooth is very worn.

Tribe REDUNCINI. A complete right horn core 1247 and a frontlet with complete left and nearly



**Table 10** Numbers of bovid bones from JK2 III

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
<i>Tragelaphus</i> sp.	-	-	-	4 (1)	1	5	1	1
<i>Syncerus acoelotus</i>	-	1	2	26	8	37	3	-
<i>Kobus</i> spp.	-	-	-	3 (1)	1	4	-	-
<i>Redunca</i> sp.	-	-	-	1	-	1	1	-
<i>Hippotragus gigas</i>	1	-	-	3	-	4	1	-
<i>Megalotragus kottwinkeli</i>	2	-	-	-	-	2	2	-
<i>Damaliscus niro</i>	6	-	-	-	-	6	3	-
<i>D. agelaius</i>	3	-	-	-	-	3	1	-
<i>Rabaticeras arambourgi</i>	2	-	-	-	-	2	2	-
<i>Parmularius rugosus</i>	1	-	-	-	-	1	1	-
Alcelaphini size group (i)	-	-	2	39	15	56	-	-
Alcelaphini size group (ii)	-	3	10 (1)	336	30 (1)	379	-	-
Smaller Alcelaphini, group (ii)	-	-	4	-	10	14	-	-
Alcelaphini total	14	3	16 (1)	375	55 (1)	463	-	-
<i>Antidorcas recki</i>	-	-	2	16	-	18	2	-



complete right horn cores 068/6694, both excavated in 1962, are of *Kobus kob* but with some differences from the living representatives of this species. The postcornual fossae are not preserved. A reduncine left M<sub>3</sub> GN 47 can probably be regarded as conspecific with the horn cores. It is larger than the teeth of the MNK II kob and the left M<sub>3</sub> from SHK II attributed to a kob.

The lower part of a damaged left horn core 1654 found in 1961 is probably of *Kobus ellipsiprymnus*. It has almost no mediolateral compression.

Tribe ALCELAPHINI. Two complete right horn cores, 674 and S.6 1627a both excavated in 1962, are of *Damaliscus niro*. They are compressed with flattened lateral surfaces, wider at the front than behind, and backwardly curved in side view, as is typical of the species. 674 lacks transverse ridges on the front surface. It is fairly thick at the base, as in SHK II 1953.282, with the cross-section widest anteriorly. It has a postcornual fossa and the braincase is strongly angled on the face. Both specimens are as large as the SHK II horn cores 1953.282 and 1957.1184. A partial horn core GN 44 also belongs to this species.

Left mandibles GN 16 and Sec 5 1614+1615 are the size of group (ii) dentitions in Bed II. GN 16 can be seen to have an alveolus in the jaw for P<sub>2</sub>. A right mandible from Sec 6 is smaller than the others and is the size of dentitions of the VFK III–IV herd of *Damaliscus agelaius*. A left upper molar GN 53, right M<sub>3</sub> 286, left M<sub>3</sub>s 1501 and Sec 6, and right lower premolar GN 54 are alcelaphine. A left upper molar GN 36 is larger than the others.

A complete right metacarpal GN –, proximal end left metacarpal GN 54, complete left tibia GN 22 and proximal end right tibia GN 38 are 'small' sized alcelaphines and would go with the size group (ii) dentitions.

Tribe ANTILOPINI. A left mandible with P<sub>4</sub> and M<sub>1</sub> preserved, and a left lower molar, both labelled 'GP8 Sec 6', belong in this tribe. It is not possible to determine whether they are *Antidorcas recki* or *Gazella* sp.

#### Other remains from Bed III

Tribe TRAGELAPHINI. Part of a large tragelaphine horn core was found at JK1 in 1961 and is said to be from Bed III. The piece is from the left side and agrees with *Tragelaphus strepsiceros grandis* in its clearly triangular cross-section.

#### Remains from Beds III–IV (undivided)

Tribe BOVINI. A left maxilla with M<sup>1</sup> and M<sup>2</sup> which was a surface find from BK III–IV in 1955 could be either *Syncerus acoelotus* or *Pelorovis antiquus*.

A partial juvenile skull of *Syncerus acoelotus* came from the Bos K III–IV surface in 1962, and a frontlet from VFK high in the Beds III–IV unit in 1961. These pieces are both in Dar-es-Salaam with the numbers OF 68.274 and OF 68.196 respectively.

Tribe ALCELAPHINI. Several skulls, mandibles and associated skeletons of a herd of *Damaliscus* were excavated from VFK III–IV in 1962 and have been diagnosed as a new species, *D. agelaius*, in the preceding pages. The herd consists of a male cranium 214; skulls 133, 134, 140, 143, 150, 176, 235, 298, 350, 357, 359, 363 and one without number which are probably all females, most with complete horn cores and maxillae, and 134, 350 and 363 with associated mandibles; partial skull 172; back of a skull without number; three horn cores presumably of females; a palate; right mandibles 154 and 171 and left mandible 156; and a large number of limb bones and vertebrae, mostly rather crushed and embedded in matrix. A right horn core 068/6661 from the surface of Hoopoe Gully was found in 1962, and a frontlet 068/5730 labelled XDK was found in 1961. Both are males of this species. The first probably came from Beds III–IV (undivided) or perhaps Bed II, while the second could have come from the same units or even from Beds III or IV.

#### Remains from Bed IV

Tribe TRAGELAPHINI. The cranium of *Taurotragus arkelli* F.3665 P.P.T.4 (Leakey 1965 : 43; pls 43–44) came from the surface of Bed IV between LK and RK in 1941.

Tribe BOVINI. A right upper molar 689 from GC IV is either *Syncerus acoelotus* or *Pelorovis antiquus*.



Tribe REDUNCINI. A left horn core 068/6658 of *Kobus ellipsiprymnus* was found at the junction of Beds III and IV at EF-HR in 1962. It was a surface find.

Tribe ALCELAPHINI. A frontlet of *Megalotragus kattwinkeli* 068/6664 was found *in situ* at GTC IV in 1962. It is rather small, but agrees with other specimens in the close insertions, divergence and curvature of the horn cores, and is possibly a female. The horn cores are not dorsoventrally compressed. Part of a braincase found with the frontlet appears to belong to a small tragelaphine. The base of a right horn core with the frontal 596 from GC IV is also *M. kattwinkeli*. It is very anteroposteriorly compressed.

A partial skull 068/5976 came from east of the second fault in upper Bed IV or the Masek Beds in 1963. It is well-preserved and not crushed but lacks horn cores and teeth. It has been rather doubtfully linked with *Rabaticeras* or *Alcelaphus* (p. 417).

The distal part of a horn core from the surface of Bed IV, F.971 found in 1941, is *Damaliscus niro*.

#### Recent excavations in Beds III and IV and the Masek Beds

Since 1969 Mrs M. D. Leakey has undertaken further excavations in Bed IV, and we have been able to see some of the bovid material during a visit to Africa in autumn 1973.

JK FERRUGINOUS SAND, BED III, 1969. Part of a right mandible 356 with  $M_1$  and  $M_2$  is an alcelaphine of size group (ii). The  $M_2$  has an occlusal length of 21.4 mm. There are also six other alcelaphine teeth of size group (i) and nine of size group (ii).

JK GREY SAND, BED III, 1969. Apart from two left lower molars of *Syncerus*, 623 and 657, the other remains from this site are of Alcelaphini. Part of a left mandible 475 has  $P_4$  and the molar row, an alveolus for  $P_3$  but no alveolus for  $P_2$ . Part of a left mandible 472 has  $M_1$  to  $M_3$ , and part of a right mandible 697 has  $M_2$  and  $M_3$ . All three mandibles belong to size group (ii). In addition there are three teeth of size group (i) and nine of size group (ii).

JK SANDSTONE ABOVE PITS, BED III, 1969. There were found in two trial trenches a fragment of a left mandible with  $M_2$  and  $M_3$ , two left  $P_4$ s and an atlas vertebra, all alcelaphine.

JK, BED III, 1969. A right upper molar, III/4 607, belongs to *Pelorovis oldowayensis*, and the distal end of a right humerus, III/7 1042, is alcelaphine.

JK2, BED III, 1969. A cranium with horn cores is marked TT 1 and belongs to *Parmularius rugosus*.

HEB IV, 1969. A right lower molar is bovine and a right upper molar alcelaphine.

HEB EAST IV, 1969. A frontlet with horn cores 814 is of *Antidorcas* and may be *A. recki* or an early example of *A. marsupialis*.

HEB WEST IV, 1969. A right mandible IV/3 1540 with  $P_4$  to  $M_3$  is an alcelaphine of size group (ii) and the  $P_4$  and  $M_3$  are erupting. Another alcelaphine right mandible has deciduous  $P_4$  and  $M_1$  with an erupting  $P_3$ , but is of size group (i). Three other alcelaphine teeth are all of size group (i).

A tragelaphine and a bovine left upper molars also come from this site.

PDK IV, 1969–70. The base of a right and a left horn core, 969 and 970, belong to *Tragelaphus strepsiceros*. The anteroposterior and mediolateral diameters at the base of 969 were 56.5 and c. 47.6 mm.

The base of a left horn core 1498 from trench IV appears to be of *Rabaticeras arambourgi*. We also saw seven alcelaphine teeth of size group (i).

A left and a right upper molar belonged to the Antilopini.

WK IV, 1970. This site is discussed by M. D. Leakey (1971a).

A nearly complete left horn core 3641 belongs to *Taurotragus*.

A left  $P_3$  5353 belongs to the Bovini.

Part of a right mandible with  $P_2$  and  $P_3$  is from a large reduncine.

Part of a right mandible 2196 with deciduous  $P_4$ ,  $M_1$  and  $M_2$  is an alcelaphine of size group (i). There are seven other alcelaphine teeth of size group (i) and two of size group (ii).

Part of a left mandible 716 with  $M_2$  and  $M_3$  belongs to the Antilopini and there are five other teeth of this tribe. 1580 is a complete right radius of an antilopine with a length and least thickness of 164 and 17.1 mm.



WK EAST IV A, 1970. A right lower molar 3354 is tragelaphine.

A nearly complete right horn core 2305(5) belongs to *Pelorovis antiquus*.

A left  $M_3$  1922 with occlusal length 45.3 and height 45.1 mm and a left lower molar 1698 are both *Syncerus*. A left upper molar 3287 is also bovine.

A right lower molar 814 is reduncine.

2866 is part of a left alcelaphine mandible with  $M_2$  and  $M_3$  which can be put into size group (i). 3029 is part of an alcelaphine right mandible of size group (ii) preserving  $P_4$  and  $M_1$ . There are also eleven other alcelaphine teeth of size group (i).

A right mandible with damaged molars, 486, is antilopine.

WK EAST IV C, 1970. Two left lower molars, 190 and 660, are bovine, the second being probably an  $M_3$  and probably *Syncerus*.

A left upper molar 355 is reduncine.

Six alcelaphine teeth belong to size group (i).

Two right upper molars are of Antilopini.

FLK, MASEK BEDS, 1969. We saw from this site a reduncine right upper molar, three alcelaphine teeth and a right upper and left lower molar and a left  $M_3$  of an antilopine.

## Conclusions

### The evolution of antelope species

The array of fossil bovids at Olduvai, other east African sites and the South African sites can be seen in various ways. In one interpretation, that found in traditional palaeontological work, they represent a great many extinct species, among which one is very unlikely to find any actual ancestors of later or living species. This approach pays attention to the differences between fossils and heightens the degree of faunal endemism at different sites. It implies the contemporaneous existence of very large numbers of evolutionary lineages. In a second interpretation, which we support, the fossils are thought to represent a smaller number of evolving lineages, some or most of which have survived to the present day. The range of variation of horn core characters and even of some tooth characters changes within any lineage from one temporal level to another, and one can imagine that the geographical ranges of infraspecific varieties have fluctuated from time to time. This interpretation has to be fully stretched to account for some anomalies. If, for example, *Damaliscus agelaius* gave rise to either or both the living *Damaliscus* species, how does one account for the ancestral lack of  $P_2$ ? The shorter premolar row of *Kobus sigmoidalis* than of living waterbuck is a less acute version of the same problem. If the Olduvai kudus are a single lineage leading to living *Tragelaphus strepsiceros*, how is it that a higher proportion of  $P_4$ s lack paraconid-metaconid fusion at the present day than in Olduvai times?

While new species may occasionally have arisen from unsuccessful antelope species occupying restricted ranges, they seem more often to have arisen from within successful species or species groups. Successful species are likely to be widespread and to show morphological differences in various parts of their ranges. Some of the anomalies of dental evolution could be explained by postulating origins of new species from fringe populations in which some characters are atypical, or from the less advanced species among pairs or groups of species. Again, the less advanced tooth characters of some living antelopes may indicate that they have less narrow adaptive ranges than their extinct relatives. Perhaps the greater number of contemporaneous species in the past, of pigs as well as antelopes, necessitated a closer adaptive relationship between each species and its environment. Guthrie (1968) faced similar problems with early Tertiary North American artiodactyls, among which the limb bones of later forms were less advanced than earlier forms. He concluded that some Oligocene genera with four fully functional toes in the hind foot had descended from Eocene ancestors with smaller lateral toes. There had been a degree of evolutionary reversal in a character apparently of fundamental importance.

When sufficient numbers of new characters spread through a species, an adequate fossil record will show a smooth transition of one species (= a chronospecies) or subspecies to another. However, R. D. Martin (1972 : 316), in a discussion of lemur evolution, has proposed that a



lineage might consist of sequentially-replacing species. Newly-evolved species compete with their immediate predecessors, and the competition favours increasing refinement of features which provide incremental increase in survival value. This is a development of the concept of iteration (see Simpson 1953 : 248), and is a different evolutionary process from that of gradual infra-specific change. We have interpreted most of the changes in bovid lineages as examples of the first process, for example the transition from *Kobus sigmoidalis* to *K. ellipsiprymnus*. One could also imagine, following Simpson (1953 : 198), that there have been bursts of accelerated evolution during a transition, as in the postulated changes from *Pelorovis oldowayensis* to *P. antiquus* and from *Parmularius altidens* to *P. angusticornis*. An example of the second process, sequential replacement, might have been *Tragelaphus strepsiceros* competing successfully against the Shungura *T. gaudryi*, but in this case it is possible that *T. gaudryi* was not exterminated but turned into *T. imberbis* instead. We still do not know enough about the evolution of species. When young male antelopes, perhaps with new characters of survival value, disperse or are chased from the territories of their birth, do they wander far, are they acceptable mates to females living further away and what success do they have in leaving descendants? Perhaps no generalizations are possible about this.

### Distribution of bovid species at Olduvai

The species list given in Table 11 summarizes the general account of the Olduvai bovids given in the first part of the paper and shows simply the presence or absence of the species in the various beds. Table 12 (pp. 56–7) shows the distributions in greater detail; it summarizes the account of the various sites given in the second part of the paper and also includes material collected before the Second World War. In both tables we have distinguished between secure records and those for which there is doubt about either the species identification or stratigraphical level. In using the tables one should remember that the collections made until the 1950s included a high proportion of surface finds, and that recent changes of geological interpretation are particularly liable to affect the placing of pre-war material from Beds III and IV. For example, the occurrence of *Pelorovis oldowayensis* in Bed IV is based only on the holotype collected in 1913, and it would be good now to have further substantiation. Fortunately M. D. Leakey (1971b : 282–289) has recorded the horizons of most of the more important specimens collected in earlier decades.

### Ecology of the Olduvai bovids

The ecology of the Olduvai bovids may be compared with that of their close living relatives as deduced from Ansell (1960, 1971), Child & Wilson (1964), Hofmann & Stewart (1972), Jarman (1974), Pienaar (1974) and other sources. As a whole, they indicate a rather dry and open environment. The only tragelaphine which is even moderately common is the greater kudu which today has a widespread distribution in diverse habitats which have some degree of cover. It is commoner in Bed I than in later beds. The eland, a gregarious and mainly browsing antelope, is very rare at Olduvai. Like the greater kudu and unlike other tragelaphines it occurs in a variety of habitats, even in fairly dry areas. The buffalo of today is an unselective grazer often found among denser, ideally riverine, vegetation, and it would not have occurred away from areas in which it could find places to wallow. It is not uncommon later in Bed II. The waterbuck lineage is reasonably common only in the lower parts of Bed I, as at the sites DK and FLKNN. Its presence conforms with other evidence at these sites pointing to nearby standing water at this time. Hirst (1975 : 32) observes that waterbuck may depend on habitats which are found only near water, rather than directly on water. Another reduncine, the kob, occurs rather sparsely in the later parts of the Olduvai sequence. While the waterbuck browses less infrequently than other reduncines and sometimes enters lightly wooded country, the kob rarely enters cover. The oryx lives in very arid country, is always rare as a fossil and only one, or perhaps two, horn cores have been found in Bed I. Presumably its normal habitat lay at some distance from the area of the present Gorge, and it came only rarely to water or was hunted only rarely by the hominids. *Hippotragus gigas* could be pictured as grazing in non-arid areas of long grass adjacent to woodland, if it was at all like modern *H. equinus*. It is present but not common in Olduvai Beds I–III. The Alcelaphini are the most characteristic antelopes of Olduvai, especially in middle Bed II and later horizons.



They would have grazed on short grass in open country or in clearings with good visibility, and could have tolerated greater aridity than reduncines or *Hippotragus*. *Antidorcas* is the commonest antilopine, notably in Bed I. As with the living springbok, an important component of its diet may have been arid-country dicotyledonous plants. The rarer Olduvai *Gazella* would have been

Table 11 Bovid species list for Olduvai Gorge

		Bed I	Bed II		Bed III	Bed IV
			Lower	Mid. + Up.		
TRAGELAPHINI						
<i>Tragelaphus strepsiceros malyanus</i>	} L	X	X	O		
<i>Tragelaphus strepsiceros grandis</i>				X	X	X
<i>Tragelaphus</i> aff. <i>spekei</i> or <i>scriptus</i>	L ?	O		X		X
<i>Taurotragus arkelli</i>	A		O			X
BOVINI						
<i>Pelorovis oldowayensis</i>	} E			X	X	O
<i>Pelorovis antiquus</i>						X
<i>Syncerus acoelotus</i>	A	X	X	X		X
REDUNCINI						
<i>Kobus sigmoidalis</i>	} A	X	X	X	X	X
<i>Kobus ellipsiprymnus</i>		O				
<i>Kobus kob</i>	L			X	X	
<i>Redunca</i> sp.	L ?	X		X	X	
<i>Thaleroceros radiciformis</i>	E					X
HIPPOTRAGINI						
<i>Hippotragus gigas</i>	E ?	X	X	X	X	
<i>Oryx</i> sp.	L ?	X				
ALCELAPHINI						
<i>Megalotragus kattwinkeli</i>	E	O	O	X	X	X
<i>Connochaetes africanus</i>	A		X			
<i>Connochaetes</i> sp.	A	X		X		
<i>Connochaetes taurinus olduvaiensis</i>	} L			X	X	X
<i>Parmularius altidens</i>		X				
<i>Parmularius angusticornis</i>	E		X	X		
<i>Parmularius rugosus</i>	E		O	O	X	X
<i>Damaliscus niro</i>	E			X	X	X
<i>Damaliscus agelaius</i>	A		X	X	X	
<i>Rabaticeras arambourgi</i>	A				X	X
<i>Beatragus antiquus</i>	A	X	X	X		
Alcelaphini, sp. 1						O
Alcelaphini, sp. 2			X			
Alcelaphini, sp. 3				X		
Alcelaphini, sp. 4	E	X	O	O		
<i>Aepyceros melampus</i>	L	X		X		
NEOTRAGINI						
sp. indet.		O		X		
ANTILOPINI						
<i>Antidorcas recki</i>	} A	X	X	X	X	X
<i>Antidorcas</i> sp.		L ?				X
<i>Gazella</i> sp.	A	X		X		
Antilopini, sp. 1	E	X		X		
CAPRINAE						
? Caprinae, sp. indet.	E	X				

} = one lineage, X = secure record, O = of uncertain horizon or identification. E = extinct lineage, A = ancestral species of an extant lineage, L = living species.



more of a grazer, perhaps akin to the west African *G. rufifrons* rather than to the specialized grazing of the Serengeti *G. thomsoni*.

Fig. 36 shows the percentages of alcelaphine and antilopine bones at the excavated sites at Olduvai. The alcelaphine readings at SHK II and BK II have been brought low by the distorting effects of the herds of *Antidorcas recki* and *Pelorovis oldowayensis* found at these two sites. Otherwise the picture given from FLKNN I onwards would be of increasingly abundant alcelaphines throughout the series of excavated sites, and of *Antidorcas recki* being well-represented higher in Bed I. If these figures reflect hominid hunting preferences, one might deduce that *A. recki* was abandoned as prey after Bed I. If they should indicate the natural occurrence of bovids in the area, they are evidence for a rather dry open bushland or tree savannah plains as the predominant habitat. However, less common bovids, such as buffalo, kob and the *Hippotragus*, indicate the presence of some less arid environments in the Olduvai area. The kob is absent from nearly all of Tanzania and Kenya at the present day.

### Size of bovids at Olduvai Gorge

In the past Olduvai Gorge has been noted as a site for giant-sized animals. One important factor contributing to this reputation was the old misidentification of *Pelorovis oldowayensis* as a relative of sheep. Once *Pelorovis* had been recognized as a bovine, its large size became less startling, for its nearest living relative was now the slightly smaller buffalo *Syncerus caffer* and not the very much smaller sheep. Nevertheless, the Olduvai bovids as a whole continue to give the impression of being larger animals than those living today, even if one cannot call them giant. This impression is derived from a number of examples at different taxonomic levels of comparison. Two of the extinct lineages, *Pelorovis* and *Megalotragus*, are larger than surviving members of the same tribes, and *Thaleroceros radiciformis* could also be larger than living reduncines, although this is not certain. *Hippotragus gigas* and *Beatragus antiquus* are larger than surviving members of the same genera, and *Tragelaphus strepsiceros grandis* and the Bed III *Kobus kob* than surviving members of the same species. Also at the species level of comparison, *Damaliscus niro* is larger than its conspecific descendants at later sites in South Africa.

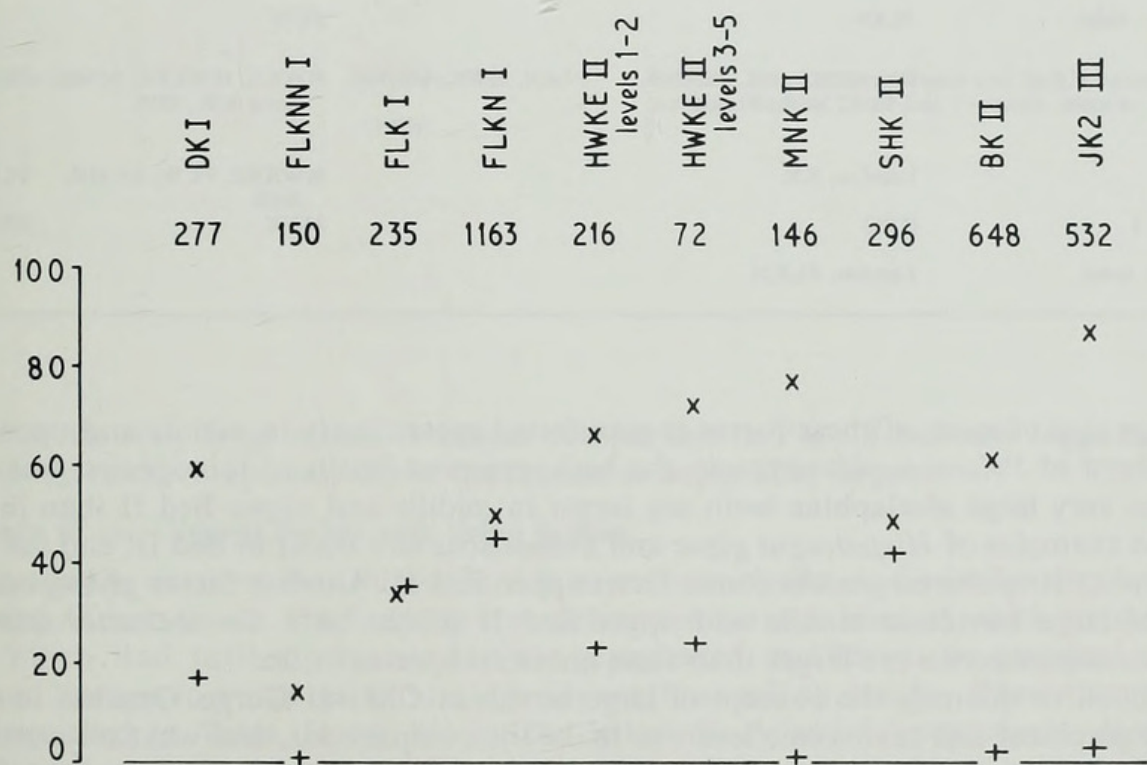


Fig. 36 Percentages of Alcelaphini and Antilopini among the bovid bones identified to tribal level or below at the excavated sites at Olduvai Gorge. The numbers along the top are the bone totals from which the percentages were calculated for each site. X = Alcelaphini, + = Antilopini.



Table 12 Stratigraphical distribution of species

Species List	Bed I	Lower Bed II	Middle Bed II	Upper Bed II
<i>Tragelaphus strepsiceros maryanus</i> <i>Tragelaphus strepsiceros grandis</i> <i>Tragelaphus aff. spekei</i> or <i>scriptus</i> <i>Taurotragus arkelli</i>	DK, FLKNN, FLK, FLKN London	HWKE, FLKN	HWKEE MNK, SHK SHK	GRC, BK, RK
<i>Pelorovis oldowayensis</i> <i>Pelorovis antiquus</i> <i>Syncerus acoelotus</i>	DK, FLK, FLKN	HWKE	HWKE, MNK, (FC), SHK MNK, Elephant K, SHK	GRC, TK, BK, PLK, MR Kar K, (Rhino K), FKV TK, SC, BK
<i>Kobus sigmoidalis</i> <i>Kobus ellipsiprymnus</i> <i>Kobus kob</i> <i>Redunca</i> sp. <i>Thaleroceros radiciformis</i>	DK, FLKNN, FLK London	FLKN, Geol. loc. 63 FLKN, HWK, HWKE	HWKEE, MNK MNK, SHK	? MRC, BK
<i>Hippotragus gigas</i> <i>Oryx</i> sp.	DK, FLKNN, FLK, FLKN, VEK FLK, London	HWKE	HWKE, MNK, FLK, SHK	TK, BK
<i>Megalotragus kattwinkeli</i>	DK, FLKNN, FLK	HWKE	HWKE, MNK, SHK	(SC), BK
<i>Connochaetes africanus</i> <i>Connochaetes</i> sp. <i>Connochaetes taurinus olduvaiensis</i>	FLKNN, FLK, FLKN		HWKEE MNK, SHK	BK
<i>Parmularius altidens</i> <i>Parmularius angusticornis</i>	DK, FLKNN, FLK, FLKN, HWK	> FLKN	HWKEE, Long KE, SHK	(SC), (MRC), BK, (DC)
<i>Parmularius rugosus</i> <i>Damaliscus niro</i> <i>Damaliscus agelaius</i>		HWK FLKW	HWKE, HWKEE, SHK Elephant K, SHK	GRC, BK Geol. loc. 54
<i>Rabaticeras arambourgi</i> <i>Beatragus antiquus</i> Alcelaphini, sp. 1 Alcelaphini, sp. 2 Alcelaphini, sp. 3 Alcelaphini, sp. 4 <i>Aepyceros melampus</i>	MJTK, FLKN	FLKN, HWKE Nairobi	SHK HWKEE (SHK)	Kit K BK BK
<i>Neotragini</i> , sp. indet.	FLKN		FCW	
<i>Antidorcas recki</i> <i>Antidorcas</i> sp.	DK, (THC), KK, FLKNN, FLK, VEK, FLKN	FLKN, HWK, HWKE	HWKE, HWKEE, MNK, Long KW, SHK	FLK, TK, BK
<i>Gazella</i> sp.	London, KK		HWKEE, FCW, EF-HR, SHK	FLK, BK
<i>Antilopini</i> sp. 1 ? <i>Caprinae</i> sp. indet.	(DK) London, FLKN		MNK	BK

The large size of most of these forms is manifested most clearly in middle and upper Bed II. Thus the herd of *Pelorovis oldowayensis*, the best-preserved fossils of this species, was found at BK II. The very large alcelaphine teeth are larger in middle and upper Bed II than in Bed III. The largest examples of *Hippotragus gigas* and *Damaliscus niro* occur in Bed II, and the holotype of *Tragelaphus strepsiceros grandis* comes from upper Bed II. Another factor giving one the impression of large bovids in middle and upper Bed II is that both *Connochaetes taurinus* and *Parmularius angusticornis* are larger than their ancestral species in Bed I.

It is difficult to quantify the concept of large bovids at Olduvai Gorge. One has to decide at what stratigraphical and taxonomic levels to make the comparisons, and what measurements or other criteria to use. Two examples of possible comparisons are available from Figs 5 (p. 302) and 15 (p. 345). In Fig. 5 *Tragelaphus strepsiceros grandis* has linear skull dimensions which are on average 17% greater than in the living greater kudu sample used as a standard, although it should be remembered that the greater kudu sample is based on museum specimens which are



Bed II, level unknown	Bed III	Beds III-IV undivided	Bed IV	Remarks
	JK1, JK2		PDK, BK, CK London (LK/RK), WK	Limb bones indicate two <i>Tragelaphus</i> species at DK I and FLK I Last three entries may not be subsp. <i>grandis</i> Large limb bones at DK I and FLK I not counted as eland
ndon				
K, HWK	London, JK	(BK)	Berlin WKE, GC	
K	JK2, JK2GP8	(Bos K), (BK), VFK	WKE, GC	Only teeth in Beds I, lower II, III and IV
-----				
	JK2, JK2GP8 JK2, JK2GP8 JK2		(EF-HR)  Munich	Teeth and limb bones above FLK are taken as transitional to <i>K. ellipsiprymnus</i> Metatarsal at FC West middle II may be reduncine
(HTK)	JK2			
-----				
(EK)	JK2	TK Fish Gully	GC, GTC	Limb bones at HWK lower II and FC West middle II are of this genus or <i>Connochaetes</i> by size
London				
(ITK)	London	VEK	London	
-----				
TEK, (GHTK)				Teeth and limb bones at MNK middle II and TK upper II are of this species or <i>Damaliscus niro</i> by size Teeth and limb bones at HWKE lower II may be this species See note above on <i>Parmularius angusticornis</i> Limb bones at MNK middle II and BK upper II may be this species
-----				
	JK2 JK, JK2, JK2GP8 JK2, JK2GP8	VFK, (Hoopoe Gully)	HWK (NGC), London, (Nairobi)	
HK	JK2		PDK  Nairobi	
(Nairobi)				
-----				
VC	JK2, JK2GP8		London, VEK  HEBE	Italicized sites have scarce teeth and limb bones not differentia- ted from <i>Gazella</i> . Large Bed I remains taken as <i>A. recki</i>
K, (MLK)				

Key
} = one lineage
Italics = doubtful identification or horizon
Brackets = records based only on known surface specimens
Names of towns = collections containing important material of unknown site

likely to be relatively large males. A similar comparison in Fig. 15 between *Hippotragus gigas* and the living roan, *H. equinus*, shows the former as being 22% larger.

### Comparison of the Olduvai bovids with living faunas

It is interesting to examine the Olduvai bovids to see how similar or dissimilar they are to those of the living African fauna. The first step is to distinguish between lineages which are now extinct, lineages which lead to living species but are represented at Olduvai by ancestral species or genera, and lineages in which the Olduvai species are those still alive today. These three categories are distinguished in Table 11 (p. 54) by the letters E, A and L respectively. It should be remembered that our opinions on phylogenies are perhaps more subjective than the species' identifications. The kudu lineage is taken as the living *Tragelaphus strepsiceros* in all the Olduvai horizons but differs at subspecies level. The fragments of *Tragelaphus* aff. *spekei* or *scriptus*, *Redunca* and *Oryx* do not allow the detection of definite differences from living species. The



eland *Taurotragus arkilli* and the buffalo *Syncerus acoelotus* are both ancestral to living species. The waterbuck lineage became the living species perhaps as early as Bed I. The kob is the living species, although its Olduvai representatives have differences which could be used to justify a subspecific separation. We regard *Hippotragus gigas* of Olduvai times as probably postdating the separation of its own lineage from that of living *Hippotragus*, but we admit that the Kanjera *Hippotragus* can be interpreted as showing either immigration of *H. equinus* or a late evolutionary transition from *H. gigas*. *Connochaetes africanus* could well be ancestral to *C. gnou*, and the other wildebeest lineage changed into the living *C. taurinus* during Bed II times. We accept *Parmularius* as constituting two lineages. *Damaliscus agelaius*, *Rabaticeras arambourgi* and *Beatragus antiquus* are taken as probably ancestral to living *Damaliscus*, *Alcelaphus buselaphus* and *Beatragus hunteri* respectively, despite the difficulties with the teeth of *D. agelaius* (p. 405). The *Antidorcas* and *Gazella* are probably ancestral to the living springbok and to *Gazella thomsoni* and *G. rufifrons*. We have not attempted to judge the Alcelaphini species 1, 2 and 3 or the very sparse neotragine remains from Olduvai.

**Table 13** Number of bovid lineages at Olduvai Gorge compared with two living faunas

	Beds I and Lower II	Middle and Upper Bed II	Beds III and IV	Olduvai Total	Serengeti National Park	Kafue National Park
Tragelaphini	1 (1)	2 (1)	3 (1)	3	3	4
Bovini	1	2	2	2	1	1
Cephalophini	—	—	—	—	4*	3
Reduncini	2	3 (1)	4 (2)	4	3	4
Hippotragini	2	1	1	2	2	2
Alcelaphini	9 (1)	9 (2)	6 (1)	11	4	3
Neotragini	—	1	—	1	4	4
Antilopini	3	3	1	3	2	—
? Caprinae	1	—	—	1	—	—
<b>TOTAL</b>	<b>19 (2)</b>	<b>21 (4)</b>	<b>17 (4)</b>	<b>27</b>	<b>23</b>	<b>21</b>

Brackets surround the numbers of extant species included in the adjacent figures.

\* Includes two doubtful records.

The table excludes from the Olduvai columns *Connochaetes africanus* and Alcelaphini sp. 1. *Tragelaphus* aff. *spekei* or *scriptus* is excluded for Bed I, *Taurotragus arkilli* for Bed II, and Alcelaphini sp. 4 for middle and upper Bed II.

Table 13 shows the number of securely identified lineages known from Olduvai as a whole and from the various beds and gives for comparison the numbers of bovid species which have been recorded from the living faunas of two ecologically different areas in tropical Africa, the Serengeti National Park in Tanzania and the Kafue National Park in Zambia (information from Swynnerton 1958 and Ansell 1960). It seems that the total number of lineages at Olduvai exceeds that in either living fauna, although this statement needs some qualifying. One should perhaps reduce the Olduvai total by two or three to allow for such possibilities as the Bed I ? caprine becoming extinct before all the other lineages had evolved, or regional fluctuations of faunas which may have masked lack of sympatry between some of the lineages. On the other hand, this notional reduction would probably need to be counterbalanced by the under-representation of Cephalophini and Neotragini, if not also Tragelaphini, arising from ecological or taphonomical factors. The two living faunas come from areas which contain a number of different habitats, and therefore they probably make a good comparison for the Olduvai fauna in which one can also detect the sampling of several different habitats. In any case the Olduvai fauna is likely to have been richer than the living ones because of the number of extinct lineages it contained. *Pelorovis*, *Thaleroceros*, *Megalotragus*, *Parmularius* and *Damaliscus niro* have no recognized counterparts in extant faunas. *Beatragus* is not quite extinct, but had become restricted to a very small part of Africa by recent centuries. *Antidorcas* no longer inhabits east Africa.

The most striking feature of Table 13 is the large number of alcelaphine lineages at Olduvai in comparison with the living faunas. Generally these Pleistocene alcelaphines were morphologically



specialized, as in the case of *Parmularius*, particularly *P. angusticornis*, in comparison with *Damaliscus* and *Rabaticeras*. One can look at the large number of lineages in relation to the account of the behaviour and ecology of living alcelaphines given in the informative review of Jarman (1974). Living alcelaphines (except *Aepyceros melampus* and perhaps *Beatragus hunteri*) are grazers, rather unselective for plant species but much more so for particular parts or growth stages of plants. They have only poorly-defined home areas and are strongly migratory, which must assist in finding grasses at their optimum growth stages. They aggregate into cohesive super-herds which split up temporarily for breeding. Finally, the territory of a male during the nomadic phase is no longer a permanent piece of ground but a temporary area around a group of females. One presumes that this advanced social organization and feeding behaviour have been important in the evolutionary success of the living alcelaphines. Could they have been developed only recently, and could they have played a part in the extermination of *Megalotragus*, *Parmularius* and *Damaliscus niro* and the diminution in the range of *Beatragus*?

Finally, Table 13 shows the number of living species which can be identified at Olduvai, omitting poorly-known forms of uncertain status. It is interesting that the number is so low. Converting the numbers of living species into percentages of the total number of species in each of the beds, one gets the figures of 11 % for Beds I and lower II, 19 % for middle and upper Bed II and 23 % for Beds III and IV. These rising percentages are perhaps spuriously impressive, but probably give a true impression that the Olduvai antelope fauna was becoming increasingly like the living fauna as time advanced through the Pleistocene. Three lineages crossed species boundaries at Olduvai in Beds I and II (*Kobus sigmoidalis*, *Connochaetes* sp. and *Parmularius altidens*), two in Beds III and IV (*Pelorovis oldowayensis* and *Antidorcas recki*) and four have done so at some time after their latest recorded occurrences in Beds III or IV (*Taurotragus arkelli*, *Syncerus acoelotus*, *Damaliscus agelaius* and *Rabaticeras arambourgi*).

### Faunal changes at Olduvai Gorge

The conception that there is a faunal break between lower and middle Bed II at Olduvai is now familiar (Leakey 1965 : 4, 75, 76), and one wonders how far the bovids support or refute the idea. Changes which occur in the vicinity of this level are:

*Tragelaphus strepsiceros maryanus* is last known at HWK East II level 2 in lower Bed II, and *T. s. grandis* first appears in MNK middle Bed II. A tragelaphine maxilla from HWK EE low in middle Bed II has an M<sup>2</sup> of a size to fit *T. s. maryanus* but perhaps too small for later subspecies. More evidence is needed to substantiate the identification for this level.

*Pelorovis oldowayensis* first appears at Olduvai in HWK East II levels 3–5, the lowest levels of middle Bed II.

A reduncine tooth of the size of *Kobus sigmoidalis* or *K. ellipsiprymnus* last appears in HWK EE low in middle Bed II. Metatarsals, probably reduncine and large enough for waterbuck, appear at MNK and FC West; otherwise this lineage is absent until Bed III.

*Kobus kob* first appears at MNK in middle Bed II.

*Connochaetes taurinus* replaces an earlier *Connochaetes* species above the lower part of middle Bed II. It is definitely known from SHK II, while its predecessor is last known from HWK EE II. There is a *Connochaetes* horn core at MNK II, but it is too poorly preserved for identification at species level.

*Parmularius altidens* is known at FLKN I, while its descendant *P. angusticornis* is known from HWK EE II onwards. A cranium likely to be intermediate between them comes from the clay with root casts at FLKN II.

An early relative or representative of the *Parmularius rugosus* lineage occurs at HWK in lower Bed II and at HWK East and HWK EE in the lower part of middle Bed II. A more evolved form appears higher in middle Bed II.

*Damaliscus niro* is first known from Elephant K and SHK II.

Horn cores of *Antidorcas recki* are usually without distal divergence at HWK East II level 2 and below. Those from SHK II and later generally have distal divergence.

At least two lineages pass through this period without appreciable change, so far as we know them at present. These are *Hippotragus gigas* and *Beatragus antiquus*. *Damaliscus agelaius* may



also do so. The situation is more uncertain with *Megalotragus kattwinkeli*; only teeth and limb bones are known in the period preceding the lower-middle Bed II change, so their species attribution is unknown.

There are some changes in the bovids at other levels in Olduvai Gorge. *Pelorovis oldowayensis* disappears in Bed III or IV, and *P. antiquus* is present in Bed IV. *Parmularius angusticornis* disappears after upper Bed II (but note the interesting Isimila record, p. 390). *Damaliscus agelaius* and *Parmularius rugosus* seem to become more common in Beds III and IV. *Rabaticeras arambourgi* appears in Bed III, *Beatragus antiquus* is not known after upper Bed II, and a larger *Antidorcas* than *A. recki* appears in Bed IV.

It appears then that over the period between FLKN I and SHK II there was quite a substantial change in the bovids which were becoming fossilized in the Olduvai sites. The degree to which the change was sharply localized at the lower/middle Bed II boundary is not yet clear; it might be better placed shortly after the start of middle Bed II. If the fossil bovids do reflect accurately a change in the composition of the then living fauna, they support Leakey's concept of a faunal break. The cause of such a change would have been environmental changes at Olduvai. Local movements of bovid populations and morphological changes on some lineages could produce the fossil record as known to us. *Tragelaphus strepsiceros maryanus* with its very compressed horn cores need have been only a local variant of the kudu. The *Pelorovis* lineage is known to have existed in the Shungura Formation, Omo, at a period before it first became fossilized at Olduvai, and the *Kobus sigmoidalis/ellipsiprymnus* lineage was only temporarily absent from Olduvai during middle and upper Bed II. There is some evidence for ecological instability in part of Bed II with the passing appearance in the HWK group of sites of *Parmularius* aff. *rugosus* and a variety of *Antidorcas recki* with unusually compressed horn cores. We conclude that it is reasonable to postulate a faunal change somewhere near or just above the lower-middle Bed II boundary.

The changes among the alcelaphine species after upper Bed II are not yet sufficiently clear to support the idea of another faunal break. *Damaliscus agelaius* and the *Rabaticeras* are probably ancestral to living alcelaphines whereas the middle and upper Bed II *Damaliscus niro* and *Parmularius angusticornis* were not. Their presence, even alongside *Parmularius rugosus* and the surviving *Damaliscus niro*, helps to give the fauna a more modern aspect. Morphologically, *Damaliscus agelaius* is a species with few advanced characters, and *Parmularius rugosus* is less specialized than *P. angusticornis*. The lower numbers of large alcelaphine teeth and limb bones than at BK II and the smaller size of the large *Megalotragus kattwinkeli* also suggest modernity, but this may be an illusory consequence of a change in hominid hunting preferences.

### Bovid extinctions

The evidence for bovid extinctions within the span of Olduvai Beds I–IV is slight. Five lineages which are now extinct survived into Bed IV; these are *Pelorovis*, *Megalotragus*, a lineage of *Parmularius*, *Damaliscus niro* and *Thaleroceros radiciformis*. Terminal populations of *Pelorovis* and *Megalotragus* species have been discovered as late as 11 000 and 15 000–14 000 BP respectively in southern South Africa (Klein 1972 : 141; personal communication), and *Damaliscus niro* certainly survived into the late Pleistocene in the Orange Free State. The times of extinction of *Parmularius rugosus* and *Thaleroceros radiciformis* are not earlier than during the time span of Bed IV, but for these genera there are no late records from other sites. *Hippotragus gigas* survived at Olduvai into Bed III, but has not yet been found in Bed IV. However, it does occur at Elandsfontein and perhaps Florisbad, so the argument is not strong for extinction preceding the end of Bed IV. *Parmularius angusticornis* is the most likely candidate for a species disappearing without issue, an event which would have taken place at the end of upper Bed II. It is also likely that an ovibovine or caprine has become extinct since Bed I times. The two species *Tragelaphus nakuae* and *Menelikia lyrocera*, unrepresented at Olduvai, are last recorded in the Shungura Formation, Omo, in members H and J respectively, equivalent in time to Olduvai Beds I and II.

The main North American extinction of mammals which were mostly large-sized (megafaunal extinction) is known to have taken place close to 11 000 years ago, and the idea has been put forward (P. S. Martin 1967 : 111) that the main Pleistocene extinction in Africa long predated that



in the Americas and Australia. The evidence which is now beginning to appear for African bovids does not support this idea.

### Correlations with other sites

The contribution of Olduvai bovids to the correlation of different sites, Fig. 37, can be considered in order of their geographical proximity to the Gorge.

The bovids from the **Laetolil Beds** must be earlier than those of Olduvai. Our identifications of this material compared with those of Dietrich are shown in the following table. In this and following lists, the symbol (T) indicates a species represented by dental remains or dental and postcranial remains.

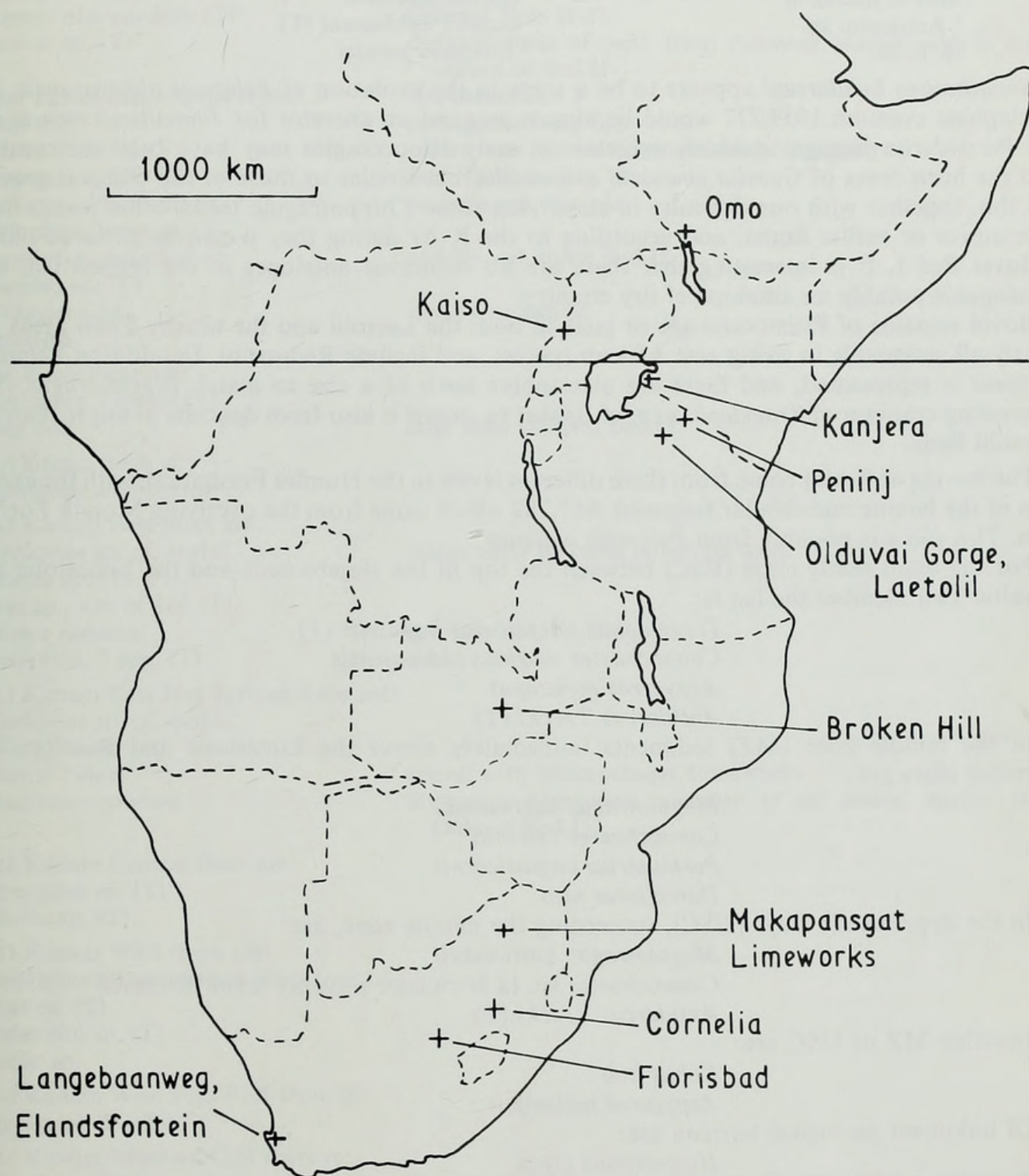


Fig. 37 Map of part of Africa to show the more important fossil localities mentioned in this paper.



Present authors

*Simatherium kohllarseni*

*Praedamalis deturi*

? *Hippotragini* sp.

? *Parmularius* sp.

*Alcelaphini* sp. indet. (1959.233)

*Alcelaphini* sp. indet.

? *Raphicerus* sp. indet.

*Madoqua avifluminis*

? *Antidorcas* sp.

*Gazella janenschi*

? *Antilopini* sp.

sp. indet.

Dietrich (1942, 1950)

*Simatherium kohllarseni*

{ *Praedamalis deturi*

{ *Aeotragus garussi* (T)

{ ? *Hippotragus* sp. (T)

{ *Gazella kohllarseni*

{ *Aepycerotinae* gen. et sp. indet. (1950 : 30)

*Reduncini* gen. et sp. indet. (1950 : 36)

—

*Parestigorgon gadjingeri*

*Gazella hennigi* (T)

*Praemadoqua avifluminis*

*Gazella hennigi*

*Gazella janenschi*

*Gazella kohllarseni* (T)

*Aeotragus garussi*

*Simatherium kohllarseni* appears to be a stage in the evolution of *Pelorovis oldowayensis*, the alcelaphine cranium 1959.277 would be almost as good an ancestor for *Damaliscus niro* as for the *Parmularius* lineage to which we relate it, early *Hippotragini* may have been represented, and the horn cores of *Gazella janenschi* are smaller but similar to those of the Olduvai gazelle. All this, together with our difficulty in classifying some ? hippotragine teeth, befits fossils from a primitive or earlier fauna, and according to the K-Ar dating they would be twice as old as Olduvai Bed I. It is interesting that there are no reduncine antelopes in the revised list, and *Madoqua* is notably an antelope of dry country.

Bovoid remains of Pleistocene age or later in both the Laetolil and the nearby Eyasi areas are nearly all assignable to living east African species, and include *Reduncini*. In addition *Pelorovis antiquus* is represented, and there are alcelaphine teeth of a size to match *Megalotragus*. The interesting cranium of *Tragelaphus* sp. cf. *spekei* or *angasi* is also from deposits younger than the Laetolil Beds.

The bovids at **Peninj** come from three different levels in the Humbu Formation, with the exception of the bovine mandibular fragment A67.282 which came from the overlying Moinik Formation. This piece is possibly from *Pelorovis antiquus*.

For the basal sandy clays (BSC) between the top of the Hajaro beds and the Limestone and Basaltic Tuff member the list is:

*Tragelaphus strepsiceros* ? *grandis* (T)

*Connochaetes taurinus olduvaiensis*

*Aepyceros melampus*

*Antidorcas* ? *recki* (T)

In the middle zone (MZ) sediments immediately above the Limestone and Basaltic Tuff Member there are:

*Megalotragus kattwinkeli*

*Connochaetes taurinus*

*Parmularius angusticornis*

*Damaliscus niro*

In the upper sandy clays (USC), succeeding the middle zone, are:

*Megalotragus kattwinkeli*

*Connochaetes* sp. (a horn core possibly from this level)

*Antidorcas* ? *recki* (T)

In either MZ or USC are:

*Kobus kob*

*Aepyceros melampus*

Of unknown geological horizon are:

*Hippotragus gigas*

*Antidorcas recki*

*Gazella* sp.



The Peninj antelopes all occur at Olduvai. *Parmularius angusticornis* equates with middle and upper Bed II at Olduvai, *Damaliscus niro* with middle Bed II or later, the *Kobus kob* is like those of Bed II and the *Gazella* sp. is the one found in middle and upper Bed II. Obviously the best placing of these deposits according to their bovids is to have MZ correlating with some part of Olduvai middle or upper Bed II. USC is likely to be of the same broad age. If *Pelorovis antiquus* were confirmed for the Moinik Formation, its age might be later than Bed III. The ecology of the area would have been similar to Olduvai.

The bovids make a limited contribution to the correlation of the **Kavirondo Gulf sites** in Kenya.

Species	Implication for correlation
At Kanjera there are:	
<i>Tragelaphus</i> ? <i>spekei</i>	perhaps not very old (younger than lower Pleistocene ?)
<i>Pelorovis oldowayensis</i> (T)	Olduvai Beds II-IV
<i>Syncerus</i> sp. (T)	distinctiveness of teeth from <i>Pelorovis oldowayensis</i> is reminiscent of Bed II
<i>Kobus sigmoidalis/ellipsiprymnus</i>	not before Bed I
<i>Kobus kob</i>	perhaps not very old
<i>Redunca redunca</i>	rather late, but material is scarcely fossilized
<i>Hippotragus gigas</i>	Bed III or earlier
<i>Hippotragus</i> ? <i>equinus</i> (T)	perhaps not very old
Alcelaphini, large sp. (T)	
<i>Parmularius angusticornis</i>	middle and upper Bed II
? <i>Ourebia</i> sp. (T)	
<i>Antidorcas recki</i>	Bed IV or earlier
<i>Gazella</i> sp.	
At Rawe there are:	
<i>Tragelaphus</i> ? <i>spekei</i> (T)	
<i>Kobus kob</i>	later than Olduvai Bed II
At Kagua there is:	
<i>Tragelaphus strepsiceros</i>	
At Kanam East there are:	
<i>Tragelaphus</i> sp. cf. <i>spekei</i>	rather early by basal pillars on teeth
<i>Syncerus</i> sp. (T)	
<i>Kobus</i> sp., size of <i>kob</i> (T)	
<i>Redunca redunca</i>	not very old
Alcelaphini, 2 spp. (T)	
At Kanam East Hot Springs there are:	
<i>Tragelaphus</i> sp. cf. <i>spekei</i>	
<i>Kobus</i> aff. <i>kob</i>	
<i>Redunca</i> ? <i>darti</i>	coeval with Makapansgat Limeworks
<i>Kobus</i> ? <i>ancystroceras</i>	Shungura Formation member G or above, earlier than Olduvai Bed IV
At Kanam Central there are:	
<i>Tragelaphus</i> sp. (T)	
<i>Redunca</i> sp. (T)	
At Kanam West there are:	
<i>Tragelaphus</i> aff. <i>gaudryi</i> or <i>strepsiceros</i>	
<i>Kobus</i> sp. (T)	
Alcelaphini sp. (T)	
<i>Gazella</i> sp.	
At Kanam West Fish Cliff there is:	
<i>Tragelaphus</i> sp. (T)	
At Kanam Museum Cliff there is:	
<i>Kobus</i> ? <i>ancystroceras</i>	Shungura Formation member G or above, earlier than Olduvai Bed IV



It looks as if reedbuck (*Redunca* spp.) and sitatunga (*Tragelaphus* of *spekei* group) have often been in past ages the source species for fossils along the Kavirondo Gulf, and they make no or little contribution to correlation. Apart from this, most material comes from Kanjera and could have an age equivalent to Olduvai Bed II. Some Kanam fossils could be older.

The bovids at **Kaiso** belong to early or late assemblages, for which the species lists are as follows.

Present authors

Cooke & Coryndon (1970)

(a) EARLY

*Tragelaphus* sp. cf. *spekei*

*Strepsiceros* cf. *maryanus* M 26402

Bovini indet. (T)

*Syncerus* sp.

*Kobus sigmoidalis*

*Pultiphagonides* cf. *africanus*

*Aepyceros* sp.

*Aepyceros* cf. *melampus*

(b) LATE

Bovini indet. (T)

{ Bovini incertae sedis  
*Syncerus* sp.  
*Hippotragus* sp. M 12595a, M 12601

*Kobus* aff. *kob*

{ *Kobus* sp. M 26622  
 cf. *Parmularius altidens* M 12590

? *Kobus* sp.

*Beatragus* cf. *antiquus* M 26623

*Menelikia lyrocera*

Various identifications, registered numbers listed previously

*Redunca* sp. (T)

*Redunca* sp. M 26620, M 26621

*Oreonagor/Connochaetes* sp.

cf. *Menelikia lyrocera* M 12584 (see this paper, p. 368, footnote 3)

Alcelaphini sp.

{ *Pultiphagonides* cf. *africanus* M 26624  
 cf. *Damaliscus* sp.  
 cf. *Parmularius altidens*

*Aepyceros* sp.

{ *Aepyceros* cf. *melampus* M 12592, M 12596  
*Gazella* cf. *wellsi*

In addition there are from the Kazinga Channel *Ugandax gautieri* of unknown age and *Kobus kob* of late Pleistocene age. The bovids of the late fauna are likely to predate Olduvai, and would best fit a time level around member F of the Shungura Formation. This verdict is chiefly based on the *Menelikia lyrocera*, but other bovids are consistent with it. The prominence of reduncines, the weaker representation of alcelaphines and the absence of antilopines implies an ecological situation closer to that of the Shungura Formation up to member G than to Olduvai Gorge. The tragelaphine horn core of the early fauna seems insufficiently primitive to match the accepted age of the fauna well before the Shungura Formation (Cooke & Coryndon 1970 : 220, fig. 17; Maglio 1973 : fig. 12), and the *Kobus sigmoidalis* is notably early.

The Shungura Formation of **Omo** is known to predate and partly overlap Olduvai. In contrast to Olduvai the tragelaphines and reduncines are abundant, while alcelaphines other than impala are poorly represented. The species list is as follows.

	Members				
	B	C-D	E-F	G	H-L
<i>Tragelaphus strepsiceros</i>				O	?
<i>Tragelaphus gaudryi</i>	O	O	X	X	O
<i>Tragelaphus ? pricei</i>		O			
<i>Tragelaphus</i> sp. (T)		O	O		
<i>Tragelaphus nakuae</i>	X	X	X	X	O
<i>Taurotragus</i> sp.	O				O
<i>Syncerus</i> sp.	O	X		O	
<i>Pelorovis</i> sp.	O	O	O	O	
Bovini spp. (T)	X	X	O	O	O
<i>Kobus sigmoidalis</i>		O	X	X	
<i>Kobus ellipsiprymnus</i>				O	O
<i>Kobus kob</i>	?	?		?	X
<i>Kobus</i> sp. nov.	X				
<i>Kobus ancystrocera</i>	O	X	O	X	O



	Members				
	B	C-D	E-F	G	H-L
<i>Menelikia</i> sp.		X			
<i>Menelikia lyrocera</i>		?	X	X	X*
<i>Redunca</i> sp. (T)	O	O	O	O	O
<i>Hippotragus</i> sp.				O	
<i>Oryx</i> sp.				O	
Hippotragini sp. (T)		O			
<i>Megalotragus</i> ? <i>kattwinkeli</i>				O	O
<i>Oreonagor/Connochaetes</i> spp.	O			O	
<i>Beatragus antiquus</i>				O	
<i>Parmularius altidens</i>				?	O
<i>Parmularius/Damaliscus</i> sp.		O			
Alcelaphini spp. (T)	O	O	X	O	O
<i>Aepyceros</i> sp. nov.	X	X	X	X	X
cf. <i>Aepyceros</i> sp.			O	O	
Neotragini spp.		?	O	O	
<i>Antidorcas recki</i>	O		O	O	O
<i>Gazella praethomsoni</i>			O	O	O
<i>Antilope</i> aff. <i>subtorta</i>		O			
'Antilopini sp. 1'					O
Ovibovini sp.		O		O	

In the above list O = rare finds, X = common finds, \* = an advanced variety.

During or soon after member G, *Tragelaphus gaudryi* and *T. nakuae* (both unknown at Olduvai) disappear, *T. strepsiceros* appears, *Kobus sigmoidalis* begins changing into *ellipsiprymnus*, *K. kob* becomes common, *Menelikia lyrocera* evolves an advanced variety, alcelaphine genera appear or become commoner and *Antidorcas* becomes more common. All this is a change towards greater faunal and ecological similarity to Olduvai, except that *Menelikia* is unrepresented at Olduvai. The Shungura Formation bovids are generally in accord with the idea that members G-L are contemporary with Olduvai Beds I-III or IV. Thus the boselaphine-like *Tragelaphus nakuae* disappears in member H and is unknown at Olduvai, the *Kobus sigmoidalis-ellipsiprymnus* transition of member G and above also appears in Olduvai Bed I, *K. kob* of member L is rather large as in Bed III, the pair of *Megalotragus* horn cores from member G are more different from those of Olduvai middle Bed II to Bed IV than are those of member K, *Parmularius altidens* is in member H and Bed I and the Antilopini sp. 1 occurs in members K and L and in middle and upper Bed II. The bovid evidence also supports the idea that members B-G predate Olduvai: *Tragelaphus gaudryi* is a smaller and more primitive kudu than *T. strepsiceros*, *T. ? pricei* has anteroposteriorly thicker horn cores than comparable *Tragelaphus* horn cores at Olduvai, the bovine and alcelaphine teeth are generally smaller and the *Aepyceros* and *Antidorcas* horn cores are smaller and more primitive.

The bovids which occur at **Broken Hill**, Zambia, are:

Present authors	Leakey (in Clark 1959)
<i>Tragelaphus strepsiceros</i>	<i>Strepsiceros</i> sp.
<i>Taurotragus oryx</i>	<i>Taurotragus</i> cf. <i>oryx</i>
<i>Pelorovis antiquus</i>	<i>Homoioceros</i> sp.
<i>Hippotragus</i> sp.	<i>Oryx</i> sp.
<i>Connochaetes taurinus</i>	<i>Connochaetes</i> spp.
<i>Alcelaphus</i> aff. <i>lichtensteini</i>	<i>Connochaetes</i> spp.
Antilopini sp.	<i>Litocranius</i> sp.

The occurrence of *Pelorovis antiquus* and the likelihood of the hartebeest being only subspecifically different from living *Alcelaphus lichtensteini* both suggest a Pleistocene date later than Olduvai Bed III, and the *Taurotragus oryx* a date later than the level of *T. arkelli* in Olduvai Bed IV.

A number of horn cores almost certainly from Broken Hill includes two examples of *Damaliscus niro*, BM(NH) M 34416-7. They are smaller than at Olduvai or Cornelia and nearer in size to



those of Florisbad. The same collection also contains a horn core, M 34418, which looks very like the slightly smaller 'Alcelaphini sp. nov.' recorded from Cornelia and Elandsfontein (p. 67). This species was referred to as 'cf. *Damaliscus* sp.' by Cooke (1974 : 75). Leakey (in Clark 1959 : 230) recorded *Damaliscus* from Broken Hill.

Broken Hill can be taken as Middle Pleistocene in age, and probably late in this period.

The South African sites can be considered in order of age, starting with the oldest. The bovid material from the Varswater Formation in 'E' Quarry at **Langebaanweg** is as follows:

*Tragelaphus* sp. cf. *angasi*  
*Mesembriportax* *acrae*  
*Simatherium* sp.  
*Kobus* sp. (aff. *sigmoidalis* ?)  
Alcelaphini spp. A and B  
? *Raphicerus* sp.  
*Gazella* aff. *vanhoepeni*  
Ovibovini sp.

This is evidently an early fauna. The tragelaphine horn cores are less anteroposteriorly compressed than in living *Tragelaphus*, and resemble the Makapansgat Limeworks BPI M.490 in this character. *Mesembriportax* belongs to the Boselaphini which are now extinct in Africa, the alcelaphines have more primitive teeth than those from Laetolil, and the ? *Raphicerus* is more primitive than at Elandsfontein. The gazelle is alleged to have a resemblance to the Makapansgat Limeworks *G. vanhoepeni* mainly on the prior assumption that Langebaanweg is the older site, so it would be unwise to let it contribute to correlating Langebaanweg. If Laetolil has an age of 3.59–3.77 million years, then Langebaanweg would be somewhat older, and Hendey (1974 : 62) has inferred an age of about 4.5 million years.

The bovid list for **Makapansgat Limeworks** is:

Present authors	Wells & Cooke (1956)
<i>Tragelaphus</i> ? <i>strepsiceros</i> (T)	<i>Strepsiceros</i> cf. <i>strepsiceros</i>
<i>Tragelaphus</i> sp. cf. <i>angasi</i>	<i>Strepsiceros</i> cf. <i>angasi</i>
<i>Tragelaphus pricei</i>	<i>Cephalophus pricei</i> (T)
? <i>Taurotragus</i> sp. (T)	<i>Taurotragus</i> cf. <i>oryx</i>
Bovini sp. or spp. (T)	cf. <i>Syncerus caffer</i>
<i>Cephalophus</i> sp. cf. <i>monticola</i> (T)	cf. <i>Cephalophus caerulus</i>
<i>Redunca darti</i>	{ <i>Redunca darti</i>
<i>Hippotragus gigas</i>	{ <i>Redunca</i> cf. <i>fulvorufula</i>
<i>Megalotragus</i> sp. (T)	cf. <i>Oryx gazella</i>
? <i>Connochaetes</i> sp. (T)	cf. <i>Pelorocerus helmei</i>
Alcelaphini sp.	{ cf. <i>Gorgon taurinus</i>
? <i>Aepyceros</i> sp.	{ cf. <i>Alcelaphus robustus</i>
<i>Oreotragus</i> sp.	<i>Damaliscus</i> sp. (aff. <i>albifrons</i> )
? <i>Raphicerus</i> sp.	<i>Aepyceros</i> cf. <i>melampus</i>
<i>Gazella vanhoepeni</i>	<i>Oreotragus major</i>
<i>Makapania broomi</i>	<i>Cephalophus pricei</i> (horn core)
	{ <i>Phenacotragus vanhoepeni</i>
	{ <i>Gazella gracilior</i>
	<i>Makapania broomi</i>

Makapansgat Limeworks has a tragelaphine of greater kudu size, a nyala-sized *Tragelaphus* with a primitive horn core cross-section as at Langebaanweg and member C of the Shungura Formation, a *Redunca* which is substantially less advanced than living species or the Elandsfontein reedbuck, a possible *Raphicerus* which is similar to that at Langebaanweg and the *Makapania* which is most similar to *Megalotis latifrons* of the European Villafranchian. This collection could best be given an age between Langebaanweg and Olduvai lower Bed II. This assessment could be altered or refined by the discovery or publication of further fossils, or by the demonstration that the site contains fossils of different ages.



The bovids which we have seen from **Cornelia** are:

*Pelorovis antiquus*  
*Megalotragus priscus*  
*Connochaetes ? gnou laticornutus*  
*Damaliscus niro*  
 Alcelaphini sp. nov. (also at Elandsfontein, = cf. *Damaliscus* sp. of Cooke 1974 : 75)  
 Antilopini sp. (T) (= *Antidorcas wellsi* of Cooke 1974 : 75)  
 Gen. indet. *helmoedi*

Cooke (1974 : 77) in his much-needed revision of the Cornelia mammals has referred additionally to *Taurotragus* cf. *oryx*, cf. *Tragelaphus strepsiceros*, cf. *Kobus venterae*, *Redunca* cf. *arundinum* and cf. *Sylvicapra grimmia*. Of these the cf. *Kobus venterae* is notable as being earlier than at other sites in South Africa. Cooke believes that the age of the fauna is around that of Olduvai Beds III–IV. We largely concur. The *Pelorovis* suggests a date no earlier than Olduvai Bed IV, and the *Connochaetes* and new species of alcelaphine both suggest a date close to that of Elandsfontein. Cornelia has generally been accepted as slightly earlier than Elandsfontein (Wells 1967 : 101; Cooke 1974 : 79).

The bovid list for **Elandsfontein** is:

Species	Implication for correlation
<i>Tragelaphus</i> sp. nov.	
<i>Taurotragus oryx</i>	later than <i>T. arkelli</i> of Olduvai Bed IV
<i>Pelorovis ? antiquus</i>	Olduvai Bed IV or later
<i>Syncerus</i> sp. (postcranial)	
<i>Redunca arundinum</i>	little different from living examples
<i>Hippotragus gigas</i>	a different subspecies from Olduvai
<i>Hippotragus leucophaeus</i>	
<i>Megalotragus priscus</i>	
<i>Connochaetes gnou ? laticornutus</i>	earlier than Florisbad
<i>? Parmularius</i> sp.	
<i>Damaliscus niro</i>	Olduvai middle Bed II or later
<i>Rabaticeras arambourgi</i>	Olduvai Bed III or IV
<i>? Beatragus</i> sp.	
Alcelaphini sp. nov.	also at Cornelia
<i>Raphicerus</i> sp. nov.	ancestral to one or more of the living species
<i>Antidorcas recki</i>	Olduvai Bed IV or earlier
<i>Antidorcas australis</i>	
<i>Gazella</i> sp.	most like examples in Olduvai middle and upper Bed II

This is the most interesting and informative site in South Africa for comparison with Olduvai. It seems that some part of the assemblage could best correlate with a time level around that of Olduvai Bed IV. There is every likelihood that Elandsfontein has yielded a temporally heterogeneous fauna (Hendey 1974 : 26), and among the bovids the *Syncerus*, *Hippotragus leucophaeus* and *Damaliscus niro* are candidates for being later than the other species.

The bovids at **Florisbad** are:

*Tragelaphini* sp. (T)  
*Pelorovis antiquus*  
*Kobus leche*  
*Hippotragus ? gigas* (T)  
*Megalotragus priscus*  
*Connochaetes gnou antiquus*  
*Damaliscus niro*  
*Damaliscus ? dorcas*  
*Antidorcas bondi* (T)  
*Antidorcas marsupialis*

The *Connochaetes* is more advanced than at Cornelia or Elandsfontein, and suggests that Florisbad



is later than those sites. The rather small horn cores of *Damaliscus niro* and the occurrence of what could be *D. dorcas* are consistent with such a later date. It would be interesting if the *Antidorcas marsupialis* horn cores came from the same low Peat Layer I as the *A. bondi*. The horn cores of the wildebeest (*Connochaetes*) appear to be at about the same level of evolutionary advance in relation to the living form as are the horn cores of *Alcelaphus* aff. *lichtensteini* at Broken Hill. This implies either that Florisbad and Broken Hill have similar ages, or that evolutionary rates have differed in the two lineages.

The bovids from Vlakkraal, Mahemspan, Melkbos and Swartklip need not be listed here as they have diminishing relevance for correlations with Olduvai Gorge. Vlakkraal evidently matches Florisbad very closely, and has the same two pairs of *Damaliscus* and *Antidorcas* species. Mahemspan has two frontlets of *Connochaetes gnou*, one (C.2402) like the Florisbad *C. g. antiquus* and the other (C.2498) more advanced. The latter, together with the horn core of *Alcelaphus buselaphus caama* (Hoffman 1953 : fig. 13), suggest either a later date than Florisbad and Vlakkraal or an admixture of later fossils. Melkbos and Swartklip are both sites under continuing investigation at the South African Museum.

## Summary

### The significance of the Olduvai bovids

The Olduvai bovids have been interesting from several aspects.

1. They are of Pleistocene age and a large number of lineages is represented. The antelope fauna of northern Tanzania must have been more diverse at that time than in the past few centuries.

2. Many of them would be recognizable to persons familiar with only the living antelopes of Africa. These are the ones which are ancestral to living species, and give information about the forebears of the greater kudu, eland, buffalo, waterbuck, kob, wildebeest, hartebeest, springbok and gazelle.

3. Earlier forms generally have more primitive characters than later ones, as can be seen for example in the horn cores of the Bed I wildebeest compared with those in later beds. However, the fossils sometimes show characters which are more advanced than in their descendants. One of the explanations for this may be that new species have not always evolved from the most advanced subspecies or variety of their parent species.

4. A number of the Olduvai lineages are now extinct or, like *Beatragus* and *Antidorcas*, no longer occur in Tanzania.

5. The higher total number of lineages in the Pleistocene would have necessitated narrower adaptations for many of the species, and this too could contribute to explaining why the Pleistocene forms sometimes appear more advanced than living ones.

6. Many of the bovids are a little larger than their nearest living relatives at tribal, generic or species level.

7. The Olduvai bovids as a whole indicate a rather dry and open environment. Alcelaphini are strongly represented, especially in middle and upper Bed II.

8. There is evidence for faunal changes at Olduvai. The change is very sharp at a level just after the start of middle Bed II. The cause of the change must have been ecological alterations which brought in species new to the Olduvai area as well as morphological evolution in some lineages. Changes at other stratigraphical levels are less sharp.

9. The bovid fauna of Beds III and IV has more resemblance to the living fauna than does that from earlier levels.

10. There is little evidence for extinctions within the time span of Olduvai Beds I-IV. Most of the extinct lineages survived into Bed IV if not later. It seems that a little-known caprine and *Par-mularius angusticornis* could have been exterminated (at Olduvai) within the span of Beds I-IV.

11. The bovids contribute to broad faunal correlation of Olduvai with other African fossil localities. Laetolil, Tanzania, has a fauna substantially older than Olduvai, but a few of its fossils are much younger. The Humbu Formation at Peninj, Tanzania, correlates well with middle



and upper Bed II. Kanjera, Kenya, correlates with Olduvai Bed II. The late fauna at Kaiso, Uganda, predates Olduvai, and its bovids would best fit a time level around member F of the Shungura Formation, Omo, Ethiopia. The early fauna need not have been very much earlier. The bovids of the Shungura Formation at Omo support making members G–H equivalent in time to Bed I and member L to Bed III.

In South Africa Langebaanweg is older than Laetolil. Makapansgat Limeworks comes between Langebaanweg and Olduvai lower Bed II, but its fossils may not all be from one time level. Cornelia and Elandsfontein appear to be about the same age as Olduvai Bed IV, but once again there is the problem that Elandsfontein may contain fossils of different geological ages. Florisbad is later than Olduvai Bed IV.

Broken Hill, Zambia, is later than Olduvai Bed III.

### Taxonomic changes

The following changes in the nomenclature and classification of Olduvai bovids have been adopted in this paper:

*Tragelaphus strepsiceros maryanus* and *T. s. grandis* are taken as subspecies of the extant *T. strepsiceros* instead of as separate species.

*Homoioceras* has become a junior synonym of *Syncerus*, and the bovine previously called *H. antiquus* has become *Pelorovis antiquus*.

*Syncerus acoelotus* is a new species.

*Thaleroceros radiciformis* is included in the Reduncini.

*Megalotragus kattwinkeli* includes the species formerly called *Alcelaphus kattwinkeli*, *Xenocephalus robustus* and *Alcelaphus howardi*.

*Pulitiphagonides* has become a junior synonym of *Connochaetes*, and *C. africanus* is included in the Alcelaphini instead of the Caprinae.

*Connochaetes taurinus olduvaiensis* is taken as a subspecies of the living blue wildebeest instead of being a separate species.

*Parmularius angusticornis* includes the species formerly called *Damaliscus angusticornis* and *D. antiquus*.

*Damaliscus agelaius* is a new species.

*Phenacotragus* has become a junior synonym of *Antidorcas*.

*Antidorcas recki* includes *Gazella wellsi*.

We have abandoned three names founded by Schwarz (1932, 1937) for Olduvai antelopes: *Tragelaphus spekei stromeri*, *Taurotragus oryx pachyceros* and *Gazella gazella praecursor*. The holotypes were lost in the Second World War, the only illustrated pieces were a tibia and cervical vertebra of the gazelle, and the descriptions are insufficient to allow existing material to be compared with them.

Many reidentifications have been made of fossil bovids from sites other than Olduvai.

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