THE FOSSIL BOVIDAE OF STERKFONTEIN, SWARTKRANS AND KROMDRAAI

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INTRODUCTION

The fossil sites Swartkrans, Sterkfontein and Kromdraai are situated in close proximity, not more than three kilometres apart, in the Sterkfontein valley near Krugersdorp, Transvaal (Fig. 24). Excavation at these sites has yielded abundant faunal remains, including hominids, as well as stone artefacts. For a comprehensive review of various aspects of these sites the reader is referred to Brain (1958). The many hundreds of cranial fragments, belonging to the mammalian family Bovidae Gray, from these assemblages, form the basis for this study. The following subdivisions, or site units, of Swartkrans, Kromdraai and Sterkfontein are referred to throughout the text:

STS: Sterkfontein Type Site, as formerly known (now referred to as Sterkfontein Main Quarry or Type locality, Tobias, pers. comm.);
SE: The West Pit of the Sterkfontein Extension Site (now Extension locality);
D16: Sterkfontein Rubble Dump 16;
SK: Swartkrans;
SKa: Swartkrans assemblages from what was formerly known as the "pink" breccia (Brain, 1958), and is now referred to as "primary" breccia (Brain, pers. comm.);
SKb: Swartkrans assemblage from 1. what was formerly known as the "brown" breccia (Brain, 1958), and is now referred to as "secondary" breccia; and from 2. fills of channels that formed at a relatively late stage through both primary and secondary breccias (Brain, pers. comm.);
KA: Kromdraai Faunal Site;
KB: Kromdraai Australopithecine Site.

How these subdivisions were arrived at is discussed in the text (p.116). They are referred to, throughout this work, either in full or by the abbreviations here given. Collectively they may be referred to as the Krugersdorp site units or the Sterkfontein valley site units.

All these assemblages represent cave accumulations (Brain, 1958). Together they form a succession, occasionally referred to below as the Krugersdorp succession, which encompasses close on two million years of South African hominid and faunal Pleistocene history.

Bovids have radiated into a wide range of environmental niches during their African history. Many are sensitive indicators of environment, having more or less restricted feeding and water requirements. Not only are they informative in their capacity as "eaters" of the surrounding vegetation, but also in their role of forming the bulk of the "eaten". As such, and because they generally constitute a large proportion of African fossil accumulations, bovids are potentially useful in the interpretation of assemblages.

This work is presented in two volumes. In this first volume bovid specimens are described and, as far as possible, taxonomically placed. Unless otherwise stated, Ansell's (1968) classification of extant African Bovidae is followed. Volume I also contains a discussion of these taxonomic results. The relative and absolute chronology of these sites and their subdivisions represents a major problem, as none of them have as yet been radiometrically or palaeomagnetically dated. The discussion contains a small contribution towards a solution of this problem. Some tentative palaeoecological inferences have also been drawn.

Volume II contains the 96 Tables, 41 Plates and 30 Figures which are constantly referred to in the text of Volume I.

Four papers, which are being submitted as parts of this thesis, have been published. They have been firmly tied into the text of Volume I at appropriate points:

1. Vrba, E.S., 1970. Evaluation of Springbok-like Fossils: Measurement and Statistical Treatment of the Teeth of the Springbok, *Antidorcas marsupialis marsupialis* Zimmermann (Artiodactyla: Bovidae). **Ann. Transv. Mus. 26**: 285–99.
2. Vrba, E.S., 1971. A new fossil Alcelaphine (Artiodactyla: Bovidae) from Swartkrans. **Ann. Transv. Mus. 27** : 59–89.

3. Vrba, E.S., 1973. Two Species of *Antidorcas* Sundevall at Swartkrans (Mammalia: Bovidae). **Ann. Transv. Mus.** 28: 287–361.
4. Vrba, E.S., 1974. Chronological and ecological Implications of the fossil Bovidae at the Sterkfontein Australopithecine Site. **Nature, Lond. 250** (5461): 19–23.

The following paper is submitted in support of the thesis, although forming no part of it:

Laubscher, N.F., Steffens, F.E. and Vrba, E.S., 1972. Statistical Evaluation of the taxonomic Status of a fossil Member of the Bovidae (Mammalia: Artiodactyla). **Ann. Transv. Mus. 28** : 17–26.

DESCRIPTION AND TAXONOMY

DESCRIPTION AND TAXONOMY OF THE SWARTKRANS BOVIDAE

Subfamily: HIPPOTRAGINAE

Tribe: ALCELAPHINI

A. Horn Core and Skull Material

●**Rabaticeras porrocornutus*: The type specimen of this species is SK 3211. It It was described as *Damaliscus porrocornutus* in a paper (Vrba, 1971) which forms part of this thesis and is intended to be included at this point. In a paper that is submitted in support of the thesis (Laubscher, Steffens & Vrba, 1972) various statistical methods suggested that SK 3211 is closer to the genus *Damaliscus* Sclater & Thomas than to *Alcelaphus* De Blainville. The multivariate analysis based on Rao's statistic (Laubscher et al., 1972: 24) indicates that SK 3211 is likely to belong to a third genus. Members of the genus *Rabaticeras* Ennouchi from Rabat, Elandsfontein and Olduvai Beds III–IV, at present all classified as *Rabaticeras arambourgi* Ennouchi (Gentry, Wells; pers. comm.), are all so similar to SK 3211 in the extremely unusual curvature and orientation of the horn cores with respect to the face, that at present *Rabaticeras* must be considered the best genus to accommodate SK 3211. It is hoped that a subsequent study (involving the collaboration of Wells and Vrba on the biological, Laubscher and Steffens on the mathematical aspects) will further examine this postulated relationship of SK 3211 to *Rabaticeras*. Several features, some of which were briefly outlined in Vrba (1971: 69 and 70), indicate that SK 3211 belongs to a *Rabaticeras* species distinct from *R. arambourgi* as we know it from the holotype cast, Q 1776, from Rabat, from Olduvai Bed III and from Elandsfontein:

1. The latter *R. arambourgi* material consistently has a considerably greater (approximately 140°–150°) angle between the posterior horn core bases and the top of the skull than has SK 3211 (estimated at approximately 100°), while the angle between anterior horn core bases and the forehead is smaller

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* Each start of the description of fossil material belonging to a particular species (or occasionally to a less well-defined taxonomic category) is announced by the symbol ●.

than on SK 3211. Thus the said *R. arambourgi* material seems to differ from the Swartkrans species in having horn cores that are orientated more forward with respect to the skull as a whole, when held in normal posture.

2. The estimated basal horn core dimensions of SK 3211 show more mesio-lateral compression (with a horn core index of 68%; see Vrba, 1971: 61) than do those of *R. arambourgi* from Olduvai Bed III and Elandsfontein (with indices varying from 80–86%) or that of Q 1776 (approximately 75%).

3. Perhaps a minor point, but again one that is consistently observable, is the fact that in *R. arambourgi* the postcornual groove is hardly demarcated by anterior and posterior edges as is so distinctly the case on the Swartkrans specimen.

4. Most *R. arambourgi* specimens lack anterior horn core ribbing, which is quite pronounced on SK 3211.

Further points could probably be established by careful comparison and measurement, e.g. the general forehead shape and the apparently considerably greater distance between the supra-orbital foramina on SK 3211. Together these differences, especially point 1 which is so consistently and dramatically different on Olduvai Bed III, Elandsfontein and North African *R. arambourgi*, probably indicate that SK 3211 belongs to a separate species and should therefore be called *Rabaticeras porrocornutus.* It is very interesting to note at this point that the Olduvai *Rabaticeras* skull (Old. 1970. Geologic Locality 208) which hails from the Lemuta Tuff at the base of Middle Bed II and dated approximately 1.65 million years, is definitely closer to SK 3211 than is other *Rabaticeras arambourgi* material. While having a basal horn core index of approximately 80%, its posterior horn core/top of skull angle is no greater than 80–90°. It has the same wide, flat, well-demarcated postcornual groove as have SK 3211 and SK 14104 (see below). The question arises whether this Olduvai Bed II form could be *R. porrocornutus* (or at least the same species if both turn out to be misplaced in *Rabaticeras*). Gentry (pers. comm.) feels that *R. arambourgi* from Olduvai Bed III, Elandsfontein and North Africa is a possible ancestor for *Alcelaphus buselaphus* Pallas. A similar line of reasoning was adopted with respect to the Swartkrans species in Vrba (1971: 68), before comparison with other *Rabaticeras* had been possible. Gentry (pers. comm.) also suspects that there may not be a simple succession from the Bed II to the Bed III form to *A. buselaphus,* because it is difficult to visualize the "successive" horn core insertion angles observed on the relevant forms (i.e. from low to high and back to low angle; see also Fig. 3 in Vrba, 1971) as belonging to the same lineage. Rather Gentry suggests that the Olduvai Bed II *Rabaticeras* may be ancestral to *Alcelaphus lichtensteini* (Peters). If the Swartkrans *R. porrocornutus* were indeed as close to the Olduvai Bed II *Rabaticeras* as I suspect (but am unable to confirm because of the fragmentary nature of the Swartkrans fossils), its horn core to skull relationship would certainly not contradict such ancestry to *A. lichtensteini.* Alternatively if *R. arambourgi* were to turn out not to be ancestral to *A. buselaphus,* I could see no reason why the Swartkrans and Olduvai Bed II forms should not have evolved into later *R. arambourgi,* one of the changes being that in horn core/skull orientation.

Another Swartkrans specimen, SK 14104, consists of most of the dorsal cranial and basioccipital regions of a skull, including the bases of both horn pedicels, portions of the orbital rims and of the frontal anterior to the horn cores (Plates 1–3). The nature of the sutures and the consistency of some of the exposed bone suggest that SK 14104 could have belonged to a subadult individual. It is extensively weathered and crushed, and such areas as can be reliably evaluated are unfortunately almost mutually exclusive from those present on the type specimen of *R. porrocornutus,* SK 3211. The closeness of the horn core bases (Plate 1), their general size and orientation with respect to the cranium, what can be seen of the forehead shape and the extent of the cornual diverticulum are all very similar. SK 14104 has more of the orbital rim and postcornual groove preserved on its left side than was visible on SK 3211. The postcornual groove is wide and flat as in SK 3211, and has a prominent anterior edge. Plate 1 shows that SK 14104 has a prominently jutting orbit. It is impossible to measure the basal horn core compression on this specimen, but hazarding a guess one could say that the horn cores were probably less strongly compressed than those of the *R. porrocornutus* holotype.

Comparison of SK 14104 with the Elandsfontein *R. arambourgi* shows some marked differences, such as the significantly wider foramen magnum, occipital condyles and nuchal crest area on SK 14104 (Plate 3), although the bregma-occiput distance is much the same. I was unable to compare the Olduvai Lemuta Tuff skull, mentioned above, directly with SK 14104. Such measurements as I have of the Olduvai skull, such as bregma-occiput distance, paroccipital and orbital widths, compare excellently with SK 14104, as do the wide, flat forehead and orbital rim shape. A point of disagreement seems to be the greater parieto-occipital angle on SK 14104 (approximately 160°) compared with about 130° on the Olduvai specimen (and approximately 140° on the Elandsfontein *R. arambourgi* skull, 9470). It is however evident that SK 14104 was crushed in this region and the actual parieto-occipital angle may have been lower (Plate 2).

An alternative assignation would place SK 14104 on a *Parmularius* Hopwood lineage, possibly close to *P. angusticornis* (Schwarz). The species was first described as *Damaliscus angusticornis* by Schwarz (1937:55) and subsequently placed into *Parmularius* by Gentry (Appendix in Hendey, 1970). Several specimens of this species (“*Damaliscus antiquus*” Leakey = *Parmularius angusticornis* according to a personal communication from Gentry) have comparable parieto-occipital angles and resemble SK 14104 in other respects. The Swartkrans skull also has a small but unmistakeable parietal eminence, so characteristic of *Parmularius* (also found in *Damaliscus* species). Where the measurement cateogries below correspond to those used for *Damaliscus angusticornis* and *D. antiquus* by Leakey (1965), SK 14104 seems rather smaller by comparison. This however would be in no way strange if SK 14104 really belongs to a subadult individual.

For the moment assignation to *Parmularius* of this single specimen remains a rather daring step: The presence of this genus in South African assemblages, as a whole, has not yet been firmly established. At present, therefore, SK 14104 is placed tentatively with the Swartkrans *R. porrocornutus* material, and the possibility of a specific identity, or at least a close taxonomic relationship, with the Olduvai Lemuta Tuff *Rabaticeras* is put forward.

The condition of SK 14104 allowed only a few measurements to be estimated:

bregma to occiput ≈ 59 mm (≈ stands for: "equals approximately")
anteroposterior basal horn core diameter ≈ 44 mm
mesiolateral " " " " ≈ 38 mm
minimum distance from bregma to upper foramen magnum edge ≈ 102 mm
maximum distance across paroccipital processeses ≈ 100 mm
maximum width across posterior tuberosities of basioccipital ≈ 37 mm
maximum width across occipital condyles ≈ 75 mm

- *Beatragus* Heller* sp. (Plate 4B): Sk 14183, consisting of a small part of the forehead and orbital rim area as well as the base of the left horncore, has the following points of interest:

1. The base of the horn core is round to slightly flattened antero-posteriorly: mesiolateral diameter = ± 55 mm; antero-posterior diameter = ± 54 mm.
2. About 30 mm. above the base of the horn core the antero-posterior flattening becomes more marked: mesio-lateral diameter = ± 51 mm; antero-posterior diameter = ± 45 mm. The broken extremity of the horn core indicates that it curved gently backwards in this area (30–65 mm above the base).
3. Torsion in the right horn core, looking along it from pedicle to tip, would have been anticlockwise.
4. There is a large smooth-walled cornual diverticulum, which occupies almost the entire volume (widthwise) at the base of the horn core.

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* In Vrba (1971: 72) it was pointed out that as a consequence of following Ansell's (1968) classification of extant African Bovidae, the "genus" *Beatragus* must be considered as being sunk in *Damaliscus.* Since that paper was written, however, further consideration has led me to accept *Beatragus* as a full genus.

5. At the antero-lateral boundary between pedicel and horn core is a number of small round pits. They occur at regular intervals, about 9 mm apart, and get shallower as one progresses from a lateral to an anterior direction. These structures (which I have never seen occurring like this in extant South African bovids) were probably occupied by blood-vessels during life, as attested by the grooves running onto the pedicel from one or two of them.

6. The distance between the base of the horn core and the orbital rim is short, and the latter juts out sharply (Plate 4B).

7. Only the upper part of the supra-orbital foramen has been preserved. It is ± 47 mm from the base of the horn core. The supra-orbital canal, ± 25 mm long, is slightly curved.

8. The postcornual groove is situated more posteriorly than is usual in extant South African *Damaliscus,* where it extends in a lateral position. Its flat base is almost parallel to the plane of the forehead.

9. The wide flat postcornual groove has a marked anterior rim (only the part near the horn core is preserved in SK 14183).

10. There is an indication of a postero-lateral keel starting about 20 mm in front of the postcornual groove.

11. There is a mesial keel. Unlike the postero-lateral one which represents an undulation in the horn core surface, the mesial keel is a ridge which lifts out of the horn core surface (arrow in Plate 4B).

Gentry, in his unpublished assessment of Elandsfontein Bovidae, tentatively identified a number of frontlets and horn cores as *Beatragus* sp. The characters mentioned above in points 1–8 occur to a greater or lesser extent on all Elandsfontein specimens. Some of the latter, among the smaller apparently female specimens, are identical to SK 14183 with respect to points 1–8. However, there are some small but consistently present differences between the Elandsfontein *Beatragus* sp. and SK 14183: The postcornual groove (point 9), where seen on Elandsfontein specimens, is narrower and much less marked, especially the upper (anterior) rim, than in SK 14183. The postero-lateral keel (point 10) originates more posteriorly, i.e. more or less from the position of the postcornual groove, on such Elandsfontein specimens where its origin is visible. The greatest difference concerns the mesial keel (point 11): Only in a couple of Elandsfontein specimens is there a hint of a mesial keel, while most have none at all.

SK 14183 is thus undoubtedly very closely related to the Elandsfontein *Beatragus* sp., perhaps representing a geographically separated race of the same species, or at most a different species. SK 14183 is here called *Beatragus* sp.

There are two further horn core specimens which could possibly belong to this species: SK 14008, the base of a right horn core, is so battered and distorted that any attempts at identifying it must be very tentative. However, the general shape of the base of the horn core, the cornual diverticulum, the posterior flattening with the suggestion of a postero-lateral keel would all agree with *Beatragus* sp. The horn core is of course much smaller (basal dimensions: antero-posterior diameter = ± 39 mm; mesio-lateral diameter = ± 40–45 mm) but the apparently spongy nature of the horn core bone suggests that SK 14008 might have belonged to a young individual. (An alternative affinity of this specimen could be with *Damaliscus lunatus lunatus* [Burchell], the tsessebe. In this case SK 14008 would have to be from an adult).

SK 14208 is a short (± 73 mm long) piece of horn core, curved and with base-to-tip clockwise torsion. This could conceivably have belonged well above the pedicel of the left horn core of a *Beatragus* sp.

The species *Beatragus antiquus* Leakey is reasonably common through the Olduvai beds (Gentry, pers. comm.). It is essentially similar to SK 14183, but has a slightly less pronounced postero-lateral keel and no mesial keel. It differs from both the Elandsfontein and Swartkrans *Beatragus* in having larger and longer horn cores. I accept the opinion of Gentry (pers. comm.) that *Beatragus* was probably formerly more wide-spread, with a southern species (so far found at Elandsfontein, and now also at Swartkrans) replacing *B. antiquus* geographically.

- *Damaliscus* cf. *dorcas* (Plate 4A): SK 14206, a partial horn core, is in every respect indistinguishable from the left horn core of a young *D. dorcas.*

- cf. *Damaliscus niro* (Hopwood) (Plate 5): SK 2862 is a piece of horn core about 155 mm long, with an eroded surface. It shows the following features:

  1. At its base can be seen the top of what must have been an extensive cornual diverticulum.
  2. Although the base of the horn core is missing, it would not have been much lower than the preserved lower edge, which permits the following measurements: antero-posterior diameter = ± 44 mm; mesio-lateral diameter = ± 36 mm (i.e. index = ± 82%); perimeter = ± 130 mm. 100 mm Further up from the place where these measurements were taken, the following were recorded: antero-posterior diameter = ± 39 mm; mesio-lateral diameter = ± 23.5 mm; (i.e. index = ± 60%); perimeter = ± 105 mm. There is thus an abrupt mesiolateral flattening as one proceeds towards the tip of the horn core.
  3. Plate 5 shows that the cross-section of the horn core about 130 mm above the horn core base was roughly D-shaped.
  4. There appear to be "bumps" on the anterior horn core surface, about 400 mm apart. This must remain a tentative point because of the eroded horn core surface.

SK 2862 differs decisively with respect to point 1, and in dimensions and/or shape from horn cores of both *Hippotragus niger* (Harris) and *Hippotragus equinus* (Desmarest). The rapid rate of thinning in anterior view (while the antero-posterior diameter diminishes less rapidly as one progresses from pedicle to tip) separates SK 2862 from all hippotragines, including *Hippotragus leucophaeus* (Pallas) as known from some Elandsfontein horn cores. It is interesting to note that the latter species, like the fossil *Hippotragus gigas* Leakey, seems to differ from extant hippotragines in having a more extensive cornual diverticulum. Point 4, if valid, would separate SK 2862 from all hippotragines.

On the other hand points 1, 3 and 4 are characteristic of the fossil *Damaliscus niro* which has been found at Olduvai from middle Bed II onwards

(Gentry, pers. comm.) and at various South African sites (Wells, 1970). The size of *D. niro* cores seems to have fluctuated in the fossil record: At Olduvai, while those from SHK in upper Middle Bed II look slightly larger than SK 2862, those from BK II in Upper Bed II seem to be of the same size. *D. niro* horn cores from JK 2 in Bed III are decisively larger. In South Africa horn cores of this species from Cornelia are larger than SK 2862, those from Florisbad of similar size. Because SK 2862 is incomplete and an isolated occurrence not only at Swartkrans, but so far in the Krugersdorp sites as a whole, and because it is too weathered to determine whether it is subadult or fully adult (not to mention sexual dimorphism in alcelaphine horn cores), such size comparisons must remain very tentative.

- cf. *Connochaetes* sp. aff. *africanus* (see footnote on p. 16 concerning the applicability in this case of the specific name *africanus*): SK 3812A, shown in Plate 6, is a piece of the top of a skull. It shows the following features:

1. Partially preserved supra-orbital foramina have mesial walls ± 64 mm apart, i.e. ± 32 mm from the midline frontal suture. The left foramen has a groove running out of it anteriorly. The supra-orbital canals are ± 25 mm long.
2. The specimen has an extensive frontal sinus which is broken open on the right side to show its extent posteriorly up to the fronto-parietal suture. The sinus extends ± 80 mm behind the supra-orbital foramen.
3. The facial surfaces of frontal and lachrymal form an obtuse angle of $\pm 120^{o} - 130^{o}$; i.e. there was apparently a pre-orbital fossa present (see arrow 1 in Plate 6B).
4. On the right side of SK 3812A the surface of the parietal sloping backwards from the coronal suture can be seen to form an angle of $\pm 95^{o}$ with the plane of the anterior frontal surface (between the two supra-orbital foramina and the nasion).
5. If SK 3812A had horn cores (and as discussed below there is reason to believe that it had) these must have been wide apart and arising closely behind the orbit.

6. The forehead above and between the supra-orbital foramina is convex, with only a slight localized concavity at the midfrontal suture between the foramina.

A comparison with living local bovids, if only with respect to the character combination of size, lack of supra-orbital pits and extensive frontal hollowing argues for affinity to the Alcelaphini rather than to any other extant South African tribe. Let us assume for the moment that SK 3812A is alcelaphine. It would have had horn cores which would have arisen far apart as alcelaphines go. This latter fact leaves only three alcelaphine genera for consideration: *Connochaetes* Lichtenstein (more especially *Connochaetes taurinus* (Burchell)), *Damaliscus* (i.e. *D. lunatus lunatus*) and the fossil *Beatragus* species.

If SK 3812 belongs to a species of *Connochaetes* (and this possibility merits serious consideration as some Swartkrans teeth have been thus assigned; see p. 33), the similarly sized *C. taurinus* would differ in the following respects from it:

1. Supra-orbital foramina of *C. taurinus* tend to be multiple with sharp upper edges.
2. *C. taurinus* has only a gentle dip to house the pre-orbital gland, unlike the marked fossa present in many other bovids. SK 3812A had at least the upper (posterior) part of such a marked depression.
3. The parietal of *C. taurinus* is smaller and more sharply bent down on the plane of the anterior frontal surface (between the two supra-orbital foramina and the nasion) than is the case in SK 3812A (see arrow 2 in Plate 6).
4. The horn cores of *C. taurinus* arise much further back behind the orbit than those of SK 3812A would have done.
5. The forehead above and between the supra-orbital foramina of *C. taurinus* is concave.
6. The orbit of *C. taurinus* is further forward, with respect to such reference points as bregma and level of supra-orbital foramina, than in SK 3812A.

Elsewhere in this work (p. 33) some Swartkrans teeth are tentatively assigned to *Connochaetes*, and it is discussed why this form could have been on or near the lineage leading up to *C. taurinus*. None of the above points would really contradict such a possibility if SK 3812A belonged to the said teeth. Concerning point 3, for instance, Pilgrim's (1939:63) observation is interesting: Correlated with the bending down of the face on the basicranial axis is the formation of an acute angle between face and braincase in more progressive alcelaphines. In earlier forms (in this case it is suggested that SK 3812A might be an earlier form of *C. taurinus*) this angle was greater.

A second possibility among alcelaphines is *Damaliscus lunatus lunatus*. The latter is essentially similar to SK 3812A with respect to points 1 to 5. It differs from the fossil in being flatter between and above the supra-orbital foramina. Horn core SK 14008, at present tentatively associated with *Beatragus* sp., could well belong to a tsessebe or cf. tsessebe. One rather awkward point would be that among the numerous Swartkrans teeth no trace of the characteristic tsessebe premolars, or precursors thereof, have been found.

A third possibility would be that SK 3812A belongs to the same *Beatragus* sp. as SK 14183. There is little overlap between the two specimens as to what structures are preserved, ruling out a comparison. All that can be said is that the postcornual groove and orbital regions look as though they might have been different in the complete state. If SK 3812A were indeed a *Beatragus* sp., the latter would certainly be specifically distinct from the Hopefield *Beatragus* sp., which differs significantly from SK 3812A in its forehead shape.

One possible non-alcelaphine affiliation for SK 3812A could be mentioned: The specimen is not unlike the corresponding part of the skull of a very young ($M_{\overline{1}}$ erupting) *Syncerus caffer*. It differs in forehead and supra-orbital foramen shape, as well as in having sutures which are fused more firmly. A more serious difference is the total lack of preorbital glands and fossae in the buffalo. Although in *C. taurinus* the preorbital area is shallower than in SK 3812A, the blue wildebeest at least has an (albeit reduced) preorbital gland, which was probably larger in its ancestors.

In fact early *Connochaetes* from East Africa, which may be ancestral to *C. taurinus*, especially material from east of Lake Rudolf (probably dated

1.5–1.9 million years, Maglio, 1972), and also from Olduvai Bed I*, seem very close to SK 3812A. Measurement proportions, relative positions of horn core and orbit, the convex shape of the forehead and other visible features compare very well. On the East Rudolf skull one can even perceive a preorbital depression which was more marked than on *C. taurinus,* while the associated upper teeth correspond well with Swartkrans Gp III alcelaphine teeth. Other dentitions, especially mandibles, from the same East Rudolf locality as well as from Olduvai Bed I are indistinguishable from the Gp III teeth (p. 37).

B. Alcelaphine dentitions: Introduction

Grouping of teeth: The first thing that strikes one on looking at the Swartkrans alcelaphine teeth is that roughly four size groups appear to be present. Let us call them for the moment Groups I–IV. Unfortunately Gp IV, consisting of the largest teeth, is represented by so few specimens that histograms of tooth lengths such as Figs. 6–9 cannot be spoken of as "four-peaked". Nonetheless a faint, recurrent tendency can be seen among Figs. 6–9 to form four main size groups. A more searching look at these size groups was taken by the clustering method, the results of which are given in the dendrogram in

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* The tentative linking of SK 3812 A and of *Connochaetes* dentitions from Swartkrans and other Krugersdorp assemblages, to the specific name *africanus* resulted from the assumption that the wildebeest in the early Olduvai sediments (up to and including the lowest levels of Middle Bed II) belongs to the same species as the holotype skull of *Connochaetes africanus* (Hopwood), originally the type species of a genus *Pultiphagonides* Hopwood. Recently, at a time when this work was already in print, it was pointed out by Gentry (pers. comm.) that this Bed II holotype skull shows greater resemblances to *Connochaetes gnou* than to *C. taurinus.* If the name *africanus* were indeed thus occupied by a black wildebeest ancestor, then possible blue wildebeest precursors, specifically distinct from *C. taurinus*, from the basal Olduvai sediments, East Rudolf and perhaps also from Swartkrans and other local assemblages, would have to be given (a) different name(s). The linking of the present Krugersdorp site material to *C. taurinus* ancestry is very tentative; the material is too scant to rule out other affinities, as for example to *C. gnou* ancestry. Consequently I am not altering the cautious appelation, cf. *C.* sp. aff. *africanus,* for the present, while recognizing the strong possibility that this may have to be revised, perhaps to a specific name chosen for more complete Olduvai or East Rudolf material.

Fig. 1. Here, with respect $M_{\overline{3}}$ length and breadth, four clearly separated size clusters emerge at, for instance, the d = 4.5 horizontal line.

Because alcelaphines have speciated so extensively in past and present Africa, any taxonomic evaluation must consider a number of fossil and recent contenders for each size group of alcelaphine dentitions. Unfortunately only in one or two instances throughout the Krugersdorp sites were alcelaphine dentitions associated with horn core material, making the taxonomic treatment of these dentitions very difficult. Consequently measurements of alcelaphine dentitions were not separated into tables, each representing a single species, as was done for the other bovid dentitions, but a more loose arrangement was adopted in Tables 4 and 5: Superimposed on the basic size Groups I–IV, are further subdivisions determined by even finer size distinctions and other morphological characters as described in detail below. Size-descriptive names appended to these subdivisions, are here introduced (like "smaller small" and "larger large") and referred to throughout the work on alcelaphines for the convenience of the reader. In the succeeding section these groups and size-descriptive names are tentatively linked with specific names and with the horn core material. The subdivisions, including a minimum of seven alcelaphine species, are as follows:

Gp. Ia:	"smaller small" dentitions
b:	"larger small" dentitions
c:	
Gp. IIa:	"medium" dentitions with Type I $PM_{\overline{4}}$ ("smaller medium"?)
b:	" " : " II " ("larger medium"?)
c:	upper "smaller medium" dentitions (probably belonging to Gp IIa)
d:	upper "larger medium" dentitions (probably belonging to Gp IIb)
e:	upper "medium" dentitions belonging to either Gp IIc or Gp IId.
Gp. III:	"smaller large" dentitions
Gp. IV:	"larger large" dentitions

Some teeth were represented in their groups in length-breadth scatter diagrams (Figs. 2–5). Points on Fig. 2 have intentionally been labelled with their SK numbers as this provides an interesting comparison with the same specimens in Fig. 1: The placing of right $M_{\overline{3}}$'s into groups, shown in Fig. 2, can be said to be the result of a subjective (in the sense of non-numerical) summary of all morphological, size and other data available. It is interesting how closely the groupings obtained of the same $M_{\overline{3}}$'s, purely on size by the clustering method, tally with those in Fig. 2.

It must be pointed out here that size-descriptive terms may not be strictly analogous to those used by other workers in the field. I am thinking particularly of the category "larger small" dentitions, which may be regarded as belonging to medium-sized alcelaphines by other workers. The teeth here placed into this category do in fact show some size overlap with smaller specimens of smaller extant individuals generally regarded as "medium-sized" alcelaphines, like some dentitions of the tsessebe.

Juvenile dentitions (i.e. specimens including deciduous teeth) could only be divided into three size categories: "Small" dentitions belonging to Gp. 1; "medium" dentitions belonging to Gp. II; and "large" dentitions belonging to G. III (Tables 7,8). No juvenile alcelaphine dentitions large enough to belong to Gp. IV were found at Swartkrans.

Matching upper and lower teeth: It is reasonable to suppose that the ratios between upper and lower tooth sizes were much the same among alcelaphines of Swartkrans times as they are among the extant ones. Even if this were untrue, extrapolation from the extant case is the closest we can hope to come to a systematic approach to matching unassociated upper and lower fossil teeth. Table 1 shows upper/lower second molar ratios for some extant alcelaphines. In Table 2 all mismatches (in composing the said ratios) among the South African extant alcelaphines were examined. Any wrongly composed ratio that fits within the total ranges obtained in Table 1 was ringed. It augurs well for the usefulness of the obtained (correct) ranges that in only two of the mismatched cases were both length *and* breadth ratios ringed: $\frac{\textit{A. buselaphus}}{\textit{C. gnou}}$ and $\frac{\textit{D. l. lunatus.}}{\textit{A. buselaphus}}$

The three species involved are all medium-sized alcelaphines of much the same body weight (Dorst & Dandelot, 1970) and similar tooth size (Table 6). Thus one could cautiously say that, by using as testing criteria the total ranges of Table I, wrong association of upper and lower teeth, although possible among species of the same size, is unlikely among species of different sizes. Armed with this tentative guideline the main Swartkrans alcelaphine tooth groups, decided upon and constituted as outlined above, were tested with respect to the same ratios. The results are given in Table 3: Again ratios falling within the Table 1 ranges were ringed. Simultaneous ringing of length *and* breadth ratios, for any one combination of groups, occurred only in those cases where numerator and denominator have the same group name. One must add at once that this is by no means regarded as proof of the correctness of present grouping and assignation. The method here used is crude and full of potential pitfalls (e.g. the use of means in Tables 2 and 3, in the latter case means of arbitrarily constituted groups; the small numbers of individuals measured for Table 3). However, it can be said that this method, which after all showed up all known wrong combinations in Table 2, did not contradict the present assignations to upper and lower size groups; i.e. it gives no cause to doubt that they are broadly correct.

B. Alcelaphine dentitions: Discussion and Assignation

"Small" dentitions: "Smaller small" Gp. Ia: *Damaliscus* cf. *dorcas;* "larger small" Gp. Ib: *Damaliscus* sp. 2; "larger small" Gp. Ic: *Damaliscus* sp. 1 or *Parmularius* sp. (Plates 7–9)

Small alcelaphine teeth at Swartkrans form quite a uniform group with little size overlap with those teeth called "medium" sized in this work (See Tables 4–6 and Figs. 1–5). Nonetheless the problem remains whether this group of teeth contains one or more species.

The first question to be answered is whether the only "small" extant alcelaphine, *D. dorcas,* is present at Swartkrans. *D. dorcas* dentitions, on present knowledge, can be distinguished from all other extant or extinct alcelaphine species by the unique combination of 1. being among the smallest alcelaphine dentitions known, 2. having long premolar rows with $PM_{\overline{2}}$ and $PM^{\underline{2}}$ generally present and $PM_{\overline{3}}$ and $PM^{\underline{3}}$ well developed, and 3. having a complicated molar occlusal surface enamel pattern. Extinct alcelaphine species almost always seem to have a distinctly less complicated dental enamel configuration. Such dentitions of small extinct species as I have seen to date have also generally been a bit larger than those of *D. dorcas* (we have not yet found or recognised the dentitions of the very small alcelaphine form, probably a member species of *Damaliscus,* which occurs at several South African sites). Extinct alcelaphines as a whole more often than not seem to have short premolar rows, without $PM_{\overline{2}}$'s. An exception among small alcelaphine fossils to this generalization is *Damaliscus agelaius* Gentry from Olduvai Bed IV, which Gentry (pers. comm.) sees as a likely ancestor for both living species of the genus *Damaliscus.* It must therefore be stressed that the element diagnostic of *D. dorcas* dentitions, on present knowledge, is the *combination* of the three characteristics and not the possession of any one of them. Using this criterion dentitions like upper SK 3123 (on points 1, 2 and 3) and lower SK 10867 (on points 1 and 3) proclaim the presence at Swartkrans of *D. dorcas,* or at least of a very closely related, advanced form which was no larger than the extant bles- or bontebok. The Swartkrans adult dentitions of *D.* cf. *dorcas* are tabulated as "smaller small", Gp. Ia, in Tables 4 and 5 and their special characteristics are shown in Plates 7 and 8. The conclusion that *D. dorcas* is present is supported by the convincing horn core SK 14206. Applying the said three dental criteria simultaneously we find *D.* cf. *dorcas* in the SE and D16 assemblages from Sterkfontein. Teeth, without premolar rows, of the right size and occlusal surface morphology also come from Dumps 2, 3 and 8. All these dump occurrences of *D.* cf. *dorcas* belong to a later Sterkfontein context (Vrba, 1974) than does the type locality material. *D.* cf. *dorcas* dentitions are probably entirely absent from the STS and KA assemblages, although from the latter a single horn core base could belong to this species.

A comparison of upper and lower tooth length means between the "Small" category as a whole on the one hand and the extant *D. dorcas* on the other (Table 6), makes it unlikely that all "Small" teeth belong to *D. dorcas.* The data suggest that a slightly larger, closely related alcelaphine lived alongside *D. dorcas* at Swartkrans. Was this "larger small" (Gp. Ib) alcelaphine a species of *Damaliscus* or of *Alcelaphus*? With respect to tooth shape, it is very difficult to pinpoint differences among alcelaphine species which will invariably separate them. However, it is my impression that the characteristic "pinched" portion of the molar lobes (buccal in lower, lingual in upper teeth) which exists in both

Alcelaphus and *Damaliscus,* is generally narrower in *Alcelaphus* with respect to tooth size, giving the teeth a more pointed appearance in this genus, which persists into old age. In *D. dorcas* this pinched portion is wider with respect to tooth size and flatter, giving the teeth more of a square look, especially in older dentitions. In this respect the fossil is unmistakably more like *Damaliscus* (Plate 7). The origin of the masseter on the maxilla is very localized and prominent in *D. dorcas* and in "Larger small" fossils (e.g. SK 3129, SK 5954), but less so in the *A. buselaphus* skulls examined. Finally, there is no fossil *Alcelaphus* smaller than *A. buselaphus* known at present in the South African fossil record. Accordingly these dentitions have been referred to *Damaliscus* sp. 2 (to distinguish them from another small fossil alcelaphine at the Krugersdorp caves which has been named *Damaliscus* sp. 1 or *Parmularius* sp.; see below).

Damaliscus sp. 2 is similar to *D. dorcas,* and unusual among extinct *Damaliscus* species as discussed above, in apparently possessing a long premolar row: SK 5979, shown in Fig. 10 A and Plate 7, is very likely to belong to *Damaliscus* sp. 2. It has a strong $\mathrm{PM}_{\overline{2}}$ and large $\mathrm{PM}_{\overline{3}}$ with completed paraconid-metaconid fusion. If it were typical of premolar rows in this species, or at least representative of a large proportion of them, SK 5979 would signify a degree of "molarization" (see pp. 41, 42) of $\mathrm{PM}_{\overline{3}}$ which was observed on none of the six *D. dorcas* specimens available at the Transvaal Museum (Table 9). Another Swartkrans mandible assigned to *Damaliscus* sp. 2 which gives some information on premolar length, SK 11390, has a large $\mathrm{PM}_{\overline{3}}$ root suggesting that the tooth was well developed. Although Swartkrans "small" alcelaphine juvenile dentitions were not separated into Gps. 1a, b, and c (Table 8) the high number of adults in Gp. 1b, i.e. *Damaliscus* sp. 2, relative to those in Gps. 1a and c, suggests that some of these juvenile lower dentitions belonged to *Damaliscus*, sp. 2. On the only three specimens where the entire deciduous premolar row is visible, i.e. SK 11003, SK 7050 and SK 5920, it is consistently longer, with a $\mathrm{DPM}_{\overline{2}}$, than in for instance *Damaliscus* sp. 1 or *Parmularius* sp. (p. 68), and comparable to that in *D. dorcas* (one or two of these juvenile mandibles may in fact belong to Gp. 1a, i.e. *D.* cf. *dorcas*). Upper dentitions assigned to *Damaliscus* sp. 2 confirm this conclusion of a longish premolar row in that species. SK 3129, SK 1520 and SK 5954 variously show the presence of strong $\mathrm{PM}^{\underline{3}}$'s and $\mathrm{PM}^{\underline{2}}$ (See Plate 8).

Damaliscus sp. 2 differs from *D. dorcas* by having dentitions that are on the average larger (Fig. 11, Tables 4–6, Plates 7 and 8), with perhaps less of a tendency to a complex occlusal surface enamel pattern: Although both species have lower molars with a tendency to buccally flattened surfaces, *D. dorcas* has the greater incidence of "kinks", i.e. "pinching", on either side of the flat portion (see arrows in Plate 7). *D. dorcas* also has greater tendency to goat-folds on its lower molars than has *Damaliscus* sp. 2. In some (maybe all?) bovid lineages the length-breadth relationships of dental occlusal surfaces change with time, the teeth becoming progessively (bucco-lingually) broader with respect to (medio-distal) length. In this respect *Damaliscus* sp. 2 is quite as advanced as *D. dorcas* (Fig. 11). On the whole, I would regard these dentitions as advanced with respect to other extinct damaliscines. The species is totally and conspicuously absent among the numerous small alcelaphine dentitions at KA. At Sterkfontein similar sized, i.e. "larger small" dentitions are found at STS, SE and Dumps H2, D1, D5, D8, D12, D13 and D16 (Vrba, 1974). At STS these dentitions represent another species, *Damaliscus* sp. 1 or *Parmularius* sp. (p. 92). Only one STS specimen could belong to *Damaliscus* sp. 2 (STS 2582, Plate 7). This specimen may have been misplaced in the type site assemblage, as there is evidence of a previously wiped out catalogue number, as well as the present STS reference number. At least some dental material from SE is too large for *Damaliscus* sp. 1 or *Parmularius* sp., and much too large for *D. dorcas,* and probably belongs to *Damaliscus* sp. 2. I would say that the rather distinctive combination of size and morphology of *Damaliscus* sp. 2 dentitions is certainly present at D16 (see Plate 7), although "larger small" material from other above-mentioned Sterkfontein dumps is too scant to make a similar statement about it. However, on the whole, there are indications that this species might have been present at Sterkfontein in a context later than that of the famous australopithecine assemblage (Vrba, 1974).

What exactly is *Damaliscus* sp. 2? Its dental characteristics certainly conform to what one might expect in an ancestor of *D. dorcas.* At both D16 at Sterkfontein and at Swartkrans the two species seem to occur together. Therefore *Damaliscus* sp. 2 should rather be seen as a species surviving until a relatively late stage in South Africa, side by side with *D. dorcas,* and not directly ancestral to it.

The extant medium-sized alcelaphine species which has the greatest resemblance in size and molar morphology to *Damaliscus* sp. 2 is *Damaliscus lunatus lunatus*, the tsessebe. Could the Swartkrans form be a tsessebe, or perhaps ancestral to it? One or two dentitions, especially among the upper dentitions, like SK 5954 and SK 3129, are very close indeed to those of the tsessebe. If, however, one compares the "larger small" assemblage as a whole with extant tsessebe dentitions, one gains the firm impression that a form with averagely smaller teeth which generally have less complex molar occlusal surface enamel configurations, than the tsessebe is present at Swartkrans. Only one premolar specimen is available for the Swartkrans form, but this shows a degree of molarization, i.e. paraconid-metaconid fusion on $\mathrm{PM}_{\overline{4}}$ and $\mathrm{PM}_{\overline{3}}$, that is very advanced even among extant alcelaphines (SK 5979, Plate 7). The tsessebe, on the other hand, among alcelaphines as a whole, is probably one of the species with the least advanced molarization of premolars (Table 9 and Plate 10). Nonetheless the possibility that what is here called *Damaliscus* sp. 2 includes some extant tsessebe material, or is on the same lineage, cannot be convincingly discounted on the available material.

It has been pointed out that the horn core assigned to cf. *D. niro* (p.13) probably belongs to a small population of that species, such as are found at Florisbad and Olduvai Upper Bed II (BK II); in fact small enough to go with these "larger small" Gp. 1b teeth. At both Florisbad and Olduvai BK II there are dentitions of similar size as Gp. Ib (and at both sites the teeth in question were the smallest alcelaphine teeth I saw, while the smallest alcelaphine horn cores seemed to be those of *D. niro*). While the few BK II dentitions which I saw lacked $\mathrm{PM}_{\overline{2}}$, those from Florisbad had $\mathrm{PM}_{\overline{2}}$ and in fact seemed to be morphologically very similar to *Damaliscus* sp. 2 specimens. The hypothesis preferred here, therefore, is that *Damaliscus* sp. 2 dentitions belong with the cf. *D. niro* horn core to a small variant of that species.

At least one small dentition, SK 3127 (Plate 7), shows a molar morphology so idiosyncratic among Swartkrans alcelaphines that it clearly represents a third small species. The occlusal surface is long with respect to (bucco-lingual) breadth (Fig. 11) and the enamel pattern is relatively simple with smooth round buccal lobes. Small alcelaphine dentitions of similar size and morphology occur quite numerously in the STS assemblage. At KA they constitute the only small alcelaphine specimens. A single specimen from the West Pit (SE) at Sterkfontein could belong to this species too. From KA and STS we know that teeth of this species are a little larger than those of *D. dorcas* (Fig. 11 and Table 37). Therefore this species, Gp. 1c at Swartkrans (Table 4) and named *Damaliscus* sp. 1 or *Parmularius* sp. (p. 72), can also be thought of as belonging to the "larger small" alcelaphine size group. No upper dentitions of this form were noticed among the Swartkrans material.

A number of small alcelaphine lower dentitions could not be placed with any confidence into one of the three small species, although I suspect that most of them belong to Gp. 1b. These are recorded as "Small (Gp. 1; indeterminate)" in Table 4.

Juvenile small dentitions (Table 7) belong either to *D.* cf. *dorcas* or to *Damaliscus* sp. 2.

A short summary of the differences between the dentitions of *D. dorcas*, *Damaliscus* sp. 2 and *Damaliscus* sp. 1 or *Parmularius* sp. are given on p. 71.

• "Medium" dentitions, including those of *R. porrocornutus* and *Beatragus* sp.? (Gp. II a–e, Plates 10–13)

In Group II (Tables 4–6), containing medium sized teeth, there are 13 specimens where the presence or absence of $\mathrm{PM}_{\overline{2}}$ during adult life can be determined:

SK 2529, SK 3046, SK 2316, SK 3213 A and D,
SK 3141, SK 2971, SK 3089, SK 2492, SK 1656(a),
SK 2083, SK 1961, SK 2287.

$\mathrm{PM}_{\overline{2}}$ is absent in all but the last specimen. Among $\mathrm{PM}_{\overline{4}}$'s in this size group there are basically two types:

Type I $\mathrm{PM}_{\overline{4}}$: Paraconid and metaconid are fused from an early developmental stage onwards. Metaconid and entoconid are sometimes apart (SK 3141, SK 3002), even in old age (SK 1623); while in other specimens (SK 3213 A and D) they have begun to fuse, or have completely fused (SK 2492, SK 3043). Fig. 10 H, I and J illustrate this type of $PM_{\overline{4}}$ (see also Plate 10).

Type II $PM_{\overline{4}}$: Paraconid and metaconid remain unfused (SK 2529, SK 3046, SK 2287), even in extreme old age (SK 3146); and sometimes on the same tooth where metaconid-entoconid fusion has taken place (SK 2478, SK 2983), which is again variable in this as in Type I. Type II $PM_{\overline{4}}$ is illustrated in Fig. 10 M and N. (See also Plate 10).

The $PM_{\overline{3}}$ associated with Type II $PM_{\overline{4}}$ has in two out of three available cases (SK 2529, SK 2478) nearly completed entoconid-entostylid fusion and fully fused entoconid and metaconid. The third available premolar series with Type II $PM_{\overline{4}}$ (SK 2287) is somewhat aberrant. It has a strong $PM_{\overline{2}}$ which would agree with the next largest size group, Group III, where it would just fit into the lowest part of the size range. However, because the mandible looks too thin for Group III, and because the variable presence of $PM_{\overline{2}}$ in alcelaphine species is well-known (See pp. 38 – 41) it has been provisionally placed into the Medium sized Type II $PM_{\overline{4}}$ category. It differs from the latter in having separated metaconid and entoconid. All three $PM_{\overline{3}}$'s shown no sign, in spite of their ages, of paraconid-metaconid fusion.

The $PM_{\overline{3}}$ associated with Type I $PM_{\overline{4}}$ is essentially similar, except that in two cases (SK 3213 D and SK 2492) there are signs of approaching paraconid-metaconid fusion. More material might well confirm the suggestion that $PM_{\overline{3}}$ associated with this type of $PM_{\overline{4}}$ is more molarized than $PM_{\overline{3}}$ of Type II. (This would be as expected from the respective degrees of molarization of the two types of $PM_{\overline{4}}$, as discussed on pp. 41, 42).

The nomenclature followed in sorting out these medium sized teeth warrants some explanation. Whereas in Tables 4–6 size groups I, II and IV among lower jaws have analogous counterparts among upper jaws (e.g. Gp. Ia among lower teeth is assumed to belong to the same species as Gp. Ia among upper teeth), the case among Gp. II (Medium) teeth is more complicated. The difference in premolar morphology may signify the presence of more than one species. Type I $PM_{\overline{4}}$ and associated teeth are regarded as Gp. IIa′(i) while Type II $PM_{\overline{4}}$

is regarded as belonging to Gp. IIb (i). Specimens including only molars are then tentatively assigned to the premolar types (Gps. IIa (ii) and IIb (ii)). This was difficult in the case of Gp. IIb where very little molar material was definitely associated with the characteristic premolars. This inability to define with confidence the size and shape of Gp. II b molars naturally hampered the assignation of upper teeth to Gps. IIa and b respectively. Because of the apparently larger molars found with Type II PM$_{\overline{4}}$ (Table 6) it was suspected that on the whole the larger upper Gp. II teeth might be associated with this type. Upper teeth were accordingly sorted mainly by size, and by some other characters mentioned below which appeared to be correlated with difference in size, into Gp. IIc (smaller medium), Gp. IId (larger medium) and Gp. IIe (teeth that could belong to either Gp. IIc or d). It is suggested that at least a good proportion of Gp. IIc might belong to Gp. IIa lowers, and Gp. IId to Gp. IIb lowers. This is tentative as suggested by the use of different letters for upper and lower Gp. II teeth. It is likely that a certain amount of overlap exists at present between Gps. IIc and d as here constituted; i.e. a number of Gp. IIc may be females of the supposedly larger species contained in Gp. IId, and vice versa. However, I do not think that sexual tooth dimorphism (and consequent misplacement of specimens) among bovid teeth in general, and this case in particular, is marked enough to be entirely responsible for the apparent effect of a larger and smaller species among medium sized Swartkrans alcelaphines. (I am drawing here too upon the ranges and means obtained for the teeth of a large number of springbok, *Antidorcas marsupialis marsupialis* Zimmerman by Vrba (1970)). In other words I think that this effect exists genuinely (as backed up by size differences between lower molar means associated with the two premolar types [Table 6]. The sexual dimorphism merely emplifies the existing effect.

The following is a short and of necessity very tentative summary of some of the characteristics of, and differences between, smaller medium (Gp IIa–Gp IIc) and larger medium (Gp. IIb–Gp IId) alcelaphine Swartkrans specimens (Plates 10–13 show some of these):

1. Gp. IIa appears to have *smaller teeth* than Gp. IIb.
2. Relative to a size measure, such as tooth row length, Gp. IIa (e.g. SK 3213 D) seems to have a *deeper mandible* than Gp IIb.
3. Upper Gp II b teeth appear to be *wider with respect to length* than their Gp IIa counterparts (Table 6). The fact that this does not seem to be borne out by lower teeth measurements may be due to the small Gp IIb sample.

   Comparison of fully adult specimens, like the Gp IIa SK 3213 D, SK 3141 and Gp IIb SK 2992 among lower teeth, and Gp IIa SK 2107, SK 3108 and Gp IIb SK 3111, SK 2987, suggests that:
4. Molar lobes, lingual among upper and buccal among lower teeth, tend to be *less rounded in Gp IIa,* i.e. more pointed.
5. Certainly among the lower teeth Gp IIa seems to have the more *complicated central enamel islands* of the two groups. This is more difficult to comment on among upper teeth. SK 3111 certainly bears it out but is from a fairly old adult (Plate 12).
6. There appears to be a greater **tendency to transverse ridges** on molars of Gp IIa, which is again more obvious among lower teeth.
7. The only Gp IIa upper toothrow which indicates the **presence or absence of** $PM_{\overline{2}}$ is SK 2107 (Plate 11). It has a small $PM^{\underline{2}}$. Unfortunately no reasonably complete Gp IIb upper toothrow showing the position of $PM^{\underline{2}}$ exists. There are however two Gp II specimens (SK 2510, SK 2286) bearing two premolars each. These premolars could not be $PM^{\underline{2}}$ and $PM^{\underline{3}}$ of Gp III, because what would then have to be $PM^{\underline{2}}$, especially on SK 2510, is too large both absolutely (in comparison with $PM^{\underline{2}}$ of *C. taurinus*) and relatively (in comparison with what would then have to be $PM^{\underline{3}}$). The two specimens have therefore both been accepted as each being $PM^{\underline{3}}$ and $PM^{\underline{4}}$ of Gp. II. A further specimen (SK 2318) confirms that at least some specimens in Gp II lacked $PM^{\underline{2}}$. Although Gp IIa SK 2107 has a $PM^{\underline{2}}$ it cannot be ruled out that one or more of these specimens belong to Gp IIa. Vrba (1970) found the presence or absence of $PM^{\underline{2}}$ in the springbok, *A.m. marsupialis,* variable. The same could be the case with Gp IIa or Gp IIb or

both. Nevertheless, because the only available complete toothrow having $PM^{\underline{2}}$ definitely belongs to Gp IIa, and because among all extant alcelaphines examined for this work $PM^{\underline{2}}$ was invariably present, it is here preferred to tentatively assign all three specimens lacking $PM^{\underline{2}}$ to the larger Gp IId. An alternative could be assignation to Gp III (pp. 96, 97).

Before attempting to assign or name these medium sized teeth, the **separation of Gp II from adjacent Gp I and Gp III** teeth requires comment. Although there exists a certain amount of size overlap between **Gp Ib and Gp IIa teeth** (Table 6) there are several distinguishing features between the two groups, some of which can be seen by comparing Plates 7–9 with Plates 10–13:

1. Comparison of Gp Ib mandibles with one of the smallest Group IIa specimens, like SK 3141, suggests that the latter has a much **deeper mandible**.
2. The **metastyle of** $M_{\overline{3}}$ invariably tapers to a point in Gp IIa, while in Gp Ib it is generally rounded (Plates 7 and 10).
3. Gp IIa lower molars show a tendency to have a **rib lingually on the most posterior part of anterior molar lobes** (Plate 10), while the corresponding part on Gp Ib is more rounded.
4. Both upper and lower teeth of Gp IIa have a greater tendency to **goatfolds** than do teeth of Gp Ib.
5. Both upper and lower molars of Gp Ib show the tendency towards **central enamel islands** of an exaggerated **dumbell** shape. In Gp IIa teeth the buccal (on lower teeth) part of the dumbell is less pronounced (Plates 7 and 10).
6. Both upper and lower **molars** of Gp IIa have **more pointed lobes** (buccally in lower, lingually in upper teeth) than do Gp Ib teeth. The latter tend to be rounded, and with aging, even flattened (e.g. SK 11827).
7. The maxillary **origin of the masseter** is not so pronounced in Gp IIa specimens, like SK 1523, as in Gp Ib specimens, like SK 5954 and SK 3129.

8. Among Gp IIa there is a tendency for **$PM^{\underline{4}}$ to be large in comparison to the molars** (e.g. SK 2092, SK 1523, SK 2032); the tooth is proportionately smaller among Gp Ib specimens like SK 5954, SK 3129 and SK 2989.
9. SK 2107 (Gp IIa) and SK 3129 (Gp Ib) suggest that $PM^{\underline{2}}$ may have been larger in the latter group, probably correlated with the generally longer premolars in Gp Ib (p. 21).

Differences between Gp III and Gp IIb are more difficult to pinpoint because the latter is so sparsely and uncertainly represented:

1. One striking feature can be noticed when comparing the shape of the mandibular rami of specimens like Gp III SK 6073, SK 3002, SK 3105 with Gp IIb SK 3046 or Gp IIa SK 3213. Gp III mandibles, deep under the molars, become rapidly shallow under the premolars (Plate 15). Broken as it is, SK 3046 nonetheless tentatively suggests that Gp IIb was relatively deeper under the premolars and shallower under the molars. Gp IIa specimens, like SK 3213 D, have deep rami under both premolars and molars (Plate 13). Such differing ramus depth under the premolars is probably correlated with difference in premolar hypsodonty (which seems in fact to be borne out by such premolars as were found in Gps II and III).
2. $PM_{\overline{2}}$ seems to have been at least occasionally present in Gp III mandibles (see p. 33 below) while being consistently absent in Gp II (with the possible exception of one specimen which will be discussed below).
3. The small buccally situated anterior foramen (behind the mental foramen) in Gp III mandibles (e.g. SK 3105) is further forward with respect to $PM_{\overline{3}}$ than not only that of Gp IIa (e.g. SK 3213 D) or Gp IIb (e.g. SK 3046) but also that of extant alcelaphine skulls examined in the course of this work.

It is perhaps best to record at this point that the separation of upper dentitions of Gp IId on the one hand and GP III on the other, as tentatively effected in Table 5 is regarded as highly unsatisfactory: Although comparison of some specimens like SK 3128 (Gp III) with SK 2987 or SK 3111 (Gp IId) seems to indicate a significant size difference, the bulk of tooth sizes in the two groups form a continuous distribution. Neither do there seem to be any associated features other than size which could help in the separation of these upper teeth, although on lower teeth both premolar morphology and size separate the two groups effectively (See also pp. 96, 97).

Because Gp IIa has no PM$_{\overline{2}}$, its teeth show little striking size difference from the teeth of *C. gnou*, and PM$_{\overline{4}}$ has completed paraconid-metaconid fusion (Fig. 10 H, I and J), the question arises whether it could be indistinguishable from *C. gnou*. However, several differences exist:

1. Table 6 suggests that both lower premolars are longer in the fossil than in *C. gnou*. This is especially the case with PM$_{\overline{3}}$. The mean of six Gp IIa PM$_{\overline{3}}$ measurements, no two of which could have belonged to the same animal, was found by a Student's t-test to be significantly larger than that of six *C. gnou* PM$_{\overline{3}}$'s, at the 1% level of significance ($t_{10} = 6.17$).
2. As could be expected from point (1), the mean of six *C. gnou* lower premolar/molar ratios (34%) is lower than that for the only two fossil mandibles which allowed estimation of the ratio (37% obtained from SK 3213 D and SK 3141).
3. Measurement of the whole lower toothrow, PM$_{\overline{3}}$ – M$_{\overline{3}}$, in six *C. gnou* mandibles showed that not one of them was as long as the corresponding measurement estimated on SK 3213 D (94.0 mm) or on SK 3141 (92.5 mm).
4. The small samples of extant and fossil PM$_{\overline{4}}$'s suggest the following difference (See also Fig. 10 H–L): Neither the exaggerated lingual incision between metaconid and entoconid in several fully adult Gp II specimens (SK 3141, SK 3002, SK 1623 and others), nor the occasional fusion of these two cusps in older dentitions (SK 3213 D, SK 2971) can be seen on any of the six *C. gnou* dentitions studied (See Plate 10).
5. On pp. 20, 21 was discussed the relative width and flattening of the "pinched" portion of the molar lobes (buccal in lower, lingual in upper teeth) in *Alcelaphus* and *D. dorcas*. In *C. gnou* this part of the

upper and lower molars is relatively wide and flat (apparently more so than in other extant alcelaphines). In Gp IIa molars there is less "pinching" of the lobes than in extant forms, and hardly any flattening. In fact upper teeth specimens like SK 3108, SK 2107 and SK 1523 have among the most pointed molar lobes I have seen among alcelaphines. With respect to toothshape Gp IIa therefore seems to be further removed from *C. gnou* than from other extant alcelaphines.

6. Although the mandibular depth under the molars in Gp IIa (e.g. SK 3213 D) is just as in *C. gnou*, it is perhaps relatively deeper underneath and in front of the premolars in the fossil.
7. The mental foramen in Gp IIa SK 3213 D is situated further in front of the toothrow than its counterpart in *C. gnou*.
8. The other small buccally situated foramen is in *C. gnou* generally situated below the junction of $\mathrm{PM}_{\overline{3}}$ and $\mathrm{PM}_{\overline{4}}$, at its most anterior under $\mathrm{PM}_{\overline{3}}$. In the fossil its position varies from below $\mathrm{PM}_{\overline{3}}$ (SK 3141) to one in front of $\mathrm{PM}_{\overline{3}}$ (SK 3213 D).
9. The strong outward flare at the level of the mandibular symphysis in *C. gnou* is absent on SK 3213 D. The anterior part of the diastema posterior to the symphysis is wider buccolingually in *C. gnou* than in Gp IIa, as represented by SK 3213D.

Points 7, 8 and 9 may be a corollary of Gp IIa having a more elongated, "stretched" and slender muzzle than *C. gnou*.

10. The ascending mandibular ramus ascends less steeply in SK 3213A than in any of the *C. gnou* mandibles studied, and its broken end in the fossil suggests that the jaw articulation was higher up than in *C. gnou*.

The assignation of Gp II teeth to the medium-sized alcelaphine horn core and skull types from Swartkrans is difficult and must remain tentative. The best preserved pair of Gp. 11a mandibles, SK 3213 A and D, typical of this category in every respect, were found closely associated (in fact pressed against) two horn core fragments, SK 3213 B and C. Both fragments show unmistakable signs of twisting and less certain evidence of ribbing. They are definitely too small to be considered as *Beatragus* sp. horn cores. The twist eliminates

P. angusticornis, as also *D. niro*. At least some, if not most, of the Gp. IIa teeth are therefore likely to belong to *R. porrocornutus*. Additional evidence on this point comes from Olduvai: It has already been stated under "Alcelaphini: Horn Core and Skull Material" that a specimen resembling the Swartkrans *Rabaticeras* was found in the Lemuta Tuff in Bed II. From below this Tuff in Lower Bed II, where I saw no horn cores of *P. angusticornis* or *D. niro*, hail mandibles, like HWK E II 25 from Level 1, which are identical in every respect to Gp. IIa. Similar premolar morphology and depth of mandible, as well as almost identical tooth size, seem to occur in Olduvai mandibles assigned to *Parmularius augusticornis* (Gentry, pers. comm.).

Could all or some of the Gp. IIb teeth belong to ***Beatragus*** sp? Is Gp IIb in fact a valid group? These questions cannot be answered here (see p. 119).

Among SE dentitions there are a few medium-sized alcelaphine teeth that agree well with respect to premolar and general morphology with Gp. IIa teeth. Also several damaged horn core fragments have the right compression, size and suggestion of a twist to be considered as possibly belonging to a *Rabaticeras*. In the STS assemblage some medium-sized alcelaphine teeth agree exceptionally well with Gp. IIa in every respect. A few upper dentitions could belong to Gp IIb (Table 62). The only medium-sized frontlet is too broken to be sure, but looks more like a *Rabaticeras* than anything else. In the later dumps at Sterkfontein medium-sized alcelaphine teeth are isolated and fragmentary. Some of both Gps IIa and b could be there, as well as some that are indistinguishable from extant alcelaphines, but nothing more definite can be said. Similarly the evidence at Kromdraai A is scant, leaning more towards Gp IIa and the modern hartebeest (more likely the former as medium-sized juvenile dentitions, the only ones on which premolar length could be assessed, had short premolar rows).

Finally it might be mentioned that two aberrant (with respect to Types I and II) premolar phenomena were found among medium sized alcelaphines. The first is SK 2287. A specimen from an old animal, it has a strong $PM_{\overline{2}}$. Because of the latter one might be inclined to group it with Group III, rather than Gp II teeth, were not the mandible much too slender for Group III. The well-known variable presence of $\mathrm{PM}_{\overline{2}}$ among certain alcelaphines, notably *Damaliscus*, has been mentioned before. SK 2287 has therefore been grouped together with Gp IIb in this study.

Three fragments (SK 2083, SK 1656(a), SK 1961), coming from at least two individuals (the former two look like the right and left sides of the same individual), have a $\mathrm{PM}_{\overline{4}}$ which is slightly atypical for Gp IIa, i.e. Type I $\mathrm{PM}_{\overline{4}}$. This $\mathrm{PM}_{\overline{4}}$ (shown in Fig. 10H) differs essentially from Type I (Fig. 10 I and J) in having an extra lingual rib posterior to the paraconid-metaconid fusion, and in being a little larger (Table 4). Although a rib of this nature is occasionally found in Gp III $\mathrm{PM}_{\overline{4}}$'s (e.g. the broken $\mathrm{PM}_{\overline{4}}$ of SK 2065 looks as though it could have had one), the three specimens in question are significantly smaller than Gp III specimens. In addition there is no hint of a $\mathrm{PM}_{\overline{2}}$. This latter fact prompts a comparison with *Connochaetes taurinus*. Of six *C. taurinus* studied during this work not one had the deep parallel-sided lingual incision (between metaconid and entoconid) nor the pronounced lingual rib, mentioned above, seen on the three fossils. In addition *C. taurinus* had in all cases a larger and more molarized (i.e. with complete or near complete paraconid-metaconid fusion) $\mathrm{PM}_{\overline{3}}$ than the one seen on SK 1656(a). The three specimens have been retained as slightly aberrant members of Gp IIa.

- **"Smaller Large" dentitions: Gp. III: cf.** *Connochaetes* **sp. aff.** *africanus* (see footnote on p. 16 concerning the applicability in this case of the specific name *africanus*):

Table 6 shows that this group of teeth is close in size to those of *Connochaetes taurinus*, from which they differ as follows (most of these features are visible on Plates 14 and 15):

1. The presence of $\mathrm{PM}_{\overline{2}}$ in the fossil is variable. Of the four cases where its presence or absence could be ascertained it was absent in one and present in the others. Of a dozen *C. taurinus* mandibles not one was found to have a $\mathrm{PM}_{\overline{2}}$ once the adult premolars were growing out.

2. The $\mathrm{PM}_{\overline{3}}$ of Gp. III is in all visible cases a simple four-lobed tooth with no lingual fusion of any cusps. (Fig. 10 O and P). *C. taurinus* invariably

has not only a larger but a much more complex $\text{PM}_{\overline{3}}$, with a strong tendency towards paraconid-metaconid fusion. Four out of six *C. taurinus* $\text{PM}_{\overline{3}}$'s exhibited such fusion (as in Fig. 10R), while the other two cases were approaching it (as in Fig. 10 Q).

3. $\text{PM}_{\overline{4}}$ of Gp III varies in sometimes having completed (e.g. SK 2065), sometimes incomplete (e.g. SK 3010) paraconid-metaconid fusion. All adult *C. taurinus* examined had $\text{PM}_{\overline{4}}$'s with completed fusion of the two cusps.

4. On Gp III $\text{PM}_{\overline{4}}$'s entoconid and entostylid tend to be directed lingually, as is their point of fusion, while in *C. taurinus* $\text{PM}_{\overline{4}}$'s the tendency is towards posterior direction and point of fusion, i.e. against the anterior surface of $\text{M}_{\overline{1}}$ (See also Fig. 10 O–R).

5. *C. taurinus* $\text{PM}_{\overline{4}}$'s tend to have a characteristic two-lobed appearance, with a pinched "waist" resulting from sharp indentations, lingually and buccally, posterior to entoconid and hypoconid respectively. Gp. III $\text{PM}_{\overline{4}}$'s at least sometimes have the sharp lingual identation. The fact that this identation is deeper and more parallelsided, i.e. less V-shaped, than in *C. taurinus,* while the buccal indentation is barely marked, gives the fossil $\text{PM}_{\overline{4}}$ and altogether different, less two-lobed look (Fig. 10 O–R).

6. Enamel islands on both upper and lower teeth tend to be simpler in the fossil than in *C. taurinus.*

7. The shape of the teeth in general is simpler in the fossil. Molar lobes, lingual on upper, buccal on lower teeth, are more smoothly rounded and show less to no tendency towards the antero-posterior "pinching" of *C. taurinus* teeth (which is even more marked on *C. gnou* teeth).

8. The small buccally situated foramen (behind the mental foramen) in Gp III mandibles is consistently situated further forward with respect to $\text{PM}_{\overline{3}}$ (e.g. SK 3105), as well as nearer to the toothrow, than in *C. taurinus* mandibles.

9. Fossil mandibles are much shallower under the premolars, both absolutely and proportionally (to mandibular depth under the molars), than are *C. taurinus* mandibles. This is shown in Fig. 23.

10. In *C. taurinus* mandibles the anterior point of emergence of $PM_{\overline{3}}$ is usually raised quite considerably above the level of the top of the diastema. In Gp III fossils this point of emergence is nearly level with the top of the diastema (e.g. SK 2065, SK 3010).

11. *C. taurinus* premolars, especially upper and lower $PM_{\overline{3}}$'s, seem to be wider with respect to length than their counterparts among Gp III fossils.

There is nothing about Gp III teeth to indicate that more than one species is included (excepting possible mistaken inclusion of Gp IIb molars). This species seems to be distinct from the nearest extant alcelaphine, *C. taurinus*, on teeth alone. However, not one of the eleven features discussed above contradicts the hypothesis that this form is on or near the lineage leading up to *C. taurinus*. In fact most points mentioned actively encourage such a hypothesis, which could go as follows:

From a species represented by Gp III teeth to *C. taurinus* several changes took place. The simple tooth shape became more complicated and specialized (6 and 7). Although $PM_{\overline{2}}$ is gradually lost altogether there is increased emphasis on the role of the anterior toothrow. This leads to widening of $PM_{\overline{3}}$, $PM_{\overline{4}}$ and $M_{\overline{1}}$ (11), and increasing molarization of the premolars. The latter is expressed not only in the enlargement and fusion of premolar cusps (2 and 3) but also in their basic reorientation: For instance, it is possible to visualize that the change in endoconid and entostylid orientation to a backward one (mentioned in point 4 and illustrated in Fig. 10 O and Q), could produce the two-lobed premolar situation of *C. taurinus,* discussed in point 5: Backward rotation from a lingual direction of the said cusps would open the steep-sided lingual indentation of Gp III $PM_{\overline{4}}$'s to a V-shape, while at the same time deepening the buccal one. Also along this hypothetical evolutionary line premolars become more hypsodont, causing the mandible to deepen beneath them (9). This may result perhaps in the development mentioned in point 8, and certainly in that mentioned in point 9.

Of described alcelaphine fossil teeth only those on which the species *Pelorocerus broomi* and *Alcelaphus robustus*, were founded (Cooke, 1949) have any relevance by their size and shape to Gp III teeth. *(Makapania broomi* (Wells and Cooke, 1956) although approximately similar in size seems to have a consistently complicated $\mathrm{PM}_{\overline{3}}$ and strong $\mathrm{PM}_{\overline{2}}$, and on the whole more pointed molar lobes). Before comparing these two species to Gp III, it might be as well to briefly discuss one or two points in connection with their present status:

Do teeth ascribed to these two species not really belong to one and the same species? Thus for example a comparison of *A. robustus* teeth (e.g. Wells and Cooke, 1956: 25) with those of *P. broomi* (Cooke, 1949: 100) shows no substantial difference in size or shape, even without allowing for well-known intraspecific tooth variability among bovids. I should like to suggest that only one species with hartebeest type teeth, intermediate in size between *M. priscus* and extant *A. buselaphus*, be retained. Of the two species descriptions in Cooke (1949) *Pelorocerus broomi* preceded *A. robustus.* Furthermore Wells (1959) argued convincingly for regarding the generic name *Pelorocerus* as a synonym of *Alcelaphus.* The species would therefore be called *Alcelaphus broomi* (Cooke).

Does *A. broomi* exist at Swartkrans? On the one hand some specimens like SK 3104 show the rounded buccal lobes of lower molars mentioned by Cooke (1949: 24) for *A. "robustus"* teeth. On the other hand there seems to be a difference in tooth size: *A. broomi* is known mainly from upper and lower third molars. All $\mathrm{M}^{\underline{3}}$'s of *A. broomi* are larger than the largest Gp III $\mathrm{M}^{\underline{3}}$'s with respect to both length and breadth. All $\mathrm{M}_{\overline{3}}$ lengths fit into the very top of the Gp III range, while two of four $\mathrm{M}_{\overline{3}}$ breadths obtainable from Cooke (1949) exceed the range of Gp III.

In summary the following has here been concluded regarding the assignation of Gp III teeth: On the available evidence it is impossible to exclude any of the following possibilities:

1. Gp III belongs to *A. broomi.*
2. Gp III belongs to a *Connochaetes.*
3. A permutation of the preceding possibilities.

Here alternative 2 is regarded as the most likely one. Earlier on in the Swartkrans alcelaphine section, the skull fragment SK 3812A was assigned to *Connochaetes* and its similarity to East Rudolf and Olduvai Bed I *Connochaetes* material was discussed. Associated with the East Rudolf material were found mandibles identical in all respects to Gp III dentitions. Similarly some dentitions from Olduvai Bed I, like FLK I B17, FLK I 067/1093 and premolar row FLK N I T.T./1–2 208, are very close to Gp III teeth. This is especially significant as Gp III lower premolar shape is in some respects unique among the alcelaphines of the australopithecine deposits. The Gp. III teeth probably belong to the same species as does SK 3812A and have been similarly assigned (see footnote on p. 16 concerning the applicability in this case of the specific name *africanus*).

Similar teeth, with identical $PM_{\overline{4}}$ morphology, are found at KA. Here, however, there are indications of a more complex $PM_{\overline{3}}$ and a slight size increase in teeth and depth of mandibular ramus. These are differences from the Swartkrans *Connochaetes* teeth which place the KA material closer to *C. taurinus*. Some of the KA lower molars have goatfolds. There is undoubted juvenile dental and horn core, as well as adult dental, *Connochaetes* material at KB. From STS there are Gp III-sized teeth with a similar morphology, but as no lower premolars are present no more definite comparisons can be made. From SE we have only one lower molar tooth fragment large enough for Gp. III with a slight goatfold, as present on some KA *Connochaetes* teeth. In several of the Sterkfontein Dumps, like D13, D8, H2, are large alcelaphine teeth which are slightly smaller than Swartkrans Gp III, with very round molar lobes. They are unfortunately too fragmentary and isolated to tell whether they belong to *Connochaetes* at all.

- **"Larger large" teeth: cf. *Megalotragus* sp. (Gp IV)**: There are a few teeth at Swartkrans (Plate 16) which are too large for both the extant *C. taurinus*, and the next largest Swartkrans alcelaphine, i.e. cf. *C.* sp. aff. *africanus* (Table 6 and Figs 1–9). *"Pelorocerus" broomi* (see discussion in previous section), although of similar size with respect to $M^{\underline{2}}$ and $M^{\underline{1}}$, is quite a bit smaller with respect to $M^{\underline{3}}$ (Cooke, 1949; Cooke and Wells, 1946) and $M_{\overline{3}}$ (Wells unpublished assessment of some Sterkfontein Bovidae). In fact, of all described extant or fossil alcelaphine species only two fossils are large enough for the "larger large" teeth: *Connochaetes grandis* from Chelmer (Cooke and Wells, 1951) and *Megalotragus priscus*. (In this latter case I am adhering to Gentry, pers. comm., who united the largest South African fossil alcelaphines i.e. *Alcelaphus helmei, Megalotragus eucornutus* and *Lunatoceras mirum,* into a single species, *M. priscus*). If Gp IV belongs to a *Megalotragus* species it was probably a smaller one that either the Olduvai *M. kattwinkeli* (the only teeth labelled *Megalotragus* which I saw among the Olduvai material were considerably larger) or the *M. priscus* from many South African sites. Gp IV teeth are definitely smaller than those of the Elandsfontein *M. priscus.* They also consistently fitted into the lower extremes of size ranges given by Hoffman (1953) for *M. priscus* from Florisbad, Prinsloo's Site, Vlakkraal, Mahemspan, Prieska and a number of other sites. However some dentitions from Cornelia seemed to be of the same size as Gp IV.

The few *C. grandis* teeth from Chelmer certainly seem to be of Gp IV size. One or two Swartkrans dentitions (e.g. SK 3031 in Plate 16, SK 6004) look morphological indistinguishable from the sketches in Fig. 2 (Cooke and Wells, 1951: 20). Nonetheless, until the presence of a *Connochaetes* larger than the *taurinus*-lineage in pleistocene Southern Africa is established more firmly, it is perhaps preferable to think of the few Gp IV teeth from the australopithecine sites (there is also one dentition from STS and two from KA) tentatively as cf. *Megalotragus* sp.

C. Comments

Premolar morphology: Premolar evolution among Bovidae has to my knowledge never been studied in detail. This brief discussion pretends to do no more than speculate, and pose a few questions, on some effects observed on some Swartkrans and modern South African alcelaphine dentitions.

There seems to be a tendency among biologists, especially those concerned with the study of fossils, to want to pinpoint which state of a character is "advanced" over another. The variations among alcelaphine and and other bovid premolars are very tempting in this respect. The "disappearance" of $\mathrm{PM}_{\overline{2}}$ is a case in point. It is well known that many members of the Bovidae lack the tooth, while their ancestors (generally accepted as being the Gelocidae [Thenius: 1969: 468]), as well as the earliest bovids such as *Eotragus* Pilgrim, had it. Is this specialization, i.e. the lack of $\mathrm{PM}_{\overline{2}}$, always to be regarded as an "advance" over its presence, when comparing supposedly related forms?

Among alcelaphines several extinct *Damaliscus* and *Parmularius* (which is possibly linked with the *Damaliscus* ancestry [Gentry, pers. comm.]) appear to lack $\mathrm{PM}_{\overline{2}}$. On the other hand most individuals in modern *Damaliscus* species have the tooth. Similarly the Swartkrans *Rabaticeras porrocornutus*, with its possible link with *Alcelaphus* ancestry (Vrba, 1971); and *Rabaticeras arambourgi* from Hopefield and Olduvai Bed III which Gentry (pers. comm.) feels might well be a possible ancestor for *Alcelaphus buselaphus,* probably both lacked $\mathrm{PM}_{\overline{2}}$ judging by the available dentitions. Extant *Alcelaphus* are generally recorded as having the tooth. This trend was already pointed out to me by Gentry with respect to alcelaphine fossils in general.

At first glance this apparent "advance" of the supposedly ancestral dentition over the descendant one seems paradoxical. Actually a difficulty would only exist if the entire populations within the relevant fossil species had lost $\mathrm{PM}_{\overline{2}}$, i.e. if the genetic mechanism responsible for its presence had been lost. In such a case, if the modern forms were indeed descendants, mutation would have been needed to re-establish the presence of $\mathrm{PM}_{\overline{2}}$.

Let us assume for the moment that the gene or genes responsible for the presence of the tooth was/were always present in populations of the said fossil species, albeit at times in low frequencies. It is well known that gene frequencies change in response to factors such as admixture from outside the population, changes in mutation frequency, and/or changes in selection forces (Burns, 1969): If the latter factor plays a role, it need of course not be the presence or absence of $PM_{\overline{2}}$ which has a selective advantage. Perhaps it is the selective advantage of another effect (e.g. some other feature of the toothrow) which is governed by the same gene or genes (i.e. a case of pleiotropism), which leads to the spread of such a gene or genes, making the presence or absence of $PM_{\overline{2}}$ merely a correlated feature. Another dimension of a consideration of the role of selection forces in the case of the alcelaphine $PM_{\overline{2}}$, is provided by the discussion on premolar and molar changes in drought-adapted bovids in Vrba (1970: 289–290).

How valid is the above assumption? There is evidence among extant alcelaphines that at least in some species $PM_{\overline{2}}$ is never entirely absent or present. Ansell (1968) quotes Halthenorth (1963) as noting that in *Damaliscus dorcas* and *D. lunatus* $PM_{\overline{2}}$, although generally present, is small and frequently absent on one or both sides. I have found for instance, that one in six *Connochaetes gnou* had $PM_{\overline{2}}$ (all others lacking it). Among Swartkrans alcelaphine fossils, three out of four species in which the presence of $PM_{\overline{2}}$ could be ascertained in at least two specimens, showed signs that the presence/absence of the tooth was variable.

Although individuals in an entire species sample from a particular site may all lack, or all have, $PM_{\overline{2}}$, this obviously does not rule out the parent population having a certain proportion of the other, unobserved state of the character.

It would merely be an expected sampling hazard, particularly likely to occur if the gene frequency for one state of the character is very low.

In summary, the apparent "disappearance" and "re-appearance" of this tooth in related and successive bovid populations can be seen as follows: Genes for both presence and absence of $PM_{\overline{2}}$ were and are probably continuously present in the populations in question, their relative frequencies altered in response to a factor or factors like environmental selection. Theoretically at least this process of alternate emphasis on presence and absence of the tooth could go on indefinitely. If this theory were true (and it is likely to be true of many morphological features dealt with by the palaeontologist), then obviously neither presence nor absence of $PM_{\overline{2}}$ can be spoken of as "advanced". Perhaps a tentative generalization may be permitted from this small example: characters which could perhaps well be said to represent an "advance" when viewed from a chronologically broad perspective, (e.g. the loss of $PM_{\overline{2}}$ during bovid evolution as a whole), should not be termed readily as such in a smaller framework (like that represented by comparison of quarternary forms).

Some related questions on premolars as a whole are:

1. Could changes in gene frequencies be playing a similar role to that discussed above in the molarization of $PM_{\overline{3}}$ and $PM_{\overline{4}}$ (i.e. changing the teeth so as to make them more like molars)? I.e. are more molarized premolars invariably or usually to be regarded as more advanced, less molarized premolars as more primitive?

2. Does molarization of $PM_{\overline{4}}$ entail a corresponding degree of molarization of $PM_{\overline{3}}$? In other words is it unlikely that one find a case where $PM_{\overline{4}}$ is in an advanced state of molarization while $PM_{\overline{3}}$ is quite the reverse, or vice versa?

3. Is an advanced state of molarization of $PM_{\overline{4}}$ and $PM_{\overline{3}}$ generally correlated positively with loss of $PM_{\overline{2}}$, while less molarized premolars occur with a $PM_{\overline{2}}$? Could the reverse, i.e. a negative correlation exist?

From the comparison possible between Swartkrans and recent South African alcelaphines none of these questions can be fully answered at the present moment. However, an attempt has been made in Table 9. Gentry (1966) has used a similar approach. He writes on p. 55: "Characteristics of P_4 have often been used in the classification of gazelles and their relatives, and some authors refer to primitive and advanced patterns of design. What seems to happen is that the inner wall of P_4 in the older fossil gazelles ... is indented by an anterior and two posterior valleys." He adds that in antilopine evolution there seems to be a progressive closing up of these valleys, first posteriorly, then anteriorly; but cautions: "But, as is usual with so many Bovid characters, there is much intraspecific variability and conclusions must be drawn with care." The closing or otherwise of "posterior valleys" was not gone into in Table 9 because it is difficult to decide on the homologies (especially in $PM_{\overline{3}}$) of the posterior cusps as referred to by Gentry, in this work and as named by Arambourg (1947: 232). Table 9 therefore approaches molarization of premolars only from the aspect of paraconid-metaconid fusion.

Regarding the first question, then, Table 9 furnishes no reason to believe that the position among alcelaphines should be any different to that discussed by Gentry for antilopines. Certainly, while the alcelaphine successions postulated on p. 39 contradict the proposition that the lack of $PM_{\overline{2}}$ is always an advanced character, they do no such thing in the case of molarization of premolars.

With respect to the second question Table 9 suggests that the answer is yes: The most "advanced" $PM_{\overline{3}}$'s occur with the most "advanced" $PM_{\overline{4}}$'s.

The answer to question three, at least with respect to this sample of fossil and extant alcelaphines, must be an emphatic no: For instance the category of most advanced molarization of $PM_{\overline{3}}$ and $PM_{\overline{4}}$ includes *A. buselaphus*, which in all cases had $PM_{\overline{2}}$, and *C. taurinus*, which in all cases lacked it. Similarly species with least advanced molarization of $PM_{\overline{3}}$ and $PM_{\overline{4}}$ include *D. lunatus lunatus* which in all cases had a $PM_{\overline{2}}$, and two fossil species which apparently lacked $PM_{\overline{2}}$ most of the time.

Subfamily: HIPPOTRAGINAE (Cont.)

Tribe: HIPPOTRAGINI

- *Hippotragus* cf. *niger*: A number of dentitions, listed in Table 10, are indistinguishable from Transvaal Museum material of this species. Klein (in press) has measured tooth lengths on a large number of *H. niger* and *H. equinuus* specimens, which he separated into four defined tooth wear categories: NW = no wear, EW = early wear, MW = medium wear, LW = late wear. Wherever similar wear categories allowed comparison, the Swartkrans measurements in every case agreed extremely well with those of *H. niger,* while they were generally smaller than those of *H. equinus.* A series of t-tests, done by Klein (pers. comm.) on the data, confirmed this: For instance, in the case of MW $M_{\overline{2}}$'s, *H. equinus* teeth were significantly larger than the Swartkrans teeth ($t_{33} = 2.88$ which has a significance level of $p = .007$), while in none of similar t-tests involving *H. niger* could a significant tooth length difference be demonstrated. The only other locations among the Krugersdorp sites where *H.* cf. *niger* has been identified, again solely on dentitions, are Dumps 6 and 16 at Sterkfontein.

- cf. *Hippotragus* sp. aff. *gigas*: Two upper dentitions, SK 3139 and SK 3107 (Table 11 and Plate 39), which should probably be stuck together, have been given this name. Dentitions thought to belong to the same species have also been found at KA, and at Sterkfontein among the STS material, in Dumps 13, 14 and 15 and more doubtfully in the SE assemblage. Dentitions from the Makapansgat Limeworks at present assigned to *Taurotragus* cf. *oryx* (Pallas) (Wells & Cooke, 1956), or at least some of these, are also thought to belong to the same species (p. 98). If such a statement can be made on two specimens, it seems as if the Swartkrans and KA versions of this hippotragine species may be larger than those at Sterkfontein (see Plate 39) and Makapansgat. SK 3139 and SK 3107 are also larger with respect to tooth length than are dentitions of the Elandsfontein *H. gigas,* again measured by Klein (in preparation).

The difficulties encountered in placing this species taxonomically (especially with respect to the possibility that these dentitions could belong on a *Taurotragus* lineage), and the reasons for deciding that it is probably a new hippotragine species, are given in the Sterkfontein section on pp. 98–101.

Tribe: REDUNCINI

- cf. *Kobus ellipsiprymnus* (Ogilby): The recording of this species at Swartkrans must be regarded as extremely tentative. One of the two specimens given this name, SK 11297, if indeed an $M^{\underline{2}}$, is somewhat smaller than any *H. niger* $M^{\underline{2}}$ measured by Klein (in press). However, it is not inconceivable that it could fall within the lower range of a larger sample of that species, which is quite well represented at Swartkrans. The other specimen, SK 2960, has teeth so worn as to render their occlusal surface morphology quite distorted. The most that can be said about it is that it looks closer in size and morphology to the waterbuck than to any other extant species (Table 12).

- *Redunca* cf. *arundinum* (Boddaert): A juvenile dentition, listed in Table 13, is indistinguisable from this extant species. Whether this Swartkrans *Redunca* H. Smith was perhaps closer to, or conspecific with, the Makapansgat Limeworks *Redunca darti* Wells & Cooke (1956) cannot be determined on this single juvenile specimen. The same is true of a similar juvenile dention from STS and an adult one from KA. No other *Redunca* material has been found in any Krugersdorp assemblage here investigated.

Tribe: PELEINI

- *Pelea capreolus* (Forster):

A. Skull material

SK 2735 a–e: The stratified brown breccia* of the Inner Cave at Swartkrans (Brain, 1958, 1970) has yielded a large part of a single skull which ap-

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* now termed secondary breccia; pp. 1, 118.

pears to belong to the Vaal Rhebuck, *Pelea capreolus*. It is separated into five very weathered and distorted pieces: SK 2735a, seen in Plate 17, comprises the top of the skull, with most of the frontals, parietal and some of the supraoccipital preserved, as well as parts of the orbital, auditory and basioccipital regions. SK 2735b consists of most of the left infra-orbital rim, the left and right molars and right $\mathrm{DPM}^{\underline{4}}$ (Plate 18). The palate of SK 2735b is almost entirely eroded away. SK 2735c is a part of the right infra-orbital rim (i.e. a part of the jugal). SK 2735d consists mainly of a part of the tympanic bulla, showing the external auditory meatus. SK 2735e comprises several fragments from the base of the skull.

Although in most respects, like the characteristic angle of protrusion of the orbit, and the straight coronal suture (Plate 17), the fossil is indistinguishable from *P. capreolus,* there are suggestions of differences:

1. As is shown in Figs 12–15, the upper dentition of SK 2735b is exceptionally large both with respect to modern and other Swartkrans and KA fossil *Pelea* Gray material. Other skull features that are preserved do not appear larger than those of the extant *P. capreolus.*

2. Although there has obviously been some flattening of the skull, it is difficult to see how it can account entirely for the fact that the slope of the cranium backward from the coronal suture makes a lesser angle with the posterior facial slope, i.e. with the straight line running from the depression above the nasion to the bregma, in the extant skulls than it does in the fossil. It also looks as if the fossil has less downward bending of the facial plane on the basicranial axis than has its extant counterpart (Fig. 17), which might be correlated with the previous point. If these two points were to signify a valid difference in cranial proportions from the extant *P. capreolus,* it would be one that is in line with what the study of other bovid lineages have taught us to expect. The progressive downward bending of the facial plane with respect to the basicranial axis and the dorsal braincase has apparently occurred in the evolution of such widely differing tribes as the alcelaphines (see also Pilgrim, 1939: 63) and the antilopines (as in gazelle-*Antidorcas* evolution). However, it must be emphasized that, because of the poor state of preservation of

SK 2735, Fig. 17 and the idea that it exemplifies are here included merely as an interesting possibility.

B. Dentitions:

Several dentitions, listed in Tables 14 and 15, some of which are shown in Plates 19 and 20, have the typical morphology of *P. capreolus*. On p. 49 is a summary of the criteria that were used in separating the Swartkrans *Pelea* dentitions from the closely similar ones of the Swartkrans gazelle.

The observed sizes of Swartkrans and KA *Pelea* dental remains raise some questions: Table 16 shows that, with respect to both lower tooth length and mandibular ramus depth, in each tooth wear group, it is almost always a fossil that is largest. This size difference is especially marked in the mandibular ramus measurements and shown in Plate 19 and graphically in Fig. 16. In both Table 16 and Fig. 16 there seem to be Swartkrans mandibular specimens which agree well in size with the extant *P. capreolus* sample and others that are clearly larger. In Figs. 12–15 of upper teeth this apparent dichotomy in sizes at Swartkrans is again suggested, with SK 2735b the only large specimen; all other Swartkrans and Kromdraai A dentitions being close to the extant material. Unfortunately there are too few specimens, and these nearly all dental, to resolve what is really happening with respect to Swartkrans and Kromdraai A *Pelea*:

1. One alternative is that large samples of measurements from, for example, Swartkrans, might show convincingly two-peaked distributions. This would mean that two distinct size groups existed, either

A. of the same species, in which case the large and small populations must have existed at separate times. (If populations of different sizes and of one species were brought together they would soon produce the intermediate sizes by interbreeding, i.e. size distribution curves would not be expected to be two-peaked). The only Swartkrans *Pelea* specimen which we can definitely place in the Swartkrans stratigraphy is the skull SK 2735b. This hails from the stratified brown breccia which is younger than the main australopithecine deposit in the outer cave. If alternative IA were correct it would therefore be the later Swartkrans breccia which contains the larger *Pelea*, while the "modern-sized" one probably comes from earlier Swartkrans breccia (see p. 121).

B. The two size groups belong to different *Pelea* species, which could have existed side by side or at different times. There is little evidence for this. The smaller material is indistinguishable from extant *P. capreolus*; of the larger material we have a skull which is very close to *P. capreolus* too.

2. Another alternative is that large samples of measurements from, for example, Swartkrans would be distributed in a single peak, i.e. closing the apparent size gaps in Table 16 and Figs. 12–16. All the Swartkrans and Kromdraai A material might belong to a single species, which is probably *P. capreolus*. The fossil form may have been on the average larger than extant *P. capreolus*, at least with respect to its teeth and horizontal mandibular ramus, and perhaps subspecifically distinct from it. KA *Pelea* also exhibits the discussed size dichotomy: There are small indistinguishable-from-modern upper teeth and undoubtedly larger mandibles, in one case apparently occurring in the same individual (KA 1766A uppers and KA 1766C lowers). This fact points strongly to alternative 2 as most likely to be true.

If, as seems likely, some of the Swartkrans *Pelea* remains come from the outer cave pink breccia (see p. 121), these probably constitute the earliest recorded occurrence of the genus at a South African or any other, fossil site. *Pelea* remains have not been found anywhere else at the Krugersdorp sites, except at Dump 16, Sterkfontein. *P. capreolus* has been recorded from the Cave of Hearths in the Makapansgat Valley (Cooke, 1962) and other more recent sites (Klein, pers. comm. and Hendey, 1947). The two Elandsfontein horn cores which alone appear to be responsible for recording the species at this site (Hendey, in press) have extensive basal cornual diverticula, and a rather longer pedicel than extant *P. capreolus* horn cores. Unless there has been rapid evolutionary change from Elandsfontein to recent times, especially with respect to the complete disappearance of the cornual diverticulum, these horn cores should probably best thought of as belonging to something else.

Subfamily: ANTILOPINAE

Tribe: ANTILOPINI

- *Antidorcas bondi* (Cooke & Wells)
- *Antidorcas australis* Hendey & Hendey

As an aid to interpreting *Antidorcas* Sundevall fossils from the Krugersdorp sites, in particular Swartkrans where the genus was most abundant, a study was made of tooth sizes of 371 skulls of the springbok, *Antidorcas marsupialis* (Zimmermann). This was published in Vrba (1970). Although the resulting information as to the degree of tooth size variation, sexual dimorphism, etc. to be expected in a bovid species has been drawn on throughout this work, the publication should be thought of as being included in the thesis at this point.

The fossil remains of two Swartkrans *Antidorcas* species have been fully described, tabulated and compared with extant and other fossil *Antidorcas* in Vrba (1973). This publication too should be incorporated into the thesis at this point.*

- cf. *Gazella vanhoepeni* (Wells & Cooke): A number of dentitions (Tables 18–20 and Plates 19 and 20) are indistinguishable from the large gazelle at the Makapansgat Limeworks, which was first described as *Phenacotragus vanhoepeni* (Wells & Cooke, 1956:43, figs. 22, 23 and 24). Subsequently these remains were referred to *Gazella* by Wells (1969). Gentry (pers. comm.) suggested that this species could be the descendant of the Langebaanweg gazelle, and have given rise to *Gazella granti* Brooke.

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* On pp. 121 – 122 it is explained why the division of Swartkrans bovid remains into SKa and SKb assemblages (the necessity of this division was not recognized until this work was almost completed) has resulted in the recognition of two additional *Antidorcas* species at Swartkrans, *A.* cf. *recki* and *A.* cf. *marsupialis*.

At Swartkrans the recognition of dentitions as cf. *G. vanhoepeni* was made difficult by the simultaneous presence of a large peleine. Both of these species have shallow mandibular rami, long premolar rows, pointed buccal lower molar lobes etc., while only in one case (the *Pelea* specimen SK 2735) a piece of the skull other than the dentition was available. As other workers may come across similar difficulties it may be useful to include here a small summary of criteria which were found to separate the Swartkrans gazelle and *Pelea* dentitions. (Some of these differences are shown in Plates 19, 20).

Dentitions of SK *Pelea* cf. *capreolus*	Dentitions of SK cf. *Gazella vanhoepeni*
Strongly pronounced, almost parallel-sided mesostyles on upper molars	Less strongly pronounced, more V-shaped mesostyles on upper molars
A greater tendency to mesostyles on lower molars	A lesser tendency to mesostyles on on lower molars
Metastyle on $M_{\overline{3}}$ often smaller and more flattened	Metastyle on $M_{\overline{3}}$ often larger and more rounded
A tendency to wide open, i.e. "gaping", irregularly shaped central cavities on molars	Central cavities of molars less "gaping" and irregular
The mandibular ramus ascends more gradually behind $M_{\overline{3}}$ (Plate 19:G)	The mandibular ramus ascends more steeply behind $M_{\overline{3}}$ (Plate 19:F)
Dentitions generally smaller	Dentitions generally larger

An interesting specimen, which was tentatively placed with the cf. *G. vanhoepeni* dentitions, is the snout SK 3155a (Plate 19). It was found closely associated with the hominid innominate SK 3155b. In Brain, Vrba and Robinson (in press) is outlined why SK 3155a is thought to belong to cf. *G. vanhoepeni* rather than to the Swartkrans antidorcines.

Although the KA remains include some large *Pelea* dentitions, there are none of *G. vanhoepeni* according to the above-mentioned criteria. STS has yielded at least one specimen which is very likely to belong to *G. vanhoepeni*, or at least to a gazelle. Some dentition fragments from Dump 13 at Sterkfontein have been assigned tentatively to this species.

Tribe: NEOTRAGINI

- *Oreotragus* cf. *major* Wells: Broom in 1934 described a new neotragine species from Taung, which he named *Palaeotragiscus longiceps*. Subsequently Cooke (unpubl.) described further remains of this species from site 5 at Taung, which he called *Oreotragus longiceps* (Broom). He wrote that the Taung *O. longiceps* is probably synonymous with *O. major* from Makapansgat Limeworks (Wells, 1951; Wells & Cooke, 1956), in which case *longiceps* has priority over *major*. However, since the type specimen of *P. longiceps* appears to be missing, and was in any case unsatisfactory, this name should perhaps be considered indeterminable and a *nomen vanum*. If this is accepted the best name for the large South African fossil *Oreotragus* A. Smith remains *O. major*.

A. **Horn cores:** SK 14243, shown in Plate 21, is a right horn core with the following dimensions:

antero-posterior basal horn core diameter = 17.0 mm
mesio-lateral " " " " = 15.7 mm
horn core length = ± 41 mm with an additional ± 5 mm
in the unbroken state.

These dimensions agree remarkably well with those given in Wells (1951:168) for the basal horn core (17 mm x 15 mm respectively) of the type skull, M 651, of *O. major* from Makapansgat Limeworks. In Wells & Cooke (1956: 35) the left and right horn core lengths of a further *O. major* frontlet, M 476, from the same fossil locality are given as approximately 43 and 46 mm respectively. I have been able to compare SK 14243 with the latter specimen, and the agreement in every respect is remarkably close.

B. **Dentitions:** Only one dentition, SK 14059 (Plate 21 and Table 21), although only consisting of $\mathrm{PM}_{\overline{3}}$ – $\mathrm{M}_{\overline{1}}$ with the root of $\mathrm{PM}_{\overline{2}}$, was definitely large enough to agree with tooth measurements recorded to date on *O. major* specimens. This is shown in Fig. 18.

At other Krugersdorp sites there are two instances of *O. major*. From SE we have almost complete upper and lower dentitions (p. 112, Plate 21 and Figs. 18–21). A single fragment with large oreotragine $\mathrm{PM}_{\overline{3}}$ and $\mathrm{PM}_{\overline{4}}$ from Dump 13 at Sterkfontein probably belongs to this species (See Fig. 18).

• *Oreotragus* cf. *oreotragus* (Zimmermann): A few dentitions (Table 22) are indistinguishable from the extant species. Fig. 18 shows how SK 4052 is close to the mean for extant *O. oreotragus* with respect to $\mathrm{PM}_{\overline{3}+\overline{4}}$ length, while SK 14059 is grouped with *O. major*.

• *Gen. et. sp. indet.*: Three dentitions (Table 24 and Plates 21 and 22) have an odd combination of features that I have been unable to place. They are included at this point because a superficial inspection might confuse them rather with *O. major* than with anything else. Their characteristics include the following:

1. Their molars are larger than those of any *O. major* specimens found to date (Figs. 19, 20 and Plate 21). The premolar series is shown on only one specimen, SK 3019, and on this seems short even for *O. oreotragus* as shown in Fig. 20. Of course, SK 3019 is of approximately tooth wear stage D (as defined in Vrba, 1973:316) and less worn dentitions of this form might have slightly longer premolars. As it is SK 3019 has a lower premolar/molar ratio of about 59% which separates it from all *Oreotragus* specimens in Fig. 20.

2. Central enamel islands get worn away very early in the life of most neotragines, other than *Ourebia ourebi* (Zimmermann), that I have seen (e.g. in a subadult *O. oreotragus*, even before the deciduous premolars are shed, the central enamel islands on $\mathrm{M}_{\overline{2}}$ are almost gone). Yet on each of the specimens, SK 2665, SK 3025 and SK 3019, central enamel islands are still present as

shown in Plate 21. On the latter specimen they are present on $M_{\overline{3}}$ while the premolars are already quite worn. So we have in these dentitions a tooth wear pattern that is quite different from that observable in most neotragines. Apparently this Swartkrans form has stronger central enamel columns in its teeth, which extend further along the crown-root axis of the tooth.

3. The central enamel islands on the specimens in question are quite straight (Plate 21).

4. The lingual walls of the lower molars are less straight and more undulating than one might expect on *Raphicerus* H. Smith, *Oreotragus,* or for that matter neotragines other than *Ourebia* Laurillard (Plate 21).

5. All three $M_{\overline{3}}$'s have a large metastyle (Plate 21).

6. The $PM_{\overline{2}}$ on SK 3019 is about half the size of $PM_{\overline{3}}$.

7. On SK 2665, where part of the mandibular bone around the tooth roots has broken, $M_{\overline{2}}$ and $M_{\overline{3}}$ appear rather more hypsodont than one would expect of most neotragines. This point is tentative.

Points 2 and 4 seem to point away from *Raphicerus, Oreotragus* and the smaller neotragine genera and rather towards *Ourebia* and the cephalophines. On the other hand points 3 (duikers I have seen invariably have curved central cavities), 5 (duikers seem to have smaller metastyles on $M_{\overline{3}}$) and 6 (duikers generally have a large $PM_{\overline{2}}$ in relation to $PM_{\overline{3}}$) do not support membership of the genera *Cephalophus* H. Smith and *Sylvicapra* Ogilby.

If the lower premolar/molar ratio of 59%, obtained on SK 3019, were close to the true mean for this species and not considerably lower due to advanced wear, it would place this species apart from all neotragines and cephalophines. This is shown below where a few relevant ratio means, obtained on Transvaal Museum specimens (except in the case of *O. major*) are given:

SPECIES	Lower PM/M Ratio Mean	Number of adults measured
Sylvicapra grimmia (Linnaeus)	66%	4
Cephalophus natalensis A. Smith	65%	3
Cephalophus monticola (Thunberg)	69%	2
Raphicerus campestris (Thunberg)	64%	5
Ourebia ourebi	49%	4
Neotragus moschatus (von Dueben)	62%	3
Madoqua kirki (Günther)	70%	3
Oreotragus oreotragus (from Table 23)	72%	9
Oreotragus major (Readings in Fig 20)	72%	3
SK 3109	59%	1

The question now arises whether these dentitions could belong to an antilopine, more specifically to a small gazelle.Such an hypothesis would be supported to a greater or lesser extent by all of points 2–7. The specimens are comparable in size to smaller extant gazelles like *Gazella dorcas* (Linnaeus). Among extant gazelles the lower PM/M ratio generally seems to be closer to 50% than to 60%. The only available value for a *Litocranius walleri* (Brooke), 56%, was the highest I have come across among any extant antilopines. Among South African fossil gazelles the position is different. While the Makapansgat and other Swartkrans gazelle dentitions have considerably lower ratio values, the gazelles from Langebaanweg and Hopefield are comparable in this respect to SK 3019. However, all the fossil gazelle dentitions in question are significantly larger than SK 3019, SK 2665 and SK 3025. These few Swartkrans specimens probably belong to a new species, either to an aberrant neotragine one or to a small gazelline species with long premolar rows. No similar teeth have come to light from other Krugersdorp sites.

- *Raphicerus campestris*:

A. **Skull material:** The female skull SK 1515, pictured in Plates 23–25, is almost complete, lacking only the snout region. It belongs to a subadult individual with $M^{\underline{3}}$ in the process of eruption. Measurements of the dentition of SK 1515 are given in Table 25. The specimen appears to be quite indistinguishable in every respect from skulls of extant *R. campestris* of similar age.

B. **Dentitions:** A few dentitions (Table 25) also conform closely in every respect to those of extant *R. campestris* (See Plate 21). Only on one specimen, SK 2108, with fairly worn teeth can the lower premolar/molar ratio be estimated at 62%, which is close to the mean obtained for extant *R. campestris* on p. 53.

Remains of this species were also found in Dumps 5 and 16 at Sterkfontein. A single mandible from KA was assigned to cf. *Raphicerus* sp., being larger than mandibles of *R. campestris*.

- *Ourebia* cf. *ourebi*: Some dentitions which are indistinguishable from *O. ourebi* are listed in Table 26. On one specimen, SK 1416, (Plate 21), the lower premolar/molar ratio could be estimated at 48% which is close to the mean obtained on extant material and given on p. 53 .

Remains of this species were also found in Dumps 8 and 16 at Sterkfontein.

- cf. *Raphicerus* sp.: Two horn cores, SK 14170 (shown in Plate 21) and SK 7880 respectively have the following dimensions:

maximum basal horn core diameters = 16.7 and 16.9 mm
minimum " " " " = 14.4 " 13.6 mm
estimated length in unbroken state = 75–85 mm in both cases.

Both horn cores lacked a cornual diverticulum. In each case it is not quite clear whether the specimen is a left or right horn core and whether its greatest horn core diameter was situated antero-posteriorly or transversely with respect to the skull. All that can be said is that in both cases the dimensions are a little smaller than, but comparable to, those taken on specimens from Makapansgat Limeworks which were assigned to *Cephalophus pricei* by Wells & Cooke (1956: 13–15). Gentry (pers. comm.) is of the opinion that horn core M 478, designated as one of the paratypes for *C. pricei,* belongs to a fossil *Raphicerus* species. This may well be the case with SK 14170 and SK 7880 too. Both have on one side of the maximum diameter a ridge which might well correspond to the prominent ridge observable on M 478. Nothing about these Swartkrans horn cores suggests that they should be placed into another neotragine genus, rather than *Raphicerus.*

Unfortunately I was unable to compare these specimens with horn cores of the large Elandsfontein *Raphicerus.* From KA hails a single mandible which has been assigned to cf. *Raphicerus* sp., and which is somewhat larger than dentitions of *R. campestris.*

Subfamily: BOVINAE

Tribe: BOVINI

• *Syncerus* cf. *acoelotus* Gentry (pers. comm.): The measurements of the Swartkrans bovine remains, which are all dentitions, are given in Table 27. Some of the specimens are shown in Plate 26.

The first thing one notices about these dentitions is that, while they are obviously comparable with extant *Syncerus caffer* Sparrman specimens, they are significantly larger, especially with respect to tooth length. Unfortunately the upper dentitions of extant *S. caffer,* that are available at the Transvaal Museum for comparison, are nearly all less worn than upper teeth at Swartkrans. In a single bovid species one would generally expect the less worn teeth to have greater length (and lesser breadth) than the analogous, more heavily worn counterparts of older individuals. Therefore the length mean differences here quoted would probably be even greater had comparably worn extant and fossil dentitions been used: Some Swartkrans tooth length means compiled from Table 27 (numbers of teeth measured are given in brackets) are $\mathrm{PM}^{\underline{4}} = 21.4(2)$, $\mathrm{M}^{\underline{2}} = 33.5e(1)$ and $\mathrm{M}^{\underline{3}} = 34e(1)$. Among extant *S. caffer* dentitions the analogous values were $\mathrm{PM}^{\underline{4}} = 19.1(4)$, $\mathrm{M}^{\underline{2}} = 31.2(5)$ and $\mathrm{M}^{\underline{3}} = 29.5(4)$.

Table 28 gives some lower tooth length and breadth means of extant *S. caffer* and the Swartkrans fossils. Here one is at once struck by the fact that, although the fossil teeth are in every case longer as was the case with the upper teeth, they are always proportionately (and in the cases of $\mathrm{PM}_{\overline{4}}$ and $\mathrm{M}_{\overline{1}}$ absolutely) less broad with respect to length than their extant counterparts. Again the fossil teeth were more worn, and the existing effect would have been even more dramatic had specimens of similar tooth wear stage been compared.

A further difference from the *S. caffer* material lies in the simpler occlusal surface enamel configurations of the Swartkrans teeth. The upper teeth of the fossils (Plate 26) have less localized and outbowed ribs between buccal styles. Lingual molar lobes are less shaped and "pinched", and more evenly rounded. On both upper and lower molars the central cavities show less tendency to infolding and complication than in *S. caffer*. Some of the dramatic difference in complexity between enamel patterns of fossil and recent lower molars seen in Plate 26 must be discounted because of the greater wear on the Swartkrans teeth. Nonetheless it is clear that the molars of the fossil form had less accentuated lingual ribs, rounder buccal lobes and less complicated central cavities than do those of *S. caffer*.

One of the most striking differences lies in the relative complexities of the $\mathrm{PM}_{\overline{4}}$'s and to a lesser extent $\mathrm{PM}_{\overline{3}}$'s, of the fossil and recent forms. On all four available $\mathrm{PM}_{\overline{4}}$'s paraconid and metaconid are unfused (see arrows in Plate 26). As with the molars one is struck by the different length-breadth relationship of the occlusal surface and the considerably simpler enamel outlines in the fossil $\mathrm{PM}_{\overline{4}}$'s. All these points are illustrated in Plate 26. It might be mentioned here that the premolar row length at root level in SK 2968 can be estimated at approximately 65 mm, while the analogous measurement on five *S. caffer* mandibles varied between 52 and 58 mm.

The single juvenile STS dentition furnishes no reason to suppose that it belongs to a different species to that (or those, see below) at Swartkrans: The erupting permanent premolars are almost identical to those at Swartkrans (Plate 26). Although only four bovine teeth were found so far at KA, their features agree quite well with those discussed for the Swartkrans dentitions, and at least one of the teeth, lower molar KA 1268, is too simple for *S. caffer* (Plate 26). What I was able to see of the Makapansgat Limeworks bovine, assigned by Wells & Cooke (1956:11) to cf. *Syncerus caffer*, furnished no reason to think of it as taxonomically separate from the Krugersdorp site species or lineage.

One might ask at this stage: Could some or all of these teeth belong to *Pelorovis* Reck, the genus of the fossil long-horned buffaloes? Gentry (pers. comm.) feels that the widespread, mostly later Pleistocene, long-horned buffaloes at present described as various species of the genus *Homoioceras* Bate, could all belong to one species. As he is intending (pers. comm.) to sink *Homoioceras* in *Pelorovis*, this species would be called *Pelorovis antiquus* (Duvernoy). A second species is *Pelorovis oldowayensis* Reck from Olduvai, which Gentry (1967) removed from the caprines and placed into the tribe Bovini. The Elandsfontein *Pelorovis* possibly constitutes a third, as yet unnamed, species. It is therefore to these three species that the bovine or bovines at the Krugersdorp sites must be compared.

P. oldowayensis molars differ chiefly in greater size, as shown by a comparison of Gentry's (1967:256–7) measurements with Tables 27, 53 and 72. Although purely on morphological grounds little difference can be discerned between lower molar shape of *P. oldowayensis* and lower molars at Swartkrans and KA, some of the upper teeth of the Olduvai species are definitely simpler, with less pronounced basal pillars and buccal styles. Although the lower or upper premolar-molar ratios of the Krugersdorp dentitions could in no case be measured, the Swartkrans specimen, SK 2968, strongly suggests that such ratios might have been considerably larger than those of *P. oldowayensis*: Although, as has already been pointed out, the Swartkrans molars are smaller, the lower premolar length as estimated along the tooth roots was 65 mm in SK 2968. This compares rather startlingly with the three values given by Gentry (1967:256–257), of 60, 60.5 and 67.5 for *P. oldowayensis*. Another important difference lies in the fact that in *P. oldowayensis* $PM_{\overline{4}}$'s are lingually anteriorly closed or almost closed, i.e. paraconid-metaconid fusion has generally occurred. Clearly the Krugersdorp dentitions are not only different to those of *P. oldowayensis* but not even likely to be on the same lineage: If Swartkrans (for instance) were later in time than the sites from which *P. oldowayensis* hails, for all these dentitions to be on the same lineage, there would have to be size reduction (possible), increase in enamel pattern complexity (likely), a dramatic lengthening of the premolar row with respect to the molars (unlikely) and a "reopening" of the paraconid-metoconid fusion on $PM_{\overline{4}}$ (highly unlikely). If Swartkrans were the earlier site there would have to be size increase (possible), shortening and morphological advancement of the premolars (likely) and a loss of enamel pattern complexity (highly unlikely).

The premolar morphology of the Elandsfontein *Pelorovis,* with its $PM_{\overline{4}}$ lacking paraconid-metaconid fusion, is amazingly close to that of the Krugersdorp site bovines. Also with respect to its larger premolar-molar ratio than that of *P. oldowayensis* it is probably closer to the Swartkrans (and perhaps KA and STS) dentitions. Again the lower molar complexity is very comparable while the uppers appear to be simpler. The most urgent argument for rejecting this species as being close to, or even on the same lineage as, the Krugersdorp bovine remains is its significantly greater size: Extra-ordinarily rapid evolution would be required to bridge the size gap between for instance Kromdraai A and Elandsfontein, assuming the former to be the earlier site.

What can be gleaned from the literature (Lönnberg, 1933:13; Bate, 1951: 14; Cooke & Wells, 1951:206, Fig. 1; Gentry, 1967:267, Fig. 9) about tooth sizes of the various "species" now lumped in *P. antiquus* by Gentry, suggests that the bovine teeth from the Krugersdorp sites are definitely smaller. The only reference to $PM_{\overline{4}}$ morphology in *P. antiquus* comes from Gentry (1967: 278): In the material that formed the basis for the former species *Homoioceras nilssoni* (Lönnberg), the paraconid and metaconid have apparently just failed to fuse, i.e. an advance on Swartkrans $\mathrm{PM}_{\overline{4}}$'s. It is difficult to compare the molar occlusal surface complexity of *P. antiquus* with that of the Krugersdorp site bovines. Some *P. antiquus* teeth (e.g. Lönnberg, 1933: plates 1, 4 and 5) seem to be more complex, while others (Wells & Cooke, 1951: Fig. 1 of upper dentition) seem to be closely comparable in this respect. While probably none of the Krugersdorp teeth belong to this species, the differences in dentitions mentioned above clearly do not eliminate *P. antiquus* (occurring mostly in a late Pleistocene context, as it does) from being the descendant of the former. This possibility could only be entertained if the other *Pelorovis* species are eliminated from the ancestry of *P. antiquus.* If it were true, it would be rather strange that no size increase can be observed from site to site at Krugersdorp.

On the whole the simplest hypothesis concerning the Krugersdorp site bovine teeth, i.e. one which would effortlessly fit all the available facts, is that they belong to one or more *Syncerus* species, probably evolving into *S. caffer.* Their overall size, less advanced occlusal surface and premolar morphology and different length-breadth relationship do not contradict ancestry of *S. caffer,* but are rather as expected in an ancestor. For instance, as Gentry (1967:277) points out: "... during their evolution the Bovini have undoubtedly widened their molars".

If one accepts the dentitions from the Krugersdorp sites as belonging to *Syncerus,* the next question arises: How many species of *Syncerus* are represented? Although at least one dentition from each site can be confidently placed into a species distinct from *S. caffer,* the question whether more than one species is represented from site to site, or whether we are dealing with a succession of species on the same lineage, can simply not be resolved because there is too little material from the Sterkfontein Type Site and Kromdraai A. In the foregoing discussion of the Swartkrans teeth a rather puzzling phenomenon has emerged: While the lower molars, with respect to occlusal surface enamel pattern complexity, seem to tend more towards *Pelorovis* at Elandsfontein and *P. oldowayensis,* the upper molars and the juvenile mandible SK 3064 are perhaps closer to *Syncerus caffer* and

P. antiquus, although generally still slightly less complicated than these. This makes one seriously consider whether there could be two bovine species at Swartkrans. The idea of a less advanced (with simpler tooth morphology) and a more advanced (with more complex tooth morphology) *Syncerus* species at Swartkrans may be quite plausible in view of the possibility that time gaps, perhaps of substantial duration, existed between the deposition of the different breccias. I have rejected this idea because:

1. On size alone there is no reason to suspect the presence of more than one species,

2. at KA the same difference between the lower and upper dentitions can be observed,

3. the Sterkfontein juvenile mandible, STS 1936 A, has an $M_{\overline{1}}$ very close to that of the Swartkrans juvenile specimen, SK 3064 (indeed, both of them are not much "simpler" than similarly aged *S. caffer* specimens). But on the STS 1936 A can be seen emerging permanent premolars which are morphologically indistinguishable, taking age difference into account, from those on other Swartkrans specimens (where such premolars are side by side with the "simple" molars). This provides a link between the supposedly advanced and less advanced factions at Swartkrans.

4. Finally the difference in occlusal surface complexity is probably simply due to the greater wear on the lower molars. Early and middle-aged adult lower dentitions, if present, would probably bridge the apparent "complexity gap".

Accordingly the Swartkrans dentitions are here accepted as belonging to a single species of *Syncerus,* closer in the complexity of its occlusal surface enamel patterns to extant *S. caffer* than to *Pelorovis* at Elandsfontein and *P. oldowayensis.*

Although *P. oldowayensis* is not considered as the correct species for the Krugersdorp site dentitions, there are other bovine teeth from Olduvai which provide an interesting comparison. Some lower molars from HWK East in

Lower Bed II (e.g. HWK E II 2688) and from MNK in lower Middle Bed II seem to be quite indistinguishable from those at Swartkrans. From BK II in Upper Bed II come two lower dentitions (BK II 2765 and BK II 2717) which are smaller than *Pelorovis* dentitions from the same site, and close in size to the Swartkrans specimens. They also have longer premolar rows (in one case only the roots of $PM_{\overline{2}}$ and $PM_{\overline{3}}$ are present) which is again reminiscent of the Swartkrans *Syncerus.* The $PM_{\overline{4}}$'s have an open anterior lingual valley, i.e. paraconid and metaconid have not fused but are perhaps a little closer to fusion than in most Swartkrans specimens. These and other similar lower teeth from BK II seemed to have a slightly more complex occlusal surface enamel pattern, which may have been due to their being less worn than Swartkrans lower teeth. An upper left $M^{\underline{2}}$ from the same site, BK II 532, which was mentioned by Gentry (1967: 295) as belonging to a bovine species other than *P. oldowayensis,* seems to compare well in every respect with Swartkrans upper molars. Gentry (pers. comm.) has named a representative of the *Syncerus* lineage from Olduvai Bed IV *Syncerus acoelotus.* The Bed II *Syncerus* teeth discussed above are taken by him to be *S. acoelotus* extending back to Bed II, or the ancestral Bed II species of the Bed IV *acoelotus.* Accordingly the Swartkrans, STS and KA specimens are here called *Syncerus* cf. *acoelotus.*

Some dentitions, presumably of *S. acoelotus*, from JK 2 in Bed III (labelled JK 2 GP8, JK 2 GP 24 and JK 2 GP 8 sec. 6) are definitely more advanced in every respect than the Swartkrans ones, and much closer to those of *S. caffer.*

On the few specimens from East and South Africa that were available for the above comparison, the Swartkrans bovine dentitions are closer to remains from Lower (HWK E) and Lower Middle (MNK) Bed II than to any others. This is of course very tentative, and on larger samples of more complete specimens the Swartkrans form might be shown to correspond more closely with *Syncerus* in BK II (Upper Bed II) after all. Let us say that the species, to which at least the Swartkrans bovine (or some of the Swartkrans bovine specimens) belongs, is likely to be found among the evolving *Syncerus* lineage somewhere in Bed II, Olduvai.

Tribe: TRAGELAPHINI

• *Tragelaphus* cf. *scriptus* Pallas: A few dentitions (Table 29) seem close to those of the extant bushbuck, *T. scriptus.* One of these, mandible SK 14205, shown together with a mandible of the extant bushbuck in Plates 20 and 29, is quite indistinguishable from this species. Fragments like SK 4261 and SK 14052 are probably a little smaller, with shallower horizontal mandibular rami, than might be expected of most modern bushbuck dentitions. $M_{\overline{3}}$, SK 2329, is perhaps too hypsodont, with insufficiently elongated buccal lobes, to qualify for inclusion in *T. scriptus,* or in tragelaphines in general, and is only very dubiously included here.

As a whole these specimens, as well as a single dentition from Kromdraai A, KA 2498 (Plate 29), could probably agree equally well with the Makapansgat Limeworks dentitions to which Wells and Cooke (1956: 12–15) gave the name *Cephalophus pricei.* Gentry (pers. comm.) is of the opinion that these Makapansgat dentitions, including both the holotype and three paratypes of *C. pricei,* are not cephalophine but tragelaphine, and that the paratype right horn core M 478 belongs to a fossil species of *Raphicerus* (See pp. 54, 55). The possibility that these dentitions should be named *Tragelaphus pricei* (Wells & Cooke) has also occurred to me independently, and at least some elements at Swartkrans and KA may belong to the same species.

Dentitions indistinguishable from extant *T. scriptus* were found at Sterkfontein in a late context (Vrba, 1974) in Dump 16.

• *Tragelaphus* Blainville sp.: A piece of a right tragelaphine horn core, SK 3171 (Plates 27 and 28), could belong to this genus. Parts of its surface are badly eroded and too little is preserved to tell whether it broke off shortly above its base or whether it belongs higher up towards the tip of a horn core. In the former case, on size alone, it would still be decisively too large for a bushbuck and probably belong to a species that is intermediate in size between the extant greater kudu, *Tragelaphus strepsiceros* (Pallas), and the nyala, *Tragelaphus angasi* Gray. In the latter case it could belong, on size alone, to extant *T. strepsiceros* or to one of the fossil forms from Olduvai designated by Gentry (pers. comm.) as sub-species of *T. strepsiceros*: viz. *Tragelaphus strepsiceros maryanus* (Leakey) from Bed I and Lower Bed II, and *Tragelaphus strepsiceros grandis* (Leakey) from Middle and Upper Bed II. The latter subspecies must be considered, in spite of its larger size than any other *T. strepsiceros* subspecies, because the spongy texture of SK 3171 suggests that it might have belonged to a subadult individual. In addition the bulk of Swartkrans tragelaphine teeth are somewhat larger than those of the extant greater kudu (See below). Apart from its size, SK 3171 looks too compressed and too strongly double-keeled to belong to either extant kudu or nyala. In both respects it is probably closer to the Olduvai fossil forms, although perhaps not compressed enough for *T. s. maryanus* horn cores.

- *Tragelaphus* cf. *strepsiceros*: A number of dentitions (Table 30 and Plate 29) are morphologically close to those of the extant greater kudu, although many of the teeth lie at or above the upper limit of size variation noted in the living material. This is exactly what Wells & Cooke (1956) noted about the Makapansgat Limeworks teeth which they called the equivalent name *Strepsiceros* cf. *strepsiceros* (Ansell [1968] who uses *Tragelaphus* comprehensively to include *Strepsiceros* Rafinesque as a subgenus, is here followed with respect to nomenclature). Similar large fossil kudu teeth hail from KA. A comparison of the specimens from Swartkrans, KA and Makapansgat furnishes no reason to think of them as different in any way. If slight size and other morphological differences exist between the fossil kudu teeth from these sites, the material is too scant for them to be discerned. This fossil form could be the same as, or close to, the large fossil kudu from Olduvai Middle and Upper Bed II, called by Gentry (pers. comm.) *T. s. grandis*, but it is impossible to say anything more definite about this on the available material, especially as I have not seen the Olduvai dentitions and am making the suggestion purely on the basis of Gentry's (pers. comm.) descriptions. At Sterkfontein only Dump 8 has yielded a few juvenile dentition fragments which have been called *T.* cf. *strepsiceros.*

- *Tragelaphus* sp. aff. *angasi*: An upper and a lower juvenile dentition (Table 31) are clearly tragelaphine but a little larger than similar dentitions of *T. angasi,* the extant nyala. They look identical to the Sterkfontein Type locality dentition assigned to *T.* sp. aff. *angasi.*

- *Taurotragus* cf. *oryx* (Pallas): A single broken $M_{\overline{3}}$ (Table 32) is indistinguishable from those seen on skulls of the extant eland.

Subfamily: CAPRINAE

Tribe: OVIBOVINI

- cf. *Makapania* sp.: There is a small number of upper and lower teeth at Swartkrans showing an interesting combination of characters. Lingual lobes of upper molars and buccal lobes of lower molars are very pointed (Plate 12) yet their hypsodonty, complex central enamel islands (especially the indentations into the walls of the rear central cavities of upper molars like SK 2759 and SK 3005), rule out their belonging to any kind of tragelaphine. The teeth have occasional weak or incipient basal pillars (as in $M_{\overline{3}}$ of SK 2965, $M^{\underline{1}}$ of SK 3005), which are too small to qualify the teeth for membership of any (at least South African) reduncine or hippotragine species. On the other hand the mere presence, albeit weak, of such pillars rules out their belonging to an *Aepyceros* Sundevall larger than the extant species (on which I have never seen even an indication of a basal pillar). From reproductions in Arambourg (1947) it would seem that the impala, very much like the extant form, occurring at Omo, had no basal pillars on its teeth either. The question arises whether this could be an aberrant alcelaphine. Looking at some Swartkrans alcelaphine smaller medium teeth, a similar but less pronounced pointedness of molar lobes can be seen. However, the teeth under discussion here and smaller medium teeth show several differences: Smaller medium teeth are narrower with respect to length. They have less well defined styles. The morphology of the cheek region seems to differ somewhat as seen when comparing specimens like SK 3005 and SK 1523. Among the numerous available smaller medium teeth there is no sign of basal pillars. The mandibular shape of smaller medium specimens, comparing for example SK 3213A with SK 3113 and SK 2965) seems different in that the lower mandibular edge rises behind $M_{\overline{3}}$. In the form under discussion the lower mandibular edge seems to slope downwards behind $M_{\overline{3}}$ (e.g. SK 2965).

Closer to the form under discussion among alcelaphines, than the Swartkrans smaller medium teeth, are some Langebaanweg alcelaphine teeth (Gentry, 1970b). The species represented by L 7257 (Gentry, 1970b: 115; also given as *Incertae sedis* occurring at E Quarry in Hendey, 1969: 102) has also very pointed molar lobes (buccally in lower, lingually in upper teeth). However, the teeth of this Langebaanweg species are less advanced than the Swartkrans teeth under discussion in the following respects: the lack of outbowed ribs between styles of upper molars, which in the Swartkrans species are moderately pronounced; the simple outline of the central cavities of molars (all points mentioned so far in connection with the Langebaanweg form are given in Gentry [1970b: 115]); the Langebaanweg species also seems to have less hypsodont teeth than the Swartkrans species. There are some other Langebaanweg alcelaphine teeth about which there seems to be some doubt as to whether they belong to the alcelaphine represented by L 7257, or to the other alcelaphine at Langebaanweg (in Hendey [1969: 102] this is referred to as ? *Parmularus angusticornis*). Although looking much like the other Langebaanweg alcelaphine teeth in having pointed buccal molar lobes and simple central enamel cavities, these lower teeth are nearer to the Swartkrans species in the following respects: the $M_{\overline{1}}$ has a basal pillar; lingual ribs between styles seem less *flat* than in lower molars of the other Langebaanweg alcelaphine, but still not nearly as pronouncedly rounded as those of the Swartkrans teeth (e.g. SK 3113).

There is a strong resemblance of the Swartkrans teeth under discussion to the species described by Wells and Cooke (1956) as *Makapania broomi,* which was subsequently placed by Gentry (1970c) into the Ovibovini. Gentry pinpoints as some of the tooth characters of the Ovibovini ".... absence of basal pillars on molar teeth, upper molars rather long relative to width, with fairly pronounced styles and rounded medial lobes, ...". Only the fairly pronounced styles tally with the Swartkrans teeth, where in fact the styles on the upper molars of specimens like SK 3005 and SK 2759 seems to be, if anything, more pronounced than those of *Makapania broomi.* The aforegoing discussion makes it clear that, on the other three points mentioned by Gentry the Swartkrans teeth in question disagree with Ovibovine tooth characters. However, since I have seen basal pillars on molars of at least one specimen of *Makapania broomi* at the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand; since those Swartkrans teeth which are widest with respect to length (SK 3005) probably belong to an older individual while others like SK 2759 are longer with respect to width; and since the degree of pointedness of molar lobes agrees very well with that of *Makapania broomi* specimens, the apparent small differences from Ovibovine teeth need not stand in the way of acknowledging affinity of the Swartkrans teeth to *Makapania broomi.* Comparison of Table 30 with Wells and Cooke's (1956) measurements of *Makapania broomi* and with Table 74 of Sterkfontein Type Site *M.* cf. *broomi* specimens, convincingly shows that the former has in every comparable case smaller teeth. Is the Swartkrans form a smaller species of *Makapania*? This is here regarded as a possible solution. However, on the scanty Swartkrans material available nothing more definite than the designation cf. *Makapania* sp. can be arrived at. An alternative solution would be that these teeth belong to an aberrant medium-sized alcelaphine.

One or two specimens, which have at present been left in the "smaller medium" alcelaphine category, could belong with the dentitions here discussed, i.e. either to a small ovibovine or aberrant alcelaphine. SK 3108 (Plate 12), an upper dentition, is particularly remarkable in this respect, with pointed lingual molar lobes, molars that are long with respect to breadth, and with a toothrow that is almost straight and shows little of the arching one usually finds in upper alcelaphine toothrows.

DESCRIPTION AND TAXONOMY OF THE KROMDRAAI A BOVIDAE

Subfamily: HIPPOTRAGINAE

Tribe: ALCELAPHINI

- *Damaliscus* cf. *dorcas*: Right horn core base KA 540 could belong to an adult male *Damaliscus dorcas*, or perhaps to another damaliscine or parmularine of similar size. The metopic and coronal sutures, compression (see Vrba, 1971: Fig. 1) and orientation of the horn core with respect to the sutures and extent of basal hollowing all look very similar to *D. dorcas*. Unfortunately the horn core is broken 35–40 mm above the base so that secure identification is impossible. It is worthy of note that the preservation of the specimen, and the matrix adhering to it, differ considerably from those of other KA specimens.

Antero-posterior basal horn core diameter = 41.0 mm
Mesio-lateral ” ” ” ” = 33e mm
(e = estimated)

- *Damaliscus* sp. 1 or *Parmularius* sp.: Small alcelaphine KA dentitions (Tables 34–36) all appear to belong to a single species. It is the dominant bovid species at the site. Some significant features of these dentitions are:

1. The premolar row is among the most abbreviated I have seen. DPM$^{\underline{2}}$'s and DPM$^{\underline{3}}$'s, wherever preserved are more slight than in the blesbok. DPM$_{\overline{2}}$ is in all available cases absent (KA 731, KA 1516, KA 913, KA 1134, KA 867, KA 1691), although it is present in Swartkrans juvenile mandibles of this size (SK 7050, SK 11003, SK 5920) and in the blesbok. DPM$_{\overline{3}}$ is more slight than in the said Swartkrans material (compare KA 731, KA 1516 with SK 7050) or in extant *D. dorcas*. In all KA adult mandibles where the presence of PM$_{\overline{2}}$ during life could be checked (KA 758, KA 1010, KA 1827 A,

KA 770, KA 1739, KA 2353, KA 646, KA 1101, KA 1687 A, KA 541, KA 1653, KA 969, KA 1004, KA 700) it was always absent while $\mathrm{PM}_{\overline{3}}$ was simple and peg-like (Plate 7). The same trend of premolar reduction can be seen in Kromdraai A $\mathrm{PM}_{\overline{4}}$'s which are significantly smaller with respect to molar dimensions than are $\mathrm{PM}_{\overline{4}}$'s of extant *D. dorcas.* This is shown in Table 38 and Fig. 22. The same trend is reflected in the upper dentitions. Where the area is preserved $\mathrm{PM}^{\underline{2}}$ is absent (e.g. KA 564 in Plate 8) and $\mathrm{PM}^{\underline{3}}$ is very slight (e.g. KA 564 and KA 1127 in Plate 8). This contrasts sharply with the position in *D. dorcas* and "larger small" *Damaliscus* sp. 2 teeth at Swartkrans. Among the latter the only specimen where the $\mathrm{PM}^{\underline{2}}$ position can be seen has a large $\mathrm{PM}^{\underline{2}}$. Both SK 3129 and SK 1520 have stout $\mathrm{PM}^{\underline{3}}$'s almost as large as $\mathrm{PM}^{\underline{4}}$'s (See Plate 8).

2. Plate 7 shows that the morphology of the KA $\mathrm{PM}_{\overline{4}}$'s is somewhat different from extant *D. dorcas.* The incision between metaconid and entoconid in KA specimens is deeper and more parallel-sided, a feature which seems to be a general difference between $\mathrm{PM}_{\overline{4}}$'s of fossil alcelaphines at all the Krugersdorp sites and extant South African alcelaphines. For instance in Fig. 10, depicting Swartkrans specimens, it is in every case the extinct species which show this type of incision between metaconid and entoconid, while extant species have a more gently V-shaped incision. This feature is speculated on extensively in the case of $\mathrm{PM}_{\overline{4}}$ evolution along the *Connochaetes taurinus* lineage (pp. 33–35). The same fossil-extant difference holds true for other alcelaphines from Kromdraai and from Sterkfontein.

3. KA molars are longer (mesio-distally) with respect to (bucco-lingual) breadth than are those of *D. dorcas* or of *Damaliscus* sp. 2. Fig. 11 shows this clearly. Table 37 and Fig. 11 suggest that with respect to overall tooth size the KA species lies between *D. dorcas* and *Damaliscus* sp. 2, and can be considered as a "larger small" alcelaphine species as opposed to *D. dorcas,* which is "smaller small" in size.

4. KA lower molars have less complex central cavities and buccal lobe enamel outlines than do those of *D. dorcas,* which have a greater tendency

to buccal pinching (Plate 7). In this respect they also differ, although to a lesser extent, from molars of *Damaliscus* sp. 2: Plate 7 shows how, especially with advanced wear, the latter (e.g. SK 1182 and the D 16 mandible) have distinctly flattened buccal lobes, while in Kromdraai A specimens like KA 1004, of similar wear pattern, buccal lobes typically remain rounded. A less certain difference is that *Damaliscus* sp. 2 lower molars seem to have slightly more complex central cavities. A similar lesser complexity of enamel pattern can be observed on the occlusal surface of KA upper molars: In general buccal styles and "ribs" between styles as well as central cavities tend to be less complex than in *D. dorcas* (Plate 8).

5. Metastyles of $M_{\overline{3}}$'s are on the whole relatively small on Kromdraai A dentitions, while being longer on those of *D. dorcas* and *Damaliscus* sp. 2. This observation is a general one and difficult to substantiate.

6. A comparison of specimens like KA 1010 and KA 731 with available extant *D. dorcas* material suggests tentatively that the small KA alcelaphine may have had a slightly shorter diastema, i.e. a shorter snout. Because the specimens with this region preserved are so few, this point must remain very tentative. It is perhaps nonetheless worth mentioning because the same effect is observable on STS specimens like STS 1800a, which have been assigned to the same species (Plate 9).

7. The mandibular symphysis has a more pronounced "bump", in the few KA and STS specimens where the area is at least partially preserved (KA 1716, KA 1010, STS 1800 a), than I have seen on extant *D. dorcas* mandibles (Plate 9).

8. Where preserved (e.g. KA 731, KA 931 A) the antero-posterior depth of the mandibular ascending ramus below the sigmoid notch-condyle level is greater than on the blesbok (Plate 9).

A short summary of these differences in dentitions, whether well-founded or tentative, between "small" alcelaphines from the Krugersdorp sites and extant *D. dorcas* is given below:

	Damaliscus sp. 1 or *Parmularius* sp.	*Damaliscus* sp. 2	*D. dorcas*
mesio-distal molar length	longer	longer (longest?)	shorter
$\frac{\text{molar breadth}}{\text{molar length}}$ %	lower	higher	higher
premolar length	very short	long?	long
$PM_{\overline{4}}$ morphology	primitive	?	advanced
occlusal enamel pattern complexity	simple	less simple?	complex
metastyle of $M_{\overline{3}}$	small	larger	larger
diastemal, i.e. snout length	shorter	?	longer
"bump" at mandibular symphysis	more pronounced	?	less pronounced
mesio-distal ascending ramus width	wider	?	narrower

The most complete specimen, KA 731, is shown in Plate 31. It consists of a large part of the cranium, mostly the right side, with both mandibles and portions of atlas and axis held approximately in their natural positions by breccia. It belongs to a juvenile with $M_{\overline{2}}$ about to erupt. Apart from the differences named above in points 1–8, KA 731 shows no startling morphological deviations from *D. dorcas.*

The dominant STS alcelaphine species is represented by a number of dentitions which consistently agree with points 1 to 7, wherever these can be evaluated, and which are in fact quite indistinguishable from the KA specimens (Plates 7, 8). On the available evidence they must therefore be assigned to the same species. A single short premolar row with $M_{\overline{1}}$, SE 192, from the West Pit of the Sterkfontein Extension locality may also belong to this species. At least one specimen from Swartkrans, SK 3127, certainly does.

Unfortunately no dentitions have as yet been found definitely associated with the small South African fossil alcelaphine known from Elandsfontein and Cornelia. I would expect its teeth to be smaller than those discussed here. However, it is tempting to compare these dentitions with those of two other small extinct alcelaphines, *Damaliscus agelaius* from Bed IV at Olduvai and the small alcelaphine* present in the *Metridiochoerus andrewsi.*

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* Harris (pers. comm.) provisionally assigned this material to *Parmularius altidens.*

zone (Maglio, 1972) at East Rudolf. *D. agelaius* differs from the dentitions under discussion by

1. its longer premolar row, and
2. larger teeth.
3. In addition the single skull fragment associated with such teeth at the Sterkfontein Type Site, STS 2368 B, seems to have a different morphology to *D. agelaius* (p. 93).

On the other hand the East Rudolf species

1. has a short premolar row,
2. similarly sized teeth, with a relatively low molar $\frac{\text{breadth}}{\text{length}}$ % as is the case in the Kromdraai A and Sterkfontein dentitions,
3. and is quite indistinguishable from STS 2368 B (p. 93).

While the KA species under discusssion certainly could be a species of *Damaliscus*, certain points like the suggestion of a short snout, and the primitive molar length/breadth relationships and occlusal enamel pattern, suggest that membership of *Parmularius* can at this stage not be ruled out. Accordingly it is provisionally named *Damaliscus* sp. 1 or *Parmularius* sp.

Does the *Damaliscus* cf. *dorcas* horn core base (p. 68) belong to these dentitions? If it does then assignation to the extant species is probably incorrect. Rather in such a case we would have a species distinct from *D. dorcas* with more primitive dental features but with a similar horn core base. Another alternative is that the horn core really belongs to the *D. dorcas* in which case, in my opinion, it cannot belong to the same species as the dentitions. In such a case it would represent an isolated occurrence at KA, and the suspicion must arise that it may not belong to the main KA assemblage. A third possibility exists that it represents quite a different alcelaphine, or even a species belonging to another tribe. Concerning the possibility of another alcelaphine it is worth noting that a Sterkfontein horn core of unknown stratigraphic origin, has a very similar base. Its rapid thinning towards the tip in anterior and lateral view, as well as the apparent lack of a twist, make it likely to belong to a damaliscine other than *D. dorcas* or perhaps to a parmularine species. It may indeed, together with KA 540, belong to the dentitions here discussed.

Addendum: At a late stage, when all taxonomic evaluations had been completed, the partial skull, KA 1601, was discovered. A single $M\frac{3}{}$, unmistakeably belonging to the *Damaliscus* sp. 1 or *Parmularius* sp. dentitions here discussed, is associated with KA 1601. Large parts of the dorsal facial area, including most of the nasals, portions of the basal horn cores and the left dorsal orbital rim have been preserved. The specimen confirms that we are dealing here with one of the smaller alcelaphine species. At the same time it is unlike any extant *Damaliscus*, or any other extant alcelaphine, species. I have not been able to see the *Parmularius rugosus* material from Olduvai Bed III–IV Junction or Bed IV. The skull measurements given in Leakey (1965: 60) for the holotype, M. 21430, agree very closely with those possible on KA 1601. Plate 75 (*op. cit.*) of M.21430 also corresponds in every visible respect with the KA specimens. Plate 76 suggests that the dentition of the Olduvai holotype, while morphologically similar, was considerably larger than KA *Damaliscus* sp. 1 or *Parmularius* sp. dentitions. The discovery of KA 1601 thus strengthens the belief, first suggested by the dentitions only, that the dominant KA alcelaphine is likely to be a *Parmularius*. The KA species could also be related to the East Rudolf small alcelaphine from the *Metridiochoerus andrewsi* zone, which appears to be a *Parmularius* as well. One would have to compare KA 1601 directly with the East Rudolf specimens, and also with Olduvai *P. altidens* and *P. rugosus* material, to resolve where exactly it might fit. My impression at the moment is that the KA species may be close to *P. rugosus*, perhaps even specifically identical with it.

The forehead region of KA 1601 is flatter than that of the STS fragment, STS 2638 B, and of the East Rudolf skull. It is possible that the STS and East Rudolf forms may be precursors, on the same lineage, of the KA *Parmularius* and Olduvai *P. rugosus.*

- *Medium-sized alcelaphines*: Unfortunately the medium-sized alcelaphine material (Tables 39 and 40) includes no horn core or skull specimens and is too fragmentary and scant to allow more than a few general observations. While, as in the case of Swartkrans and Sterkfontein fossils, the specimens seem to be closest to *Alcelaphus buselaphus* among extant alcelaphines, and one or two (e.g. KA 794 A in Plate 12) could belong to this species, the bulk of the specimens suggest differences from such extant *A. buselaphus* material as was available for study: The posterior border of the palate, lateral to the perpendicular part of the palatine, is situated further forward on the Kromdraai A specimens (arrow in Plate 11). The angle at which the recessus maxillaris rises (posterior to the palate and lateral to the perpendicular part of the palatine) is more nearly a right angle, as shown in KA 1781 and KA 1067, than that in *A. buselaphus*. In the latter species the angle formed with the palate is larger, with the recessus maxillaris sloping diagonally backwards. In alcelaphines as a whole this feature appears to be correlated with the antero-posterior length of the skull, the said angle being larger in longer skulls like those of blue wildebeest and hartebeest, and more nearly a right angle in shorter skulls, like those of the blesbok. Perhaps one could infer from this that the Kromdraai A medium-sized alcelaphine had a somewhat shorter skull, i.e. less facial lengthening, than *A. buselaphus*. Similar features of the recessus maxillaris can be observed on one or two Swartkrans "smaller medium" sized, i.e. Gp. IIc, specimens. What can be seen of Kromdraai A medium-sized alcelaphine occlusal surface enamel patterns also resembles Swartkrans Gp IIa and c rather than *A. buselaphus*: Thus lingual upper molar lobes in both fossil groups are peculiarly pointed while their enamel patterns as a whole are a bit simpler than in *A. buselaphus* (See Plates 11, 12).

Although there are no complete fully adult premolar rows among the Kromdraai A dentitions, the emerging permanent premolars on KA 542 agree excellently with premolar morphology of Swartkrans Gp IIa (Fig. 10: H–J), while the juvenile premolar row KA 2514 is too short for extant *A. buselaphus*.

On the whole, therefore, the medium-sized KA alcelaphine is likely to belong to the same species as the "smaller medium" sized Swartkrans alcelaphine dentitions. The latter were tentatively thought to belong to *Rabaticeras porrocornutus* (p. 32).

Teeth from SE and STS, and a fragmentary frontlet from the latter site, could also belong to the same medium-sized alcelaphine species.

- cf. *Connochaetes* sp. aff. *africanus* (see footnote on p. 16 concerning the applicability in this case of the specific name *africanus*): A few dentitions (Table 41) compare well with Swartkrans cf. *C.* sp. aff. *africanus* (Gp III) specimens with respect to size and complexity of their occlusal enamel pattern (Plate 14). The $PM_{\overline{4}}$'s on KA 1147, KA 1609 and KA 883 are indistinguishable from those of Swartkrans Gp III (Fig. 10: O and P; KA 1609 and KA 1147 in Plate 14), while differing from those of the extant blue wildebeest: The two latter of the Kromdraai A $PM_{\overline{4}}$'s here cited have paraconids and metaconids in an unfused state, although close to fusion (see point 3 on p. 34). On the only Kromdraai A $PM_{\overline{4}}$ where the feature could be seen (KA 1609), entoconid and entostylid are directed lingually as is their point of fusion (see point 4 on p. 34). All three show a deep, more or less parallel-sided lingual incision between metaconid and entoconid (see point 5 on p. 34).

A feature that is puzzling and difficult to explain is the tendency on lower molars to pronounced goatfolds as shown on KA 883 (Plate 14) and KA 782 B. This tendency is less pronounced in Swartkrans and extant *Connochaetes* species. If this feature were really representative of this KA form, it might represent a specialization away from the main lineage leading to *C. taurinus.*

Another interesting point is that the only specimen on which ramus depth can be assessed, KA 1147, seems to be deeper under the premolars than the Swartkrans *Connochaetes* mandibles, and closer in this respect to *C. taurinus* (Fig. 23 and Plate 15).

Among the "smaller large" Kromdraai A alcelaphine specimens, mandibular fragment KA 740 is rather unique and interesting. The teeth seem to be (bucco-lingually) wider and more robust, with more flattened buccal enamel surfaces, than Swartkrans *Connochaetes* or Kromdraai A specimens like KA 1147. They are reminiscent of some of the specimens assigned to cf. *Megalotragus* sp. but clearly smaller than these (Plate 16). Does KA 740 belong to what has variously been called in the literature *Alcelaphus robustus* and *Pelorocerus broomi* which I suspect to belong to one species and have called *Alcelaphus broomi* in the Swartkrans section (p. 36)? Is this large fossil species really an *Alcelaphus* species or could it be on, or an offshoot from, the same large *Connochaetes* lineage that recurs throughout the Krugersdorp sites? For the moment KA 740, isolated and fragmentary as it is, has been left as part of the *Connochaetes* assemblage at KA.

KB definitely has a *Connochaetes* which seems to belong to the *C. taurinus* lineage, while being less advanced than the extant blue wildebeest. A few teeth from STS seem to belong to the same lineage, but are too few in number to say whether they are closer to cf. *Connochaetes* dentitions from Swartkrans or KA. A single tooth fragment from the West Pit of the Sterkfontein Extension, SE 2601.1, is of Gp III size and clearly shows the goatfold also found on KA Gp III teeth. Similar teeth of the correct size are found in some of the Sterkfontein Dumps, but are too isolated and broken to ascertain whether they belong to a *Connochaetes* at all.

- cf. *Megalotragus* sp.: Some large teeth (Table 43 and Plate 16) are similar in size and morphology to the Swartkrans teeth tentatively assigned to cf. *Megalotragus* sp. In the shape of the central enamel cavities and the goatfold KA 1292 looks perhaps closest to the single Sterkfontein Type Site mandible, ST 1339. On the whole the specimens called cf. *Megalotragus* sp. from all the Krugersdorp sites are too scant to allow investigation of possible relationships from site to site.

Tribe: HIPPOTRAGINI

- *Hippotragus* cf. *equinus*: A single left $M_{\overline{2}}$ (Table 44), which is in the process of eruption, is indistinguishable from this species. Similar teeth are found at the Sterkfontein Type locality (p. 97).

- cf. *Hippotragus* sp. aff. *gigas*: A specimen, including the upper left dentition and parts of the skull, has not been prepared yet. What can be seen of the teeth looks almost exactly like the Swartkrans dentition (SK 3139 and SK 3107) which was assigned to this species, being of a similar tooth wear stage. This form is well represented at STS. Some specimens also come out of Sterkfontein Dumps D13, D14 and D15.

Tribe: REDUNCINI

- *Redunca* cf. *arundinum*: A single dentition fragment (Table 45) appears to be reduncine, and could belong to this species. As in the case of similarly assigned fragments from STS and Swartkrans, an alternative assignation could be *Redunca darti.*

Tribe: PELEINI

- *Pelea capreolus*: A few dentitions (Tables 46 and 47 and Plates 19 and 20) seem to belong to this species. At KA as at Swartkrans (see pp. 45 –47) there appear to be elements larger than the extant *P. capreolus*. This is shown in Table 16 and Figs. 12–14, 16.

Subfamily: ANTILOPINAE

Tribe: ANTILOPINI

- *Antidorcas recki*:

A. **Skull and horn core material**

KA 1779: This almost complete skull, which lacks the dorsal braincase, is shown in Plates 32–34 (in Plate 34 a mandible, KA 964, of the same species but not of the same individual as KA 1779, has been included). It was briefly mentioned in Vrba (1973:310). Both upper orbital rims have been broken so similarly, with the broken edges extending in semicircles towards the metopic suture (Plate 32), that the conclusion is inescapable that horn cores were present during life which were somehow knocked or torn off subsequently. The said breakages each expose an extensive frontal sinus which extends laterally to the supra-orbital foramen, and which must have continued into the horn pedicle and probably the basal horn core. The extent and placement of these breakages further indicate that horn cores, if present, must have been slender and arisen closely behind the supra-orbital foramina, in fact of a size and positioning on the skull very close to that observed in, for instance, extant female *A. marsupialis.*

The species *Adenota recki* (Schwarz, 1932) was subsequently called *Phenacotragus recki* (Schwarz, 1937) and, with the sinking of *Phenacotragus* into *Antidorcas*, became *A. recki* (Gentry, pers. comm.). A comparison of KA 1779 with the cast of the type skull, BM (NH) M. 21460, of *A. recki* from Olduvai shows that the two are indistinguishable in almost every respect. They differ in the presence of strong horn cores on the Olduvai type and in its slightly larger overall size. The obvious conclusion is that these differences are sexual. The degree of male-female horn core difference in this species has hitherto been in some doubt. Gentry (1966:79) suggested some rather large Olduvai horn cores as possible candidates for the female *A. recki.*

This would have implied a considerably lesser degree of horn core sexual dimorphism in *A. recki* than is found in gazelles, and even in *Antidorcas.* He (pers. comm.) subsequently felt that this concept cannot be maintained and suggested that a better possible female would be the slender horn core BM (NH) M. 22362, which he had previously (Gentry, 1966: 65, Pl. 7A) thought of as a female of the Olduvai *Gazella* species. KA 1779 goes some way towards resolving this whole question: If one accepts the abovementioned idea about the missing horn cores of the KA skull as correct, then the difference between it and a skull like M. 21460 would be indicative of a similar degree of sexual dimorphism in *A. recki* as is observed in *A. marsupialis* and in *A. bondi* (Vrba, 1973). This would be in perfect accord with Gentry's suggestion about the slender Olduvai horn core M. 22362, which by its size could probably fit comfortably onto KA 1779.

Bearing in mind the said size difference, points of similarity between M. 21460 and *A. recki* in general, and KA 1779 include:

1. They have almost identical preorbital fossae, much shallower and with less pronounced ventral rims than those in *A. bondi* (Vrba, 1973), and less deep posteriorly than those in *A. marsupialis.*

2. The supraorbital foramina in KA 1779 are similarly close together as in M. 21460 and other Olduvai *A. recki* specimens. This is shown in Fig. 14 (Vrba, 1973). The surrounding shallower pits are very similar (Plate 32).

3. Cooke, in his unpublished manuscript on the Bolt's Farm Bovidae, wrote about a specimen of what he calls *Antidorcas wellsi,* here accepted as *A. recki* (Gentry, pers. comm.; see also Vrba, 1973:310): "A portion of the front of the snout ..... is wide and blunt, measuring 30 mm across the premaxillary-maxillary suture .....". This description fits the snout of KA 1779 (Plate 32) almost exactly. Unfortunately there are at present no complete snouts available of either *A. australis* or *A. bondi*, but KA 1779 is significantly different in this respect from *A. marsupialis* with its anteriorly narrowed snout and different premaxillo-maxillary suture.

4. The basioccipital of KA 1779 (Plate 33) is anteriorly narrowed, similar to that on M. 21460 and to Plate 7B of M. 22371 in Gentry (1966). The anterior tuberosities of KA 1779 are more parallel and less diagonal in direction, and far less prominent than in the two Olduvai specimens, but this may again be due to sexual dimorphism. The course of the anterior tuberosities of KA 1779 is certainly quite unlike the transversely directed, widely-spaced one to be seen on *Antidorcas marsupialis* and, to a lesser extent, on *A. australis.*

5. Both KA 1779 and M. 21460 have similar pronounced angles (i.e. "upbending") between the basioccipital and basisphenoid planes, as does the modern springbok. This character appears to separate *A. recki* and *A. marsupialis* on the one hand from *A. australis* and *A. bondi* on the other. In the latter two species the basioccipital and basisphenoid form part of more or less the same plane, (Hendey & Hendey, 1968; and Vrba, 1973 respectively), or at least form an angle closer to 180° than in the former two.

6. The foramen ovale in both KA 1779 (Plate 33) and M. 21460 is markedly elongate, as it is in *A. bondi*, rather than subcircular and smaller as in *A. marsupialis* and *A. australis.* It was mentioned in Vrba (1973) that this is likely to be a phenomenon correlated with braincase length.

7. Maxillary tooth morphology, with respect to prominence of buccal styles, shape of central enamel islands, etc. is very close in M. 21460 and KA 1779 (Plate 33). The premolar/molar ratio of KA 1779 places it with Olduvai *A. recki* specimens in Fig. 7 (Vrba, 1973).

8. In both M. 21460 and KA 1779 the toothrow is situated more posteriorly with respect to the orbit than is the case in *A. marsupialis* (see also Plate 34).

There are few points of difference:

9. The size difference between M. 21460 and KA 1779, and the fact that it is probably due to sexual dimorphism, has been mentioned.

10. Gentry (1966:96) points out that in the only three *A. recki* specimens (including M. 21460) where the posterior nasal shape could be seen, the posterior fronto-nasal suture had a V-shaped, or posteriorly pointed, course. In KA 1779 this posterior suture is transverse, (Plate 32) rather as it is in *A. marsupialis.* This might be expected in a later *A. recki* (if indeed all the relevant Olduvai specimens are of a time earlier than Kromdraai A; unfortunately there is no certainty as to the stratigraphical provenance of M. 21460 at Olduvai), if the lineage was really evolving into *A. marsupialis* as is generally believed.

Distance between lateral walls of supraorbital foramina = 32e
Maximum posterior orbital width = 83e
Distance between the anterior extremity of the snout and the straight line joining the metastyles of the $M\frac{3}{}$'s = 99.5e

KA 1577 (Plate 35): Judging by the texture of the horn core bone, where it is broken more or less through the top of the pedicel, this right horn core base with pieces of the orbital rim and metopic suture belonged to a subadult male. This is perhaps the reason why KA 1577, although in horn core compression very similar, appears to be slightly smaller than the bulk of *A. recki* readings in Fig. 1 (Vrba, 1973) of basal horn core dimensions. The slightly raised metopic suture with the horn core arising close to it, as well as the nature of the post-cornual groove, all point to KA 1577 belonging to *A. recki.*

Antero-posterior basal horn core diameter = 28e
Mesio-lateral basal horn core diameter = 21.5e

KA 1567: This left horn core, broken off shortly above the base, again has a spongy bone texture and dimension that suggest a juvenile male.

Antero-posterior basal horn core diameter = 17.6
Mesio-lateral basal horn core diameter = 15.0

B. **Dentitions:** A number of typically antidorcine dentitions are listed in Tables 48 and 49, and some of them appear in Plates 34 and 35. In the characters of straightness of central cavities, straightness of lingual lower molar walls and the tendency to lower molar squaring these dentitions are distinctly of Type A (See Vrba, 1973 where the concept of two basic *Antidorcas* types, Type A and Type B, was introduced). In the only three mandibles, where the presence or absence of $PM_{\overline{2}}$ can definitely be determined, it is present in all cases while $PM_{\overline{3}}$ is similar in shape to $PM_{\overline{4}}$ and not reduced and peg-like (e.g. KA 1002 in Plate 35). This rather longer mandibular premolar row is reflected in the upper teeth as well as shown in Fig. 7 (Vrba, 1973) and firmly points to *A. recki* rather than *A. australis* and *A. marsupialis* which both lack $PM_{\overline{2}}$ and have a reduced $PM_{\overline{3}}$. The size of the Kromdraai A dentitions also points to *A. recki*: Fig. 2 (Vrba, 1973) of $M_{\overline{2}}$ dimensions shows that tooth length is especially significant in separating the KA teeth from those of *A. australis* and *A. marsupialis*. Fig. 6 (Vrba, 1973) shows how $M_{\overline{1}} - _{\overline{3}}$ length groups the Kromdraai A specimens with *A. recki* dentitions from other African fossil sites rather than with *A. australis* and *A. marsupialis* which are larger. Fig. 4 (Vrba, 1973) suggests that the KA *A. recki* probably had a greater hypsodonty index than *A. australis* and certainly than *A. marsupialis,* but more data would be needed to confirm this. It is clear that these dentitions belonged to the same species as the skull KA 1779. Not only does the upper tooth morphology correspond excellently, but the startlingly upright ascending mandibular ramus on specimens like KA 506 and KA 964A is exactly as expected in a form where the toothrow is displaced posteriorly with respect to the orbit-zygomatic arch complex. In Plate 34 this is demonstrated.

Comparison with other Krugersdorp sites: The above discussion of differences between the Kromdraai A *A. recki* and *A. australis* as known from Swartkrans and Swartklip, Elandsfontein and Melkbos (Hendey & Hendey, 1968; Hendey, 1968 and Hendey, 1974) makes it clear why the KA and Swartkrans Type A antidorcines cannot belong to the same species. In Vrba (1973: 302) there is further discussion on why the two species are likely to be on a single lineage only if KA turns out to be earlier in time that the relevant *A. australis* fossils at Swartkrans.

There is definite evidence of *A. recki* at KB (pp. 89 – 90 and Plate 37) although the remains are too scant to allow a comparison with the KA *A. recki*. The species is also represented in the SE assemblage by a single horn core (Plate 41) and, more doubtfully, by some dentitions. Some fragmentary STS dentitions have been assigned to *Antidorcas* cf. *recki*.*

Comparison with other African sites: As the KA assemblage includes no complete *A. recki* horn cores, only the teeth can be compared with those of other sites. Occasionally remains at other sites are complete enough to allow comments on how the rest of the skull compares with KA 1779. Some dentitions ascribed to *A. recki* from FLK I in Middle Bed I at Olduvai have an ascending mandibular ramus that is more robust and less steeply ascending than is the case in KA material. This robustness in relationship to teeth that are rather smaller than at KA is noticeable in the horizontal mandibular ramus as well. In Upper Bed I are at least some mandibles (e.g. FLK N I 7266 and FLK N I 7284) in which the angle of ascent of the ascending mandibular ramus has become more like that in KA specimens. However, the larger mandibular and skull structure (e.g. FLK N I III/2 7266) with respect to teeth that are smaller than, or of the same size as, at KA persisted in all specimens I was able to see up to Upper Bed I. Similarly the teeth up to this time at Olduvai seem slightly different in morphology: Lower lingual walls tend to be undulating having less of a straight Type A antidorcine edge than later *A. recki* teeth. The buccal lower molar lobes are more pointed with little or no tendency to lobar "squaring" which is quite well developed on Kromdraai A mandibles. This latter tendency persists in lower Bed II *A. recki* mandibles that I saw, as does a seemingly lesser hypsodonty than at KA. The closest (and latest) *A. recki* mandibles I was able to see came from SHK in Upper Middle Bed II. Comparisons of *A. recki* teeth from South African sites like the Vaal River Younger Gravels, Cornelia, Elandsfontein and Bolt's Farm, with those of the KA *A. recki* were discussed in Vrba (1973: 310, 311). It would not be prudent at this stage to try interpreting such slight differences as appear to exist between the relatively scant dental remains at the said sites and *A. recki* at KA, in terms of chronological succession.

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* The splitting of Swartkrans into SKa and SKb resulted in assignation of some SKa specimens to *A.* cf. *recki* (pp. 121–122).

- *Antidorcas bondi*: A few dentitions (Tables 50 and 51) immistakably represent this species. They are quite indistinguishable from Swartkrans remains of *A. bondi*. Other records of occurrence of this species are discussed fully in Vrba (1973).

Tribe: NEOTRAGINI

- cf. *Raphicerus* sp.: A single mandible, KA 1152 (Table 52 and Plates 21 and 22), while clearly neotragine, is a little different from all the extant species of that tribe as represented at the Transvaal Museum. Although in terms of general tooth size it agrees more with the klipspringer, its premolars are a little smaller in relation to the molars than is usual in extant *O. oreotragus* (Fig. 20 and Plate 21), placing it with its lower premolar/molar ratio of 65% closer to the mean obtained on p. 53 for *R. campestris* (mean = 64% of 5 individuals with range 61% – 67%) than to that obtained for extant *O. oreotragus* (mean = 72% of 9 individuals with range 67% – 78%). On the other hand it is clearly larger than any *R. campestris* specimens I have seen. For the moment it can be tentatively thought of as belonging to a slightly larger species of *Raphicerus*.

Two horn cores from Swartkrans, assigned to cf. *Raphicerus* sp. were also significantly larger than those of *R. campestris*.

Subfamily: BOVINAE

Tribe: BOVINI

- *Syncerus* cf. *acoelotus*: Four teeth (Table 53 and Plate 26) are obviously close to those of extant *S. caffer*. Earlier in this work (pp. 55 –60) it was discussed why the bovine teeth from the Krugersdorp sites as a whole are more likely to belong to *Syncerus* than to the fossil bovine genus *Pelorovis*. It was also mentioned that on the available material there seems to be no reason to think of the KA *Syncerus* as belonging to a species different from that at Swartkrans, which was called *S.* cf. *acoelotus*. As is the case with the Swartkrans teeth, the KA teeth are decisively larger than expected of extant *S. caffer*: Five individuals of the latter had a mean length and breadth of $M^{\underline{2}}$ of 31.2 mm and 21.8 mm respectively. Table 53 shows that the Kromdraai A $M^{\underline{2}}$'s, KA 1451 with length 35 mm and breadth 26.4 mm and KA 1630 with breadth 27 mm, are much larger. Similarly $M^{\underline{3}}$'s of four extant buffaloes gave a length mean of 29.5 mm and a breadth mean of 19.6 mm, as against 36.0 mm and 22.0 mm respectively for KA 752. On the other hand a comparison of Tables 27 and 53 shows that KA and Swartkrans bovine tooth sizes agree very well. The three KA upper teeth are perhaps slightly simpler in their occlusal surface enamel patterns than are their extant counterparts; while the lower $M_{\overline{2}}$, KA 1268 is decisively simpler in this respect (Plate 26) although it is still relatively high-crowned and little worn. KA 1268 is also less broad bucco-lingually with respect to mesio-distal length than are teeth of extant *S. caffer*, exactly as was observed on the Swartkrans material (p. 56 and Table 28).

Of the Krugersdorp sites, apart from Swartkrans and KA, only STS has yielded a single mandible that has been assigned to *S.* cf. *acoelotus*.

Tribe: TRAGELAPHINI

- *Tragelaphus* cf. *scriptus*: Mandibular fragment, KA 2498 (Table 54 and Plate 29) could belong to a bushbuck, or to *Tragelaphus pricei* (See p.62).

- *Tragelaphus* cf. *strepsiceros*: A few, mostly juvenile, dentitions (Table 55 and Plates 29 and 30) are thought to belong to the large fossil kudu also found at Swartkrans and Makapansgat Limeworks. What was written about the Swartkrans *T.* cf. *strepsiceros* material applies to that from KA too.

- *Taurotragus* cf. *oryx*: Two teeth (Table 56) are indistinguishable from those of the extant eland.

DESCRIPTION AND TAXONOMY OF THE KROMDRAAI B BOVIDAE

Subfamily: HIPPOTRAGINAE

Tribe: ALCELAPHINI

- *Connochaetes* sp. (on a *C. taurinus* lineage):

A. **Horn core material:** KB 376 (1) is a piece of a left horn core with some of the adjacent skull region attached. It resembles the horn core of a young (perhaps before the eruption of $M_{\overline{1}}$) *C. taurinus*, the extant blue wildebeest. KB 376 (1) differs from the latter by having a shorter distance between horn core base and orbital region (See point 4, p.14), by a more extensive cornual diverticulum extending about 30 mm up into the horn core, and possibly by a more oblique, backwardly directed course in lateral view: KB 3187 is another juvenile horn core fragment that could have belonged on the mesial surface of the right pedicel and horn core base of the same individual to which KB 376 (1) belongs.

B. **Dentitions:** The juvenile lower dentitions in Table 57 with deciduous premolars erupted but not yet in occlusion, could belong to the same individual as the horn cores mentioned above. All the teeth in Table 57, as well as additional tooth fragment seem to be comparable in size and morphology to those of the extant blue wildebeest. Perhaps the central enamel cavities on fragments like KB 3365 (2) and KB 3001 (2) are a little simpler than those on extant *C. taurinus* teeth. The $DPM_{\overline{3}}$'s on KB 382 (1) and KB 3009 (2) are less molarized than those I have seen on juvenile extant *C. taurinus* specimens, resembling in this respect similar dentitions of the Swartkrans cf. *Connochaetes* sp. aff. *africanus* (e.g. SK 4479 and SK 7315). On the whole these Kromdraai B *Connochaetes* remains appear to be less advanced than the extant *C. taurinus*, and somewhere on the lineage evolving into the blue wildebeest, members of which are present at all of the Krugersdorp Sites.

However, exactly where in this temporal sequence, i.e. closest to *Connochaetes* from which other site or sites, the KB material fits is impossible to say on these few fragments.

Subfamily: ANTILOPINAE

Tribe: ANTILOPINI

- *Gazella* sp.: The left horn core KB 380 (1) is comparable in size, and backward slope with respect to the cranium in lateral view (Plate 36 C), with female horn cores of *Antidorcas bondi* from Swartkrans (Vrba, 1973: Plate 4). However, it shows some dramatic differences from these, or any other antidorcine, female horn cores: The anterior pedicel of KB 380 (1) is broken open, showing that no sinus was present in the horn core base or pedicel. A part of the intero-dorsal surface of the orbit is preserved, and this is situated high up, almost at the level of the horn core base, showing that the level of the orbital rims was probably more or less as high as the level of the frontal between the horn bases. These features are typical of gazelles. They could also qualify KB 380 (1) for membership of the tribe Neotragini. However the slight backward bending towards the tip in lateral view, i.e. forming a convex anterior horn core surface, of KB 380 (1) (shown in Plate 36 C) is a feature which I have never observed on any neotragine horn cores which tend to have a concave anterior horn core surface in lateral view. The specimen also has a distinctly flattened lateral surface with a hint of a postero-lateral keel. In this respect, in fact in all discernible respects, the specimen resembles female horn cores of the Olduvai Middle and Upper Bed II *Gazella* sp., which is also known from Elandsfontein and Peninj (Gentry, pers. comm.). If KB 380 (1) really belongs to the said *Gazella* sp., it would be the only known occurrence of this species at any of the Krugersdorp sites.

Antero-posterior basal horn core diameter = 13e
Mesio-lateral " " " " = 11.5e

Horn core length from pedicle to broken tip = 48 mm; total length in the unbroken state was probably about 70 mm.

- *Antidorcas* cf. *recki*:

A. **Horn core material:** KB 3190 (3) is a left horn core base with parts of the surrounding frontal bone, the supra-orbital foramen, the metopic and coronal sutures preserved (Plate 37). Its basal horn core dimensions were given in Table 9 and graphically represented in Fig. 1 of Vrba (1973). The said Fig. 1 shows that KB 3190 (3) is somewhat larger than horn cores of the Olduvai *A. recki*, and closer in size to the *A. recki* from Bolt's Farm (Cooke, unpubl.) and from Elandsfontein, although it is more strongly compressed than these. The specimen had to be pieced together, is definitely a little distorted and has an extremely weathered horn core surface. If it were in a better condition its basal compression might be found to be closer to those of the Bolt's Farm and Elandsfontein specimens shown in Vrba (1973: Fig. 1). Some of its features are (e = estimated):

1. Antero-posterior horn core diameter = 42 mm e
   Mesio-lateral " " " = 30 mm e
   Basal horn core compression = 71%
2. Minimum distance between horn core base
   and supra-orbital foramen = 26 mm e
3. Distance between lateral wall of supra-
   orbital foramen and metopic suture = 17–19 mm e;
   i.e. very close for a horn core of this size.
4. The supra-orbital foramen is situated almost flush with the frontal surface and not in a pit (the part of the frontal anterior to the foramen is missing, but at most it could have constituted only a small pit).
5. The extensive cornual diverticulum extended forward lateral to the foramen, and laterally into the orbital rim.

6. Enough of the posterior horn core base and coronal suture is preserved to see that the horn core must have been bent backwards quite strongly near the base in lateral view (Plate 37 B), more so than is the case in *Antidorcas bondi* from Swartkrans (See Vrba, 1973: Plate 3).

Points 1–4 mark KB 3190 (3) as belonging to a type A (as defined in Vrba, 1973) *Antidorcas,* including at the moment *A. marsupialis,* the extant springbok, as well as fossil species *A. recki* and *A. australis,* and separate it from *A. bondi* as known from Swartkrans. *A. australis* has smaller and more upright (in lateral view) horn cores. Point 6, and probably 1, remove KB 3190 (3) from typical extant springbok material. The best assignation on all points is undoubtedly *A. recki.*

Two very fragmentary and eroded basal right horn core specimens, KB 381 and KB 377 (1) probably belong to this species too. They confirm that *A. recki* males from KB have basally more massive horn cores than does most of the Olduvai *A. recki* material, and that the grouping on size of KB 3190 (3) with *A. recki* from Elandsfontein and Bolt's Farm rather than with the Olduvai material, in Fig. 1 (Vrba, 1973) is no accident.

KB 379 is a fairly compressed horn core tip that probably belongs to the same species.

B. **Dentitions:** Two lower teeth (Table 58) are typical in size and shape of *A. recki* dentitions (and different in these respects from those of the extant springbok). They are probably lingually too straightwalled to belong to the *Gazella* sp.

- cf. *Antidrocas bondi*: Three horn core fragments, broken off above the base, KB 372 (1), KB 375 (1) and KB 3191 (3) are remarkably rounded right up to the tip and little bent. There are horn cores just like these among the Swartkrans *A. bondi* material.

- *Antidorcas* sp.: KB 374 (1), a right horn core base, and KB 499 (1) respectively have basal dimensions:

Antero-posterior basal horn core diameter = 19 mm and 18.0 mm
Mesio-lateral " " " " = 18 mm e and 15.2 mm

Both have basal horn core hollowing, which means that they could belong to *Antidorcas.* They may be juvenile stages (because of their smaller size) of one or both of the antidorcine species thought to be present at KB.

- *Incertae sedis*: KB 3193 (3), shown in Plate 36 A, is a piece of horn core about 140 mm long lacking both base and tip. It is twisted, lyrated and subcircular in cross-section. Most of its surface is very weathered but one area suggests tentatively that transverse ridges were present during life. One possibility would be assignation to the impala, *Aepyceros melampus* Lichtenstein, although KB 3193 (3) thins more rapidly towards the tip than horn cores of this species. Another possibility is that it belongs to a reduncine, but as there is no sign of a terminal forward twist on this horn core fragment, this is only a remote possibility. In compression and lyrate shape it is not unlike some *A. bondi* horn cores from Swartkrans, but it is much larger than these. Although the actual assignation of KB 3195 (3) must remain in doubt, one can say with some certainty that it is unlikely to belong to any of the species found at KA, and thus, although an unknown quantity, constitutes a difference between the fossil assemblages from KA and KB. There is a slender possibility that KB 3193 (3) belongs to the horn core of a *Rabaticeras,* in which case it would resemble, in its lack of compression, rather the *Rabaticeras* from Elandsfontein, Olduvai III–IV and Rabat than the Swartkrans holotype of *R. porrocornutus.*

DESCRIPTION AND TAXONOMY OF THE STERKFONTEIN TYPE LOCALITY BOVIDAE

Subfamily: HIPPOTRAGINAE

Tribe: ALCELAPHINI

- *Damaliscus* sp. 1 or *Parmularius* sp.: The dominant alcelaphine at the Sterkfontein Type locality (to be referred to as STS) is represented by a number of dentitions (Table 59) and a fragmentary frontlet associated with some upper molars, STS 2368 (Plate 8). In a preceding section (pp.68 –73) the features of the dentitions of a KA species, *Damaliscus* sp. 1 or *Parmularius* sp., were discussed. Suffice it here to say that on all points (1–7 on pp. 68 –70; See also summary on p. 71 and Plates 7–9) the STS dentitions agree remarkably well with those from Kromdraai A. The feature of the robust ascending mandibular ramus (point 8, p.70) of the KA form could not be compared on the STS specimens because it was never preserved.

The fragmentary frontlet, STS 2368 **B**, associated with two teeth of this species, $M\frac{1}{}$ and $M\frac{2}{}$ (the latter is not yet in full occlusion), is very tantalizing indeed. It is so weathered and incomplete, consisting of several fragments that have been pieced together (Plate 8), that nothing much can be reliably deduced from it. Yet it must be regarded as worthwhile to record an impression of its features and affinities, albeit an extremely tentative one, because it is the only skull material definitely associated with this important group of distinctive dentitions occurring throughout several Krugersdorp sites. A comparison with extant *D. dorcas* material (which it resembles in overall size) of identical tooth wear suggests the following:

1. The horn cores of the fossil species were probably closer together (basal horn core separation is approximately 25 mm) and the left horn core base, although posteriorly incomplete, provides a hint by its curvature that the horn cores may have been less compressed than those of *D. dorcas.*

2. The left frontal piece, which is complete and undistorted from left of the supra-orbital foramen to the metopic suture, is definitely flatter and forms a more pronounced wide V-shaped dip at the suture than is the case in *D. dorcas* where the said dip is shaped more like a wide U, and the adjacent frontal areas are less flat.

3. The position of the supra-orbital foramen with respect to the metopic suture and the horn core base is not noticeably different from that in *D. dorcas.*

STS 2368 B definitely seems to be larger than the smallest South African fossil alcelaphine from Elandsfontein and Cornelia. Of the two small extinct alcelaphine species mentioned on p. 71 i.e. *D. agelaius* from Olduvai Bed IV and the small East Rudolf species, STS 2368 B corresponds more closely with the latter. In fact it agrees with respect to points 1–3 and in every other visible respect, including the associated teeth.

If the horn cores were really a little closer together and rounder than is the case in *D. dorcas* for instance, such features would not contradict membership of the genus *Parmularius.* The same possibility is suggested by the morphology of the STS small alcelaphine dentitions, as also by that of similar KA dentitions. Accordingly the openended assignation to *Damaliscus* sp. 1 or *Parmularius* sp. is considered most suitable for both the STS and KA material at present. This does not mean that KA and STS small alcelaphines are necessarily thought of as belonging to the same species. Rather on the available evidence they cannot be separated and their resemblance may signify if not specific identity, perhaps membership of the same lineage. On p. 73 it was noted that the late discovery of the KA skull, KA 1601, strengthens the belief that *Parmularius* was present in the Krugersdorp succession. Before we can evaluate the suggestion made on p. 73 that the East Rudolf and STS forms may be precursors of, and on the same lineage as, the KA species, and maybe also *P. rugosus* from Olduvai, and indeed before the membership of this material to the genus *Parmularius* rather than *Damaliscus* can be assessed, a direct comparison with the relevant East African material will be necessary.

A few similar dentitions come from Swartkrans. A single fragment of three worn teeth from SE has also been similarly assigned.

- *Damaliscus* cf. sp. 2: The single right mandibular fragment, STS 2582 (Table 60) represents a problem. Of the points of comparison on pp. 68 –70 only 3, 4 and 5 can be seen on this specimen. In terms of these, and in terms of the summary on p. 71 the specimen diverges convincingly from the other small alcelaphine dentitions at STS, being closer to *D. dorcas* and *Damaliscus* sp. 2, more especially the latter (Table 37 and Plate 7). Apparently a previous catalogue number has been partially wiped out and the possibility exists that this specimen has been misplaced in the STS assemblage and really belongs to another faunal phase at Sterkfontein (Vrba, 1974) such as that represented by the West Pit assemblage.

- **Medium-sized alcelaphines:**

A. **Horn core material:** STS 2595 A is a fragmentary frontlet (Plate 38). It has half of the right horn core base preserved, showing

1. extensive basal horn core hollowing. Mesially a piece of the left horn core base is present, allowing the guess that

2. basal horn core separation was probably approximately 40 mm, and that

3. the horn cores may have diverged with a basal angle of about 45° (Plate 38).

4. Although the right horn core is posteriorly incomplete, a tentative estimate of the angle between the posterior basal horn core and the frontal-parietal surface behind it, might place it as being no larger than 100°–110°, and perhaps smaller.

5. The antero-posterior basal horn core diameter on the right side can be estimated to be between 51 and 54 mm. Extrapolating the curvature one would say that compression is likely to have been less than 80%, but this must be regarded as very tentative.

The overall size of STS 2595 A, together with point 1, strongly point towards the alcelaphines. However, among species of the correct size present at STS perhaps cf. *Hippotragus* sp. aff. *gigas* should also be considered. This is only known from dentitions at STS (p. 98). I have rejected this possibility because

a. I would not have expected a hippotragine species to have quite such a large cornual diverticulum;

b. *H. gigas* as known from Elandsfontein, and from Olduvai (Leakey, 1967) seems to be larger, with

c. possibly less compressed horn cores, and

d. a lesser angle behind the horn cores than that mentioned for STS 2595 A in point 4.

Although each of these points is difficult to substantiate, a–d nonetheless collectively strengthen the decision to see STS 2595 A as belonging to an alcelaphine. Among the species present at STS a medium-sized alcelaphine would seem most suitable. In terms of the discussion about the Swartkrans and Olduvai *Rabaticeras* horn core and skull material on pp. 5 –7, none of the visible or estimated features of STS 2595 A would contradict its belonging to the same species as Old. 1970. Geologic Locality 208 from Bed II, and SK 3211 from Swartkrans, i.e. *R. porrocornutus.* Presumably in such a case the latter specimen could be female and the former two (from Olduvai and STS) males. STS 2595 A could of course quite easily belong to another fossil alcelaphine. However, further arguments in favour of the *Rabaticeras* assignation are constituted by the morphology and affinities of the associated dentitions (p. 32 and below).

B. **Dentitions:** Several dentitions (Table 61) are in every visible respect indistinguishable from those of the Swartkrans Gp II a and c alcelaphine, which have been described on pp. 24 –33. This applies to premolar morphology (e.g. STS 1445), molar lobe and $M_{\overline{3}}$ metastyle shape e.g. STS 1445, STS 1334 and STS 1324. Why the Swartkrans Gp IIa and c dentitions could belong to *R. porrocornutus* is outlined on pp. 31, 32. Similar dentitions are also found in the KA and SE assemblages.

Some larger alcelaphine upper dentitions (Table 62 and Plate 12) have been provisionally thought of as belonging to the same species as the Swartkrans Gp IIb and d "larger medium" dentitions. The only specimen on which premolar length can be assessed (STS 2597 A; see Plate 12) lacked PM^{2}. However, these dentitions, as well as some of the Swartkrans Gp IId upper dentitions with similarly simple enamel outlines and indications of an abbreviated premolar row may well belong to the *Connochaetes* lineage, as mentioned below.

- cf. *Connochaetes* sp. aff. *africanus* (see footnote on p. 16 concerning the applicability in this case of the specific name *africanus*): At least one STS tooth, STS 2512 B, a left M_{3} (Table 63), is definitely large enough to belong to (and morphologically indistinguishable from) the species represented by Swartkrans Gp III dentitions, i.e. cf. *Connochaetes* sp. aff. *africanus* (Plate 14).

The upper STS dentitions in Table 62, while a little smaller than Swartkrans upper dentitions assigned to Gp III ("smaller large" in Table 5), may also belong to the same early *Connochaetes,* as may some of the Swartkrans specimens at present provisionally placed into Gp IId, i.e. "larger medium". Both these STS and Swartkrans groups of upper dentitions consistently have a short premolar row, lacking PM^{2}, wherever the area is preserved (above and pp. 27,28). Thus if these groups of upper dentitions are accepted as belonging to a *Connochaetes* sp. and not to a different "larger medium" alcelaphine species, it would seem that the early Krugersdorp site *Connochaetes* had basically a short premolar row. In such a case the mandibular specimens of Swartkrans Gp III which had a PM_{2} (on others it was absent, p.33), on the basis of which it was concluded that the species may have had a generally longer premolar row than extant *C. taurinus* would seem to be the exception rather than the rule. Early East African *Connochaetes* specimens from the East Rudolf *Metridiochoerus andrewsi* zone (Maglio, 1972), which could be close to the Krugersdorp form (pp. 15, 16, 37) also showed signs of a similarly reduced premolar row.

The real affinity of the STS and Swartkrans upper dentitions can, however, on available material not be resolved. Because they are smaller than most Swartkrans Gp III uppers they have for the present been left in the "larger medium" category, with a strong proviso that an alternative affinity may lie with a *Connochaetes* sp.

Teeth assigned to a *Connochaetes taurinus* lineage have also been recovered from KA, KB, SE and Sterkfontein Dumps 13, 1, 8 and 16. Only those from the latter three Dumps are indistinguishable from extant *C. taurinus.*

- cf. *Megalotragus* sp.: A single mandible, STS 1339 (Table 64 and Plate 16) could belong to a *Megalotragus* sp. smaller than the large *M. priscus* (See p. 38 for synonyms) as known from sites like Upper Bed II at Olduvai and Elandsfontein. It is difficult to tell to what extent this STS occurrence ties in with similarly assigned specimens from Swartkrans and KA, except that, if really belonging to *Megalotragus*, they all seem to belong to the lower part of the size range (see also Hoffman, 1953) within this genus, which seems to have undergone a general size increase with time. The Makapansgat Limeworks teeth, which Wells and Cooke (1956: Fig. 12) assigned to cf. *Pelorocerus helmei,* may belong to the same species.

Tribe: HIPPOTRAGINI

- *Hippotragus* cf. *equinus*: Two upper molars (Table 65) are quite indistinguishable from extant *H. equinus.* Unfortunately the type series of cheek teeth of Cooke's (1947) *Hippotragoides broomi*, which he maintained came from the "upper quarry" at Sterkfontein, seems to have been lost. Although the specimen clearly had a higher frequency of lingual basal pillars on the lower molars (Cooke, 1947: Fig. 2) than is found on extant *H. equinus* dentitions which I have seen, it is in all other respect so close to the extant roan antelope, that it may belong to the living species, or at least to a not too distant ancestor. Mohr (1967:66) concluded, from a comparison of

Cooke's (1947) Fig. 2 with extant roan antelope mandibles, that the specimen belongs to *H. equinus*. The two STS molars very likely belong to the same species as the specimen Cooke described. They are almost unique in the STS assemblage in being indistinguishable from recent material (Vrba, 1974: Fig. 2). The question could therefore be asked whether these two isolated teeth (as well as the *"Hippotragoides"* type jaw?) may not belong to a later faunal phase at Sterkfontein (Vrba, 1974), and be misplaced in the STS assemblage. A single tooth from KA is the only other Krugersdorp site material also identified as *H.* cf. *equinus.*

- cf. *Hippotragus* sp. aff. *gigas*: One of the most numerous species at STS (Fig. 25) is represented by a number of dentitions (Tables 66 and 67) which seem to belong to the same species as at least some, if not all, of the Makapansgat Limeworks specimens which Wells and Cooke (1956:10) described as *Taurotragus* cf. *oryx.* At first sight these dentitions look more like those of the eland than anything else (Plate 39). They show several features, however, which point towards their being hippotragine rather than tragelaphine:

1. The lower premolars, like STS 2584 and the D13 specimens in Plate 39, have a certain round bulbousness, with completely open lingual "valleys". In these respects they are at variance with those of tragelaphines, which tend to have a more angular look and a greater degree of fusion of the lingual cusps.

2. Dentitions like STS 1531 have teeth which are rather rugose for their size. Tragelaphine teeth in general seem to have a tendency, among bovids as a whole, towards a comparatively low degree of enamel rugosity with respect to size. The eland is a good example of this.

3. Extant tragelaphines, including the eland, do have occasional basal pillars on their teeth, and one might expect an ancestral eland to have an even greater tendency in this direction. However, even bearing this in mind, one might feel that the frequency and extent of basal pillars on most of these dentitions are rather large for a *Taurotragus* (Plate 39).

4. A more cogent feature, that is incompatible with eland dentitions and perhaps those of tragelaphines as a whole, is the occurrence of goatfolds on molars like STS 1682 and STS 1531 (Plate 39).

Admittedly these features do not conclusively rule out membership of *Taurotragus*, and some of the points above are rather subjective. Yet cumulatively they have led me to see these dentitions as hippotragine rather than tragelaphine, with the proviso that an admixture of fossil eland may be present.

Among known fossil and extant hippotragines the dentitions undoubtedly resemble those of the extinct *Hippotragus gigas* most closely. Comparing them to the Elandsfontein *H. gigas* one gains the impression that the latter has a more advanced tooth morphology, i.e. molar ribs between styles tend to be more pronounced and localized at Elandsfontein, and buccal lower molar lobes tend to have more shape. STS tooth sizes were compared with the measurements Klein (pers. comm.) obtained from the Elandsfontein dentitions, which were divided into four tooth wear stages as described on p. 43. Such comparison shows that STS mesio-distal tooth length means are sometimes (perhaps more often) a little smaller and at other times larger than those from Elandsfontein, but on the whole comparable. The overall impression, in spite of different degrees of advancement of the molar occlusal pattern and slight size differences, is that the two assemblages are very close in character. Especially among lower dentitions, where material of similar wear stages was more readily available from both STS and Elandsfontein, some striking parallels can be found; e.g. STS 1531, D13–12/269 compared with 8362 C from Elandsfontein. Lower premolar configuration at STS (e.g. STS 2584, STS 2228), and also Makapansgat Limeworks (M 597), seems almost identical to that at Elandsfontein.

Another South African occurrence of *H. gigas* may be the dentitions M8 and M34 from Makapansgat Limeworks (Gentry, pers. comm.) described by Wells and Cooke (1956: 23) as cf. *Oryx gazella*. The upper dentition M34 is again more advanced than comparable STS specimens, with more pronounced buccal styles and ribs between the styles. M8 has almost exact counterparts at STS. It seems to me that there may be two large hippotragine species at Makapansgat Limeworks, one represented by M34 and the other by at least some of the material described by Wells and Cooke (1956:10) as *Taurotragus* cf. *oryx* together with M8. Could one be an early *Oryx* sp., the other a *Hippotragus* sp.? An alternative would be that the two forms are not separate contemporanous species, but on the same lineage separated by time.

Gentry (pers. comm.) feels that the Olduvai *H. gigas* might be subspecifically distinct from the Elandsfontein one, the latter being a later development of the former. Unfortunately I was only able to see one or two of the Olduvai dentitions from BK in Upper Bed II. These again seemed to be more advanced in molar occlusal surface pattern, although one cannot be certain of such a statement on so little material. The interesting material from the point of view of comparison with the STS and Makapansgat Limeworks species would seem to be the *H. gigas* dentitions from the lower Olduvai levels, and these I did not see. From the present perspective, therefore, it is impossible to eliminate any of the following four alternatives:

If the material under discussion is really hippotragine

1. it could represent a new early species or subspecies ancestral to the Elandsfontein and other later South African *H. gigas*, as well as to the Olduvai *H. gigas*;

2. it could be identical with early Olduvai *H. gigas* and together with this form a subspecies separate from the Elandsfontein *H. gigas*;

3. it could represent a new hippotragine species separate from the *H. gigas* lineage as known to date, perhaps an early offshoot from a common ancestor which remained conservative in its molar occlusal pattern and was developing parallel with *H. gigas.*

4. A strong possibility is that it could represent an early *Oryx* Blainville species. What can be seen of its premolar length indicates that this must have been quite short, maybe very short, for a hippotragine. This fact

and the simple occlusal enamel molar pattern would support assignation to an *Oryx* sp.. However, these features are also distinguishing characteristics of *H. gigas.*

One certainly cannot rule out that the material under discussion may belong to *Oryx*. There is of course no fossil dental material of an extinct *Oryx* sp. available for comparison, while we do know of a large *Hippotragus*, i.e. *H. gigas* of similar size and morphology. The simplest hypothesis for the moment would therefore seem to lean in one's evaluation of these dentitions towards the known *H. gigas* material. To express all these uncertainties, the loose appelation cf. *Hippotragus* sp. aff. *gigas* is proposed for the present.

How close these teeth might be to early bovine dentitions, like those of *Ugandax gautieri* Cooke and Coryndon (1970) from the Kaiso Formation, which Gentry (pers. comm.) considers to be the earliest known member of the *Syncerus* lineage, or possibly even to boselaphine dentitions, I am unable to comment on. From this perspective such a possibility can certainly not be ruled out.

Whatever its correct name may eventually be, it seems fairly certain that at least some Makapansgat Limeworks material belong to the same species, that it is also represented in Sterkfontein Dumps 13, 14, 15 (all forming together with STS the earliest faunal phase at Sterkfontein as suggested in Vrba, 1974), and by a single specimen each at KA, Swartkrans and SE.

Tribe: REDUNCINI

- *Redunca* cf. *arundinum*: A single juvenile dentition (Table 68) seems to be indistinguishable from extant reedbuck dentitions. As this specimen, together with the two teeth of *H.* cf. *equinus* constitute the only STS material that is indistinguishable from recent species one wonders whether it may not perhaps belong to *Redunca darti*, described by Wells and Cooke (1956) from the Makapansgat Limeworks. Wells (1969) includes *R. darti* among species common to Sterkfontein and Limeworks. This was based (Wells, pers. comm.) on a *Redunca* frontlet, in the Anatomical Museum at the University of the Witwatersrand, collected in about 1935 either from STS or one of the related dumps. This specimen was not included among the material on which this study is based.

Single dentitions from each of Swartkrans and KA were also assigned to *R.* cf. *arundinum.*

Subfamily: ANTILOPINAE

Tribe: ANTILOPINI

- *Antidorcas* cf. *recki*: A few dentitions (Table 69) are very close in every respect to those of *A. recki* as occurring at Kromdraai A (See plate 35). Comparing their sizes with the mesio-distal tooth lengths obtained by Vrba (1970: Table 2, p. 294) for a large number of extant *A. marsupialis* dentitions, the STS teeth seem to be somewhat smaller. Nearly all the length measurements in Table 69 fall below the means obtained for the extant material, and some fall outside the lower limits of ranges. *A. recki* also occurs at Kromdraai B, the apeman site, and probably also at SE, although the nomenclature of the latter is somewhat complex.

- *Antidorcas* cf. *bondi*: A single mandibular specimen (Table 70) with worn teeth probably belongs to *A. bondi*, also known from the Krugersdorp sites Swartkrans, KA and KB, the Sterkfontein Dumps H2, D1, D2, D8 and D16 and SE. Because of the possibility that material belonging to different faunal phases at Sterkfontein may occasionally have got misplaced, and because *A. bondi* generally occurs in a relatively late context in the South African fossil record, I suspect that this isolated specimen may belong to a later time than the STS assemblage. In addition the specimen seems to have lacked $PM_{\overline{2}}$ during life which I would have only expected to occur with any frequency in *A. bondi* later than Swartkrans times.

- cf. *Gazella vanhoepeni*: Two dentitions (Table 71) are too brachyodont to be antidorcine. On STS 2076 can be seen small basal pillars (arrows in Plate 19:H) and the molars of this specimen have lingual walls that are rather "wavy" and not straight. These dentitions are indistinguishable from material assigned to cf. *Gazella vanhoepeni* at Swartkrans and have parallels among the Makapansgat Limeworks material assigned to this species. Two specimens from Sterkfontein Dump D13 could also belong to this species.

- *Antilopini Gen. et. sp. indet.*: The horn core STS 2351 (a) (Plate 35), although almost certainly that of a female antilopine, could belong to a *Gazella* or an *Antidorcas*. It is more curved in lateral view than is usual for female *A. marsupialis* or *A. bondi* as known from Swartkrans. It could conceivably belong to a female *A. recki*. Perhaps this is the horn core of a female *Gazella vanhoepeni* which has to date not yet been recognized or described.

Subfamily: BOVINAE

Tribe: BOVINI

- *Syncerus* cf. *acoelotus*: A single dentition (Table 72 and Plate 26) clearly belongs to *Syncerus*, while its erupting $PM_{\overline{4}}$ is clearly less advanced than is the case in extant *S. caffer*. Why dentitions of this type from STS, Swartkrans and KA have been given the name *S.* cf. *acoelotus* has been discussed fully on pp. 55 –60.

Tribe: TRAGELAPHINI

- *Tragelaphus* sp. aff. *angasi*: A few dentitions (Table 73) appear to belong to a tragelaphine that was probably a little larger than the extant *T. angasi*. Similar dentitions were found at Swartkrans.

Subfamily: CAPRINAE

Tribe: OVIBOVINI

- *Makapania* cf. *broomi*: Several dentitions (Tables 74, 75 and Plate 40) unmistakably belong to the species from Makapansgat Limeworks which Wells and Cooke (1956:26) described and thought, at the time, to be an aberrant alcelaphine. Gentry (1970c), after seeing additional material of this species, placed it into the caprine tribe Ovibovini, close to *Megalovis latifrons* Schaub from the Villafranchian of Senèze, France. Tooth sizes in Tables 74 and 75 agree well with those given for Makapansgat specimens in Wells and Cooke (1956:27). All the typical features first noted by Wells and Cooke and later by Gentry, like the the V-shape of lingual upper and buccal lower molar lobes, the greater degree of hypsodonty than can be observed in (for instance) tragelaphines, the $PM_{\overline{4}}$ with fused paraconid and metaconid, and the indentations into the walls of the central cavities of the upper molars, can be seen on the STS specimens (Plate 40). There is also a similar tendency to goatfolds, as I have seen on Makapansgat Limeworks specimens. Gentry (1970c:64) notes that basal pillars are absent. Although this is true of most STS specimens, one does occasionally see a basal pillar on the molars, e.g. STS 1901 A (I have also seen such pillars on one or two Makapansgat Limeworks specimens).

Teeth assigned to *M.* cf. *broomi* also come from Sterkfontein Dumps D13 and D15. A single broken specimen hails from the Sterkfontein Extension West Pit (SE). Teeth with essentially similar features, but considerably smaller, from Swartkrans have been tentatively thought of as possibly belonging to a different, later *Makapania* sp.

- *Incertae sedis*: Two horn core fragments cannot be placed taxonomically. The first, STS 2351 b, is a piece of a small (about antilopine to middle alcelaphine sized) horn core with a pronounced basal hollow. STS 1261 is a flat, abraded, possibly squashed piece of horn core which must have belonged to a large bovid species.

DESCRIPTION AND TAXONOMY OF THE STERKFONTEIN EXTENSION WEST PIT (SE) BOVIDAE

Subfamily: HIPPOTRAGINAE

Tribe: ALCELAPHINI

- *Damaliscus* cf. *dorcas* A few dentitions (Table 76) are indistinguishable from extant *D. dorcas*. They resemble the extant form in their small size, similarly complex occlusal enamel pattern and long premolar row (Plate 8). Dentitions of this type were absent from the Sterkfontein Type locality (STS) and Kromdraai A and B, but present at Swartkrans and Sterkfontein Dumps H2, D3, D5, D8 and D16. At Sterkfontein they seem to be indicative of a time later than the STS assemblage (Vrba, 1974).

- *Damaliscus* cf. sp. 2: A few dentition fragments (Table 77) have been tentatively lumped under this category. Although certain features of the lower dentitions, like the molar lobe and $PM_{\overline{4}}$ morphology of SE 1233.1, agree fairly well with those of *Damaliscus* sp. 1 or *Parmularius* sp. at KA, the overall impression gained is that the SE dentitions, both upper and lower, are definitely larger. A comparison of the $M_{\overline{3}}$ of SE 1233.1 with KA $M_{\overline{3}}$'s of a similar hypsodonty stage (e.g. KA 2611, KA 922, KA 1097b) shows that the latter have a consistently smaller occlusal surface with less tendency to goatfolds and less pronounced metastyles. In all these respects the dentitions in Table 77 are more like the Swartkrans specimens assigned to *Damaliscus* sp. 2.

One or two of the upper dentitions included here, like SE 588, could belong to a tsessebe or hartebeest, and could perhaps be regarded as medium-sized alcelaphine dentitions. On the whole, however, they are definitely smaller than medium-sized teeth at Swartkrans and have here been placed in the "larger small" alcelaphine size group.

It seems thus that these few, broken dentitions resemble *Damaliscus* sp. 2, as found at Swartkrans and some Sterkfontein Dumps, notably D16, more than anything else. The present assignation must however be regarded as very tentative. What can be said with a greater degree of certainty is that the bulk of STS small alcelaphine material seems to be different from the bulk of dentitions in this size range at SE. Such a statement although restricted to a concept of difference, irrespective of the correctness of the name given to these dentitions, has importance in the unravelling of the chronology of the Sterkfontein Excavation Site as a whole (Vrba, 1974).

- *Damaliscus* cf. sp. 1 or *Parmularius* sp.: A single specimen (Table 78) including only very worn $PM_{\overline{3}}$ – $M_{\overline{1}}$ may belong to the same species as the small alcelaphines of STS and Kromdraai A. Its overall size, as well as the abbreviated premolar row with a peglike $PM_{\overline{3}}$ agree well with such an assignation.

- **Medium-sized alcelpahines:** Several specimens (Table 79) fall into this size group. What little can be seen of their morphology seems to agree well with Swartkrans medium-sized Gp IIa dentitions (e.g. features like the goatfold on SE 535 and the rather pointed buccal molar lobes on mandibular fragment SE 464) which were tentatively linked to the horn cores of *Rabaticeras porrocornutus* (p.32). One or two specimens could perhaps equally well agree with extant forms.

- cf. *Connochaetes* sp. (size of *C. taurinus*): A single $M_{\overline{2}}$ fragment (Table 80) is of similar size as the *Connochaetes* material at the other Krugersdorp sites. One interesting point is that the specimen, SE 2601.1, has a goatfold. A similar feature was noticed on Kromdraai A *Connochaetes* lower dentitions, while being very infrequent on extant *C. taurinus* or Swartkrans cf. *Connochaetes* sp. aff. *africanus.*

- **Alcelaphine horn core and skull material; Gen. et sp. indet.:** A piece of the posterior cranium, SE 571.1, including the occiput and adjacent occipital and parietal areas, seems closest to the tsessebe among extant medium-sized species. It differs from this by the relatively small amount of transgression of the supraoccipital onto the dorsal braincase surface, and by the flaring out of the parietal anterior to the medial area, suggesting a relatively wide braincase.

Three very damaged horn core fragments, SE 2031, SE 2925.1 and SE 2038, seem to be alcelaphine. In degree of compression they might be akin to *D. dorcas* and *Parmularius angusticornis* horn cores, and probably between these two in size. Only one, SE 2025.1 is complete enough to show signs of basal hollowing. There are signs of slight horn core twisting and SE 2038 has what was probably a postero-lateral keel. What can be seen of these fragments could be compatible with *Rabaticeras* horn cores. It is possible that this is also the correct assignation of the medium-sized teeth.

Tribe: HIPPOTRAGINI

- *Hippotragus* sp. aff. *gigas*: A fragmentary $M_{\overline{3}}$ (Table 81 and Plate 39) probably belongs to the large hippotragine which is also present at STS, Sterkfontein Dumps D13, D14, D15 and peripherally at Swartkrans and KA.

Subfamily: ANTILOPINAE

Tribe: ANTILOPINI

- *Antidorcas* cf. *recki*: In Vrba (1973: 305) it was suggested that species of the genus *Antidorcas* can be divided into two groups, A and B, each with its own set of distinguishing features. Both groups are undoubtedly present at SE. The group B dentitions of *A. bondi* are dealt with below (see also

Table 83). The specific assignation of the group A (with possible member species *A. marsupialis, A. recki* and *A. australis*) SE material, some of which is shown in Plates 35 and 41, is distinctly problematical. The material presents us with the following facts:

The almost complete left horn core, SE 801.1 (Plate 41) has

1. a basal compression of about 77% (antero-posterior and mesio-lateral basal horn core diameters 33 mm e and 25.5 mme respectively) which places it very close to the mean for *A. recki* in Fig. 1 (Vrba, 1973:338). SE 801.1 is even more strongly compressed further up towards the tip;

2. an approximate length from pedicel to tip (in the complete state) of 140–150 mm;

3. a pronounced basal horn core hollow;

4. the suggestion of transverse ribbing, notably on the anterior surface;

5. the hint of a postero-lateral keel;

6. a definite twist or torsion which would have been clockwise, as seen from pedicel to tip, on the right horn core;

7. a tip that diverges outward, i.e. laterally in anterior view;

8. in lateral view SE 801.1 is bent backwards more strongly than is the case in any South African material assigned to *A. australis*, including that at Swartkrans (Plate 41), while being very close in this respect to some Olduvai *A. recki* horn cores (although being perhaps less strongly bent than others).

SE 2774 looks like a juvenile horn core of the same species with a similar basal hollow, compression and torsion. The horn core tip, SE 1142, also shows signs of considerable compression and back-bending in lateral view.

Among antidorcine species *A. bondi* can be eliminated at once, and decisively, as the species to which SE 801.1 could belong, on points 1, 6, 7 and 8 (See Vrba, 1973). Among group A antidorcines, *A. marsupialis* becomes an unlikely choice on considering the combination of points 1, 5, 7 and 8. Points 4, 6, 7 and particularly 8 (Plate 41) argue against *A. australis*. There can be no doubt that the most satisfactory assignation of this SE horn core material is to *A. recki*. With respect to each of the eight points, at least some of the horn cores at present assigned to *A. recki* agree excellently with SE 801.1.

However, the few *Antidorcas* group A dentitions at SE (Table 82 and Plate 35) are somewhat surprising in the light of this horn core assignation. They are too small for *A. marsupialis*, especially 1855.1 and 1258.1, which is as might be expected. The specimen 1855.1 (Plate 35) has teeth that are probably smaller than those of most of the Swartkrans *A. australis* dentitions, and with respect to molar size and morphology seems to be closer to the KA *A. recki* dentitions. $\mathrm{PM}_{\overline{4}}$, however, is large and $\mathrm{PM}_{\overline{2}}$ was missing during life, both of which features one would expect to find in *A. australis* rather than in *A. recki*. SE 535, too, leans strongly towards *A. australis* as known from Swartkrans, rather than to KA *A. recki*, in every respect of molar and $\mathrm{PM}_{\overline{4}}$ size and morphology.

Summarizing these facts, therefore, one must conclude that while the horn core material points to *A. recki*, the dentitions lean towards *A. australis*. To rephrase this in terms of the Krugersdorp site context one might say that the SE *Antidorcas* group A horn core material points to KA (although no horn cores were found at this site, skull and dentition material allowed a fairly secure identification of *A. recki*), while the teeth are closer to the Swartkrans breccia that yielded the *A. australis* specimens. The solution to this dilemma may have one of several answers:

1. The material could belong to two different species living at the same time. In view of the facts that *A. australis* is likely to have evolved from an *A. recki* stock (Vrba, 1973: pp. 312, 313, and Fig. 16), and that the two species are likely to have occupied very similar ecological niches, this proposition is not an attractive one.

2. The material could belong to two different species which lived in the Krugersdorp site area during successive time periods. This would mean that one of the two species, for instance *A. australis* as represented by the dentitions, belongs to a different time period than the main SE assemblage. Such a possibility, viz. that the Sterkfontein assemblages may be mixed with respect to time, at least to some extent, cannot be discounted.

3. The material could belong to a single species. What we know to date of antidorcine evolution as a whole indicates that teeth (molars) became progressively larger, premolar rows progressively shorter. In terms of this it would seem that the KA form, if on the same lineage as that at Swartkrans, must have preceded it in time. This was mentioned in Vrba (1973: 32), where it was also pointed out that such case could only hold true "if all the relevant Swartkrans material belonged to a later time than Kromdraai A", Perhaps, then, we have here at SE the *Antidorcas* group A which is intermediate in time and evolution between *A. recki* of Kromdraai A and the descendant *A. australis* of Swartkrans. If this idea is accepted then horn cores of the kind present at SE must obviously have changed into the straighter, more slight version of *A. australis* (Plate 41) as present at Swartkrans and other sites. This may not be an entirely palatable proposition (See also Vrba, 1973:312), involving as it does a change from a more twisted and bent (i.e. more complex and specialized?) horn core morphology to a simpler, straighter one. It may nonetheless be correct. The fact that Swartkrans *A. australis* horn core material, like SK 3071, seemed slightly less straight then horn cores of the species from, for instance, Swartklip would support such a hypothesis.

From this perspective alternative 3 must be tentatively regarded as the simplest and best explanation of the SE *Antidorcas* group A material. Adhering more to the evidence of the horn core SE 801.1, the material is here provisionally named *Antidorcas* cf. *recki.*

- *Antidorcas bondi*: Several dentitions (Table 83) are indistinguishable from this species as known from Swartkrans, KA, STS (marginally and doubtfully) and Sterkfontein Dumps H2, D1, D2, D8 and D16.

Tribe: NEOTRAGINI

- *Oreotragus major*: Two specimens, an upper (M 8361 B) and a lower (M 8361 A) dentition, belonging to the same individual, agree excellently with those of *O. major* as found at Makapansgat Limeworks (Wells and Cooke, 1956:33–36; Fig. 17). Several points concerning this species name were mentioned on p. 50 . As in the case of the Makapansgat dentitions, M 8361 A and B (Table 84 and Plate 21), while clearly oreotragine, are considerably larger than dentitions of extant *O. oreotragus*, the klipspringer. This is shown in Figs. 18–21, where M 8361 A and B group convincingly with Makapansgat Limeworks, Taung, Swartkrans (only one) and Sterkfontein D13 (only one) specimens of this species. What is interesting, and might be worth mentioning in spite of the paucity of specimens, is that M 8361 A groups with a Taung specimen, rather than with those from Makapansgat Limeworks, with respect to the upper premolar/molar ratio in Fig. 21.

A few remains from Swartkrans and Sterkfontein Dump 13 were also assigned to this species.

Subfamily: BOVINAE

Tribe: TRAGELAPHINI

- *Taurotragus* cf. *oryx*: A single fragmentary $M_{\overline{1}}$ (Table 85) is indistinguishable from extant *T. oryx*. A few teeth from Swartkrans, KA and Sterkfontein dump D13 were also assigned to the eland.

Subfamily: CAPRINAE

Tribe: OVIBOVINI

- cf. *Makapania broomi*: The $M^{\underline{3}}$ tooth fragment, SE 1425.1 (Table 86 and Plate 40), although extensively broken, unmistakably shows the idiosyncratic combination of some of the typical features of *M. broomi* dentitions: The posterior lingual lobe is markedly pointed; the central enamel island on this lobe is posteriorly and anteriorly indented by spurs; although the tooth root is missing, the straightness of the remaining tooth, as one looks from crown to root, indicates that this $M^{\underline{3}}$ is likely to have belonged to a fairly hypsodont dentition rather than to a brachyodont one. In size it appears to resemble the dentitions from STS (the species also seems to be present in Sterkfontein dumps D13 and D15) and Makapansgat Limeworks (Wells and Cooke, 1956: Fig. 15).

THE BOVIDAE OF THE STERKFONTEIN DUMPS

At the time that this study of fossil Boviade at the Krugersdorp sites was undertaken, cranial bovid specimens, mostly dentitions, were available from Sterkfontein rubble dumps H2, D1, D2, D3, D5, D6, D8, D12, D13, D14, D15 and D16. Tooth measurements and detailed descriptions of these specimens have not been included in this work. They were, however, identified as far as possible, and a faunal list giving minimum numbers of individuals per species per dump is given in Vrba (1974: Table 1). The same publication contains an attempt to group these dumps, on the basis of their bovid content, with the Sterkfontein Type Site or locality (STS), with the West Pit assemblage (SE), and with each other into faunal phases.

DISCUSSION OF TAXONOMIC RESULTS

DISCUSSION OF TAXONOMIC RESULTS

THE BASIC UNITS UNDER DISCUSSION

This is a brief introduction of the foundations on which subsequent deliberations are based. It is presented in three parts:

1. The sites (general comments);
2. The division of Swartkrans and considerations arising therefrom;
3. The species (defining how much is known aboth them).

The sites: This study was commenced with the idea of elucidating relationships between the bovid faunas from Sterkfontein, Swartkrans and Kromdraai. For some time in the past different authors have come to the conclusion that, at Sterkfontein, SE may belong to a later time period than the immediately adjacent STS. This fact, and the relevant references, have been more fully discussed in Vrba (1974). In that publication an analysis was undertaken of the relationships between STS, SE and such rubble dumps as contained bovid cranial remains, in terms of the minimum numbers of individuals of bovid species within them. The paper is intended to be included in the thesis in this section. The conclusion was reached that STS and SE had unquestionably different and chronologically successive bovid faunas. Furthermore a third, still later time period, represented mainly by D16, was found to be present among Sterkfontein bovid remains. The dumps grouped variously (Vrba, 1974; Fig. 4) with STS, SE and D16. However, because of the high probability that most rubble dumps are likely to be mixed to a greater or lesser extent with respect to the said time periods, they have not been firmly included in the ensuing discussion, being only occasionally referred to. D16 is regarded as an exception: Because it has a relatively high minimum number of individuals (forty-two), because the taxa identified within it indicate apparent freedom from admixture, and because it represents a time period unique among Sterkfontein Valley assemblages, it has alone among Sterkfontein dumps been included in the analysis as a site unit.

Tentative suggestions, based on faunal evidence, have been made that the two assemblages from Kromdraai, KA and KB, are not coeval (Freedman & Brain, 1972; Hendey, 1973; Wells, pers. comm.) although no one has yet committed himself on the question of which of the two is the earlier.

The situation with respect to literature on Swartkrans is different. I should like to take the liberty at this point of recounting the successive availability of new information which led to the "splitting" or dividing of Swartkrans bovids into those coming from SKa and those from SKb.

The division of Swartkrans and considerations arising therefrom: When this study started, and in fact until very recently, scientific opinion, whether published or unpublished (to my knowledge), gave no indication that alongside the accumulation including *Paranthrophus robustus** there might be another assemblage of any size or note at Swartkrans. Although the presence of a "brown" breccia, later than the "pink" *P. robustus* breccia, was recognized (Brain, 1958) it was generally thought that the whole Swartkrans fossil assemblage contained no more than 5–10% of specimens and probably less, from this latter source. In accordance with this view, although bearing in mind the possibility of a negligible later admixture, the Swartkrans bovid assemblage was approached descriptively and taxonomically as forming fundamentally one time unit. However, on perusal of the resulting bovid species list from Swartkrans (Table 92), some contradictions to this view become apparent. At least twenty-eight species are present after a taxonomic evaluation that, because of the fragmentary nature of most specimens, has probably tended to "lump" rather than to "split" species. This high number is not matched by the bovid assemblages from Makapansgat Limeworks (18 species, Wells & Cooke, 1956), from any one Olduvai Bed

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* I am not in a position to make a firm judgement on whether the Swartkrans australopithecine should be called *Paranthropus* or *Australopithecus.* As at present I can see no reason why the former should be incorrect, subsequent references are to *P. robustus.*

(Gentry, pers. comm.), or, to my knowledge, from any other South African sites that are likely to represent one time period. The entire Kruger National Park today, with all its different environments, has a lower total of bovid species (20, de Graaff, pers. comm.). The range of ecological niches covered by all Swartkrans species also appears to be rather large. Furthermore, alongside several species with affinities to fossil bovids elsewhere in Africa which have an age around one to two million years, there is a large complement which is indistinguishable from recent forms. Finally one is startled to find in SK (Table 92) every single species that is found at D16 at Sterkfontein (Table 89). It was concluded in Vrba (1974) that D16 represents a very late time period, when compared to other Sterkfontein site units, perhaps the Middle Stone Age. All this clearly suggests that the later fossil component at Swartkrans is by no means peripheral, but considerably larger than had been anticipated. From this point on I shall call earlier and later Swartkrans faunas SKa and SKb respectively. SKa is clearly associated with the *P. robustus* remains in what used to be called "pink" breccia by Brain (1958) and what he now prefers to term primary breccia (pers. comm.); SKb derives from both the breccia which was formerly called "brown" and is now termed secondary breccia, as well as from fills of channels that formed at a relatively late stage through both primary and secondary breccias (Brain, pers. comm.).

An attempt was made, based purely on the taxonomic and other considerations arising from the bovid fauna, to reconstruct what the bovid species lists of SKa and SKb could look like. Subsequent to this Dr Brain very kindly consented to look at all Swartkrans bovid specimens with a view to recognizing their breccial origins. In a large proportion of cases he could place specimens certainly into either primary or secondary breccial or channel fill categories. In still other cases he was able to estimate the origins. It is remarkable, and worth recording here, to which extent the two entirely different approaches agreed in the placement of specimens into SKa or SKb. There was absolute agreement on species present, but the frequencies had to be increased in some SKb species following the breccial evaluation. The final resulting evaluation (Tables 93, 94, 96), which is used subsequently in this work, can be seen to allot considerably more than 50% of all Swartkrans bovid material to SKb. Of eleven species previously labelled, on purely taxonomic grounds, as being indistinguishable from recent species, all but one (*Redunca* cf. *arundinum*, based on a single specimen which could also belong to *R. darti*) definitely occur in SKb (13, 14, 16, 19, 20, 22, 23, 24, 25, 27 in Fig. 25). Of these the majority (19, 20, 22, 23, 25, 27) is definitely restricted to SKb, i.e. absent from SKa. *Raphicerus* cf. *campestris* (species 24 in Fig. 25) is more doubtfully restricted to SKb, as one specimen could possibly come from primary breccia. At least ten, and probably all twelve (if one counts the medium-sized alcelaphines and the *Connochaetes taurinus* lineage) of the species present in D16 also occur in SKb. Similarly, using only breccial criteria, many species are entirely restricted to SKa (e.g. species 4–8, 10, 11 in Fig. 25).

Most of the skull and horn core material could be classified as to breccial origin. As this is not always apparent from Tables 93, 94 and 96, the details are given here:

SKa includes: *Rabaticeras porrocornutus* (SK 3211, SK 14104); cf. *Connochaetes* sp. aff. *africanus* (SK 3812A); *Tragelaphus* sp. (SK 3171).

SKb includes: all *Antidorcas bondi* and *Antidorcas australis* horn cores, described in Vrba (1973); *Damaliscus* cf. *dorcas* (SK 14206); cf. *Damaliscus niro* (SK 2862); *Beatragus* sp. (SK 14183, SK 14209).

All of these results, except one, are in accord with the breccial origins of the dentitions, to which these horn cores were originally thought to belong. This gives heartening support to the possibility that horn core-skull-dentition associations are correct. The one exception concerns *Beatragus* sp.: On page 32 it was loosely speculated that alcelaphine dentitions of Gp IIb, with Type II PM$_{\overline{4}}$, may belong to this species. As all these dentitions can be firmly placed into SKa, while the *Beatragus* sp. horn core material derives from SKb, the probablity that they belong to one species decreases sharply.

An absolute division of Tables 1–33 into SKa and SKb is at present impossible, and may perhaps remain impossible in view of the many specimens about the origins of which we may never be certain. On the whole the taxonomic assessment on the joint Swartkrans bovid fauna reinforces the breccial assessment, without originally having been influenced by it. It is therefore perhaps desirable to include it in its present form. However one or two taxonomic points and possible changes, arising from the split into SKa and SKb, must be mentioned.

One of the greatest surprises arising from the breccial analysis concerns *Antidorcas bondi*: Of the numerous specimens of this species, all those on which the breccial origin could definitely be ascertained were derived from either secondary breccia or channel fill. Nonetheless a substantial number could not be placed with certainty. Based on a very rough estimate, it was decided to retain 10%, i.e. seven individuals, in SKa. However, a definite possibility exists that all of this species belongs to SKb. This possibility has been considered in the ensuing discussion in such cases where it could make a difference, e.g. the evaluation of alcelaphine and antilopine percentages per site unit in Fig. 29. The statement in Vrba (1973:287) that *A. bondi* material "probably all comes from the fossiliferous pink breccia" is clearly incorrect.

Among specimens labelled cf. *Gazella vanhoepeni* one good specimen (SK 2990) definitely, and several isolated teeth possibly, belong to SKb. It is my impression that the gazelle present at Makapansgat Limeworks (and perhaps at SKa if these remains have been correctly assigned) did not extend forwards in time to the extent of being present in SKb. It does not seem to have been found so far in any Krugersdorp or other South African site which might bridge this time gap. On the basis of such (admittedly largely subjective) reasoning I would be more inclined to view any definitely later, i.e. SKb, specimen in the present cf. *Gazella vanhoepeni* assemblage as possibly belonging to something else, e.g. a peleine. For the moment, as such specimens do not obscure the fact that a large gazelle (or at least dentitions closely similar to those of the Makapansgat Limeworks *Gazella* *vanhoepeni*) is present in SKa, I have left Tables 18 and 19 intact. Breccial evaluation of the *Pelea* material also merits comment. In the relevant taxonomic section an element larger than extant *P. capreolus* was noted (Table 16 and Figs. 12–17). Surprisingly it is not this larger element but specimens no larger than the modern form (e.g. SK 2682) which can definitely be associated with primary breccia. The question arises whether these SKa specimens should not be associated with the cf. *Gazella vanhoepeni* material. In terms of the criteria on p. 49 they appear to be closer to *Pelea,* and in fact they look very like extant *Pelea* dentitions in every respect. They have therefore been left in this taxon for the present. However the doubt remains whether *Pelea capreolus* did not make its first appearance in the Sterkfontein valley during SKb times, and whether the relevant few specimens from both SKa and KA do not in reality belong to cf. *Gazella vanhoepeni.*

The only really fundamental change in taxonomic evaluation, arising from the division into SKa and SKb, concerns the Swartkrans group A (Vrba, 1973:305) *Antidorcas* material. In deciding that this material belongs to *A. australis* (Vrba, 1973:300–302) three facts played a major role:

1. The teeth are on the average narrower than those of *A. marsupialis* (Vrba, 1973: Fig. 2), being closer in this respect to those of *A. recki.*

2. Two reasonably complete, undoubtedly antidorcine horn cores, SK 3071 (Plate 41 and Vrba, 1973: plate 18) and SK 3011 are compressed, slender and straighter in anterior and lateral view than are those of *A. recki* and *A. marsupialis.* Other horn core fragments confirm this impression.

3. The few available premolar rows are all short, with PM$_{\overline{2}}$ absent.

At the time I was puzzled to find such a relatively advanced *Antidorcas* at a site generally regarded as preceding Kromdraai A. This is fully expressed in Vrba (1973:302). At the time there seemed to be no reason to think of this fairly abundant material as belonging to more than one species.

Now it looks as though all the relevant horn cores, and probably all the short premolar rows belong to SKb. A few of the narrowest and smallest teeth are definitely associated with the primary breccia. Therefore of the three features which, simultaneously, served to diagnose the presence of *A. australis,* only feature 1. is now definitely present on the SKa *Antidorcas.* The latter is quite strikingly close to the Kromdraai A *A. recki.* For this reason, and because the species has been tentatively identified at SE and KB as well, the SKa *Antidorcas* is now called *A.* cf. *recki.* The possibility that the palate and snout, SK 3155a, which was closely associated with a hominid innominate, may belong to this species, has been raised in Brain, Vrba and Robinson (in press). A total minimum number of 13 *A.* cf. *recki* individuals has been estimated to be present at SKa. This number may, however, be less and in Fig. 29 the possibility was taken into account that more of this material should be included in SKb. The name *A. australis* still seems to be a good one for the majority of specimens of the SKb group A *Antidorcas.* An alternative would be to interpret the SKb material as being a pre-*A. marsupialis* offshoot from the *A. recki* lineage. (See Vrba, 1973: Fig. 16). This would certainly simplify the Krugersdorp site *Antidorcas* story: a continuous *A. recki* lineage throughout most site units culminating eventually in *A. marsupialis,* while leaving *A. australis* as a southern Cape endemic. While the dentitions in question would agree well with such an attractive hypothesis, the SKb horn cores do not.

Some specimens, like horn core SK 14171 and dentition SK 5982, are obviously out of loose channel fill, i.e. among the latest SKb elements, and the question arises whether the springbok may be present. This possibility that both *A. australis* and *A. marsupialis* may be present at SKb is expressed in Tables 94, 96 and Fig. 25.

The splitting of SK into SKa and SKb, as shown in Tables 93, 94 and 96 should be seen as an estimate of the true situation, which, on these specimens at least, we shall never know. Although it must therefore be regarded as tentative, it is in simultaneous excellent accord with the requirements and logical considerations of several different approaches. Deviations from the true picture are probably not large enough to alter the basic broad conclusions reached below about SKa and SKb.

The species: Determining the specific identity of material as circumscribed (i.e. the overwhelming bulk consists of teeth) and fragmentary as that present at the Krugersdorp site units, has in many cases been difficult. However, although uncertainty attaches to some of the names (e.g. cf. *Hippotragus* sp. aff. *gigas*), perhaps more confidence can be felt in the recognition of a particular species from site unit to site unit. The latter is of greater importance than the former in determining inter-site unit relationships, which predominate in this study. Information about species, that was incorporated in the species lists, includes weight classification, minimum numbers of individuals, and age determinations. All these quantities are calculated as in the explanation for Tables 87–96 in Volume II. Some isolated specimens are strongly suspected of being misplaced in the STS and SE assemblages. This is expressed by the dotted lines in Fig. 25. It must be stressed that, although one may be almost certain of such misplacement (e.g. the single *Makapania* tooth in SE is highly likely to belong to the STS assemblage), such specimens cannot, and were not, omitted from any graphs, statistical methods, Tables or other deliberations. Rather the effects of their absence were occasionally included in the discussion.

Tables 87–96, therefore, containing information on bovid species in site units STS, SE, D16, SKa, SKb, KA and KB, form the basis of the ensuing discussion and conclusions.

THE TIME SEQUENCE OF SITE UNITS

On the basis of the bovid evidence it was decided that no two of the site units are coeval, but that they succeed one another, from earliest to latest, as follows:

1. STS
2. SKa
3. KA
4. SE
5. KB
6. SKb
7. D16

The greatest measure of uncertainty attaches to the position of KB in this sequence. The reasons for these decisions are given below in three parts:

1. Crude estimation of sequence;
2. A "common-sense" approach to the species present;
3. A statistical approach to all site units simultaneously, to assess their relationship in terms of their bovid species frequency content.

An attempt to evaluate the position of site units on the absolute time scale, and with respect to other African sites, is included in a later section.

Crude estimation of sequence: The term "crude estimation", as here used, refers to methods like counting the number of species which two or more sites have in common, and estimating proportions of extinct and extant elements.

Although the total time period covered by the Krugersdorp site units is substantial, the time gaps between successive sites are in some cases relatively small. In fact, to satisfactorily statistically demonstrate such small differences one would need a sensitive method applied to uniformly large samples. The name "crude estimation" is not meant to cast aspersions on the methods to which it here refers, which undoubtedly can in many cases be usefully employed and may in fact be the only ones available. It is merely meant to express that in this case, with its special problems, they are unlikely to give conclusive results. The one advantageous aspect of this study is that numerous taxonomic details are available, unfortunately often of an inevitably subjective nature, but at least acquired by one worker over all sites in question. In this case then I would place more emphasis on the ensuing "common sense approach to species present", than on the "crude" statistical approaches. Nevertheless, the applicability of the latter to this case was investigated and some of the results are given below.

An example of this type of analysis is the count of the numbers of species occurring in more than one of the deposits, STS, SK and KA, done by Ewer (1956:41, Table 1). Several mammalian groups, excluding the Bovidae, provided the species data. The identical procedure is here followed in Table 97, on bovid species from STS, SKa (unlike Ewer, who used SK, i.e. the whole of Swartkrans) and KA. Such small differences in numbers (larger in Table 97B) as were obtained unanimously support a sequence placing STS first (i.e. earliest), KA last and SKa between the two. Yet the differences are unsatisfactorily small and cannot be statistically tested. Perhaps they are so small in this case because, apart from the possible closeness in time of the site units, the fragmentary nature of the material has resulted in insufficient specific distinction. Another factor, difficult to substantiate, may be that bovid species are generally conservative in their evolutionary rate. However, even if these difficulties could be eliminated, there is a basic fallacy in the method as used here: A site unit with less identified species has less chance of contributing "shared species". For example STS in Table 97B, even if corresponding absolutely with another site unit, can only contribute a maximum of 11 shared species, when compared with, for instance, SKa. Yet this number 11 could be argued to denote a closer relationship than, for instance, 12 or 13 shared between SKa and KA where the maximum would have been 15. A better approach would be to decide, for any site unit combination, what the possible maximum number of shared species would be. This would obviously be the total number of species in the site unit with the lowest number of species. Then the **actual** number of shared species can be related to the possible **maximum** number, e.g. by dividing the former by the latter and obtaining a percentage. This has been done in Table 98, where STS, SKa, KA, SE, SKb and D16 are considered. KB has been left out because of its small content. All species in Fig. 25, except numbers 28 and 29 (which could not be separated into species and which occur throughout all site units), have been included. The highest percentages in each column, i.e. for each site unit, were ringed. In general these results conform exceptionally well with the sequence as suggested by the consideration of taxonomic evolution (see below). Not only is the highest percentage (i.e. closest taxonomic relationship) nearly always obtained with a neighbouring site unit, but the magnitudes of all other percentages per site unit generally corroborate the suggested time sequence. SE is an exception to this: In Table 98A where "suspect" specimens are included, it is closest to STS (as might be expected if the specimens in question in SE really belong to STS, and those in STS to SE). In Table 98B, however, it is closest to a neighbour in the suggested sequence, i.e. SKb, and furthest from STS. The reason for SE showing so little distinction among its percentages, with three out of five at 56%, is partially due to the fact that it has by far the lowest bovid content of the six site units here presented. This method would be of far more value if one could test which of the observed differences in percentages are statistically significant. This could be done by the X^2 test if the numbers of species involved were higher. As Table 98 stands one can only say that these percentages agree well with the results of other approaches that were used in this work. This, although somewhat inconclusive, is in itself interesting, and justifies the inclusion of this Table.

Another approach, different in assessing not inter-site unit relationship but rather the separate antiquity of the fauna of each site unit, is the calculation of percentages of extinct, or alternatively indistinguishable-from-recent, species of the total number of species. This method too is fraught with inherent fallacies that may obscure fine distinctions: a species that is really extinct (E) may, because of low number representation at a site unit, be considered as indistinguishable from recent (IR): the few specimens may provide insufficient information for distinguishing it from a modern form.

In other words, a site unit with a high proportion of such peripheral species may assume an undeservedly modern aspect, in comparison with one of similar antiquity but containing ample material per species. There is another aspect of this method which makes it less sensitive than desirable: For example, in Fig. 25 *Makapania* cf. *broomi* and *Damaliscus* sp. 2 (*niro*?) would both be scored as being extinct, i.e. lumped together. The fact that they are diagnostic of different time periods does not come to the fore at all. Nonetheless, for providing a rough idea of site unit sequence the method has some use, and its results when applied to the present problem are given in Fig. 26. Fig. 26A and B agree in sequence with each other, as well as with the postulated sequence, but for the swtiching of SE and KA in Fig. 26A. This may be due to possible admixture from STS which was not eliminated in Fig. 26. A point of interest in the placement of SK which, when looked at as one unit, appears to postdate STS, SE and KA.

A "common–sense" approach to the species present: For this section the reader is referred to Fig. 25. A tentative placement of the small KB bovid assemblage is considered only right at the end, once all other site units have been placed into sequence. Makapansgat Limeworks, although geographically separate, is also one of the Transvaal australopithecine sites. Obviously it cannot be integrated completely into this inquiry, but references will be made to its bovid fauna as known from Wells and Cooke's (1956) account, and in some cases from personal experience. It is assumed here that it belongs to the earliest part of the South African australopithecine phase as known to date. All authors seem to concur with this although opinions differ as to whether it precedes or postdates STS: Wells and Cooke (1956) write of it as belonging "to the latest Kageran or earliest Kamasian". Ewer (1956) places it close in time, but immediately after, STS. Partridge (1973) estimates tentatively that Makapansgat and Sterkfontein caves may have opened around 3.7 and 3.3 million years ago respectively. Tobias (1973), quoting Cooke's (1970) and Maglio's (1973) faunal correlation estimates of between 2.5–3 million years for both sites, notes that there was probably a long lapse of time between the earliest opening of the caves and the deposition of the relevant faunal assemblages. Tobias (*op. cit.*) is of the opinion that an age for Makapansgat Limeworks, which places it earlier than STS, would be in keeping with the evidence of the hominids. All this is noted here, because such uniformity of opinion on an early date for Makapansgat Limeworks, placing it at least before SK and KA, is useful in assessing the sequence of the Sterkfontein valley site units.

A multitude of features in Fig. 25, all more or less relevant to the relative antiquity of the site units, could be cited. Great care must be exercised, however, in distinguishing which of them are really reliable and important. In a subsequent section (Fig. 28) the average weights per bovid individual are found to differ widely among site units. This is probably due, at least to some extent, to real differences in accumulation. It would be risky, for instance, to infer too much, if anything, about time from the absence of a large species from a site of low average weight. As an example one might cite the "absence" of *Syncerus* from SE, SKb and D16. This may mean nothing more than that it was present, but out of the range of possible prey of the predominant predators at those site units. Such negative evidence of absence of a species, especially one which is present in low numbers where it does occur, must in general be treated with caution. Species, of which the taxonomy is less than secure, should also be avoided. This is the case with some of the *Pelea* and cf. *Gazella vanhoepeni* material. It was mentioned on p. 121 that the few KA and SKa *Pelea* specimens may belong to cf. *G. vanhoepeni*. This doubt was partly induced by the closeness of the two types of dentition (especially having established the presence of a large *Pelea* among the site units), by the fragmentary nature of the specimens and by the absence of horn cores. Also partly responsible, it must be admitted, was a subjective impression of the antiquity of the site units involved. Wherever possible such cases, where a potential circularity of reasoning exists, should be avoided in making statements about time.

A phenomenon relatively free from such problems, which I therefore consider very important in this context, concerns the small to medium-sized alcelaphines. This group occurs throughout the site units. This tells us that suitable ecological conditions must have existed to a greater or lesser extent during the whole Krugersdorp site time span. Furthermore, whatever or whoever the accumulating agents were, it is clear that none of them ignored this size-and-taxonomic group. Conclusions therefore can be based on "presence" and not on "absence", and this "presence" makes one thing abundantly clear: The species change (i.e. replace one another) sharply about half-way through the suggested sequence. There can be no mistake about this because, unlike medium-sized alcelaphine dentitions, their smaller counterparts are very distinctive. Whether the species called *Damaliscus* cf. *dorcas* is really the blesbok or whether it is some related or precursor form is not at issue here. The fact that morphologically advanced, small, alcelaphine dentitions with long premolar rows suddenly appear in SE, SKb, and D16 in healthy frequencies, is important. There is nothing comparable among the numerous alcelaphine specimens of similar size from STS, SKa and KA. The latter three site units contain only small dentitions which I consider distinctively primitive in the Krugersdorp site context, and which may belong to an extinct genus (species 8 in Fig. 25). STS, SKa and KA also lack evidence (if the single doubtfully STS specimen which may even have been misplaced in the catalogueing process is discounted; see p. 94) of *Damaliscus* sp. 2 (*niro*?). This form too has distinctive, advanced dentitions which seem to be reasonably well represented at SE, SKb and D16. The SE record of this species is more tentative than the other two, but whatever it may turn out to be it certainly does not look like *Damaliscus* sp. 1 or *Parmularius* sp. from STS, SKa and KA. It is this evidence, then, which on its own would be strong enough to a. discount any possibility of SE being strictly coeval with STS, SKa or KA, and b. which splits the site units right down the middle into earlier and later factions:

STS	SE
SKa	SKb
KA	D16

The absence in the later faction of species 4–6 may be significant, but perhaps only in signifying a difference in mode of accumulation (which might also indicate a time difference but not whether in an earlier or later direction). A further point of real difference between SE and KA is constituted by the *Antidorcas* type A remains. Although the SE dentitions have been tentatively called *A.* cf. *recki,* like those at KA, they are definitely more advanced, tending towards those at SKb and D16 (p. 110).

Within this later faction a further dramatic change in species composition is evident between SE on the one hand, and SKb and D16 on the other: A host of new species, all indistinguishable from extant forms (species 22–27), is suddenly present. The proportional presence of *Antidorcas bondi* increases significantly after SE. *Antidorcas* type A horn cores at SE and SKb look different, while dentitions of type A appear more advanced in SKb (and D16) than in SE. SE is clearly of earlier age than the other two site units.

Within the earlier group, STS, SKa and KA, the most significant difference lies between STS and the other two. In this respect the presence of the unmistakeable dentitions of *Makapania* cf. *broomi* at STS is important. It is one of the four dominant species at Makapansgat Limeworks (Wells & Cooke, 1956: 48). Of all the "doubtful" specimens, dotted in Fig. 25, I regard the fragmentary tooth of *M.* cf. *broomi* in the SE assemblage as the most certainly misplaced one. If this impression is correct then the only site unit in the Sterkfontein valley that has yielded remains of this strange, undoubtedly early (in the present context) species is STS. This is a case where the "absence" of a species appears to be significant: Bovid remains at both SKa and KA are numerous by any standards. In fact the minimum number of individuals at each site is larger than twice that of STS. Several species of large body size (e.g. species 5–7 and 14 in Fig. 25) are present at both sites; and yet there is not even a peripheral trace of one of the species dominant at both Makapansgat Limeworks and STS. This species alone, therefore, provides a good indication that STS is unlikely to be contemporaneous with SKa and/or KA, but is decisively earlier.

The taxonomy of the teeth assigned to cf. *Hippotragus* sp. aff. *gigas* is a problem. It is here thought most likely that they are hippotragine but it is difficult to discount the possibility of their being tragelaphine, or even bovine. One thing is clear, however, simply as a result of looking at their morphology: In each of these three tribes the dentitions in question would have to be regarded as primitive, the more so in comparison with any members of these tribes which are present among the Krugersdorp site units. In the present context, therefore, it is an early species, which is borne out by the fact that it is present at Makapansgat Limeworks among the dentitions called *Taurotragus* cf. *oryx* (Wells and Cooke, 1956: 10). Its good representation at STS, and peripheral presence (one specimen each) in subsequent site units is a further indication that STS is earliest among the six site units in question. There are several further points that could be cited: For instance STS is unlikely to be coevel with SKa because of their vastly differing proportions in species 8 and 28 (Fig. 25), and with KA because of a convincing number of indistinguishable-from-recent KA species which are absent from STS. More convincing than such arguments, however, is the fundamental environmental change that seems to have taken place between STS on the one hand and SKa and KA on the other (see below).

These deliberations have now reached the stage where further chronological divisions among site units can be added to the first one:

STS	SKa	SE	SKb
	KA		D16

In terms of accumulation patterns (Fig. 28) and environment (Fig. 29), too, SKa and KA on the one hand, and SKb and D16 on the other seem to be naturally associated (see also Fig. 27). Nonetheless there are compelling reasons why neither group should be thought of as containing a coeval pair of site units.

D16, as it appears in Fig. 25, seems to include only two extinct species, *Antidorcas bondi* and *Damaliscus* sp. 2 (*niro*?). If the implied ascription of "larger small" alcelaphine dentitions from D16 to *D. niro* were correct, the two species may both be among the last South African fossil bovid species to become extinct (p. 162). This fact led me (Vrba, 1974) to speculate that D16 may belong to the Middle Stone Age.

It is likely that SKb, in view of its derivation from solid secondary breccia and from loose channel fill, covers more than one closely circumscribed time period. It might represent a time continuum, perhaps not a very long one, or even separate time intervals. Let us just, for the moment, determine whether SKb, as it stands in Fig. 25 provides evidence that at least a part of it was deposited during a time differing from that of D16. The answer to this is "yes". *Tragelaphus* cf. *strepsiceros* dentitions from SKb include at least some that are conspicuously larger than those of extant kudu. Are these the last manifestations in the Sterkfontein valley, and perhaps in South Africa, of the large form known as *Tragelaphus strepsiceros grandis* (Gentry, pers. comm.), which also occurs at Olduvai? In the Swartkrans taxonomic section (p. 63) it was pointed out that this is a tentative suggestion as I have not had the opportunity to see the relevant Olduvai dentitions. The fact remains that at least some kudu teeth in SKb look different from the modern form, and are of similar size as those from KA and SKa. While the few *Antidorcas* type A teeth from D16 are quite typical of modern springbok dentitions in size and every other respect, at least some of similar SKb dentitions have a smaller occlusal surface area (Vrba, 1973: Fig. 2). The horn cores assigned to *A. australis* confirm the presence of a form at SKb which is different from the springbok. The dominance at SKb of *Antidorcas bondi* is so overwhelming, as to serve as a unique feature which separates it from neighbouring (in the time sequence) site units. There is evidence of an extinct *Raphicerus* species at SKb (species 17 in Fig. 25). The horn cores in question look very close to M 478 from Makapansgat Limeworks (Wells and Cooke, 1956: 15, Fig. 6) which may also belong to an extinct *Raphicerus* species (p. 55). A strange, squat, little horn core from SKb has been assigned to *Oreotragus* cf. *major* because it closely resembles the horn cores of M 476 of *O. major* from Makapansgat Limeworks (Wells and Cooke, 1956: 35, Fig. 18). At least some elements of

Pelea from SKb are decidedly larger than comparative material of the modern species, which I have seen. The presence of the *Beatragus* sp. horn cores in SKb is a probable link with Elandsfontein.

In comparing these earlier-than-recent indications of SKb with the D16 assemblage, the negative evidence of "absence" in the latter site unit is repeatedly invoked. This is especially regrettable as D16 has a minimum number of only 42 bovid individuals, as opposed to 140 in SKb. Nevertheless, even in such a small assemblage one would expect at least some of these earlier indications to be represented if they were really there. It is really begging the question to suppose that among D16's 42 individuals nearly *all* the later indications of SKb are reproduced by chance, while nearly *all* the numerous earlier ones were there but failed to be included. Fig. 26, especially Fig. 26B, illustrates this proportional discrepancy between the two site units rather well.

A comparison of the SKa and KA assemblages is made difficult by the fact that the separation of SKa and SKb was not entirely conclusive. As an example the case of *Antidorcas bondi* might be cited. It is my opinion that *A. bondi* was not yet in the Sterkfontein valley by the SKa times (again I am discounting a single STS specimen as being misplaced from SE). Otherwise at least a few *A. bondi* specimens should surely definitely have been associated with Swartkrans primary breccia. However, we cannot be certain of this. Even if it could be proved that no *A. bondi* specimens belong to the SKa assemblage, would this necessarily mean that it was absent at that time? Or could this, like the very marked disproportion in numbers of species 8 in Fig. 25, between the KA and SKa assemblages, be due to different predation patterns going on over much the same time period? On the other hand, in such a case why would the relevant predator, or predators, at SKa ignore the abundantly present (as judged by its KA representation) species 8, while liberally sampling the only slightly larger species 29 of the same tribe and probably similar habitat?

A more positive indication of time difference is supplied by the *Connochaetes* material, which seems more advanced at KA. Although the KA

Connochaetes assemblage is rather small, it contains a. molars that seem larger than their analogues from SKa; b. a mandibular ramus that is shaped more like that of the modern blue wildebeest than are any of those at SKa (Fig. 23); c. molar goatfolds not observable at SKa. The medium-sized alcelaphines from KA, while similar in most respects to "smaller medium" specimens (tentatively assigned to *Rabaticeras porrocornutus*) from SKa, appear more modern, with greater resemblances with extant hartebeest material. The few KA fragments assigned to cf. *Megalotragus* sp. could be larger than their SKa counterpart. This, if really true, might again indicate a later age for KA as members of the genus *Megalotragus* seem to have increased in size with time. If material from STS, KA and SKa, referred to *Damaliscus* sp. 1 or *Parmularius* sp. (8 in Fig. 25) all belongs to one species, then its frequency distribution throughout the three site units would look more satisfactory if KA came after STS, with SKa the latest of the three. The possibility has, however, been raised (p. 73), that the relevant STS specimens may belong to an earlier species, on the same lineage, than the KA (and SKa?) material.

On the basis of the available material nothing more decisive can be said than this: The cumulative weight of several indications tends to place SKa as preceding KA in time.

Where does KB fit into this sequence? To say anything at all on these few KB bovid fragments requires the making of several assumptions, and can only be regarded as highly speculative. Nonetheless I should like to record my personal impressions for what they are worth.

In Table 96 can be seen that there are only five species identified from KB. Of these four appear to be extinct. Without placing too much reliance on this figure ($\frac{4}{5}$, i.e. 80%) it still places KB as decisively earlier than D16, and, probably also than SKb (although the latter is less certain as SKb seems to represent an extended time period). Furthermore, of this small sample 89–100% of individuals appear to be either alcelaphine or antilopine. This seems to further rule out D16, and the other extreme of the sequence, STS (see Fig. 29). I would say KB definitely belongs to the time span indicated by brackets:

$$\text{STS} \quad \left| \; \overbrace{\text{SKa} \quad \text{KA} \quad \text{SE} \quad \text{SKb}} \; \right| \quad \text{D16}$$

I have a vague impression that the *Connochaetes* fragments look more advanced than those of SKa or KA. Further, the KA *A. recki* material looks as though, if any horn cores had been present, they would have been less robust than KB 3190. From this would follow that the possible range of time during which KB could have been accumulated can be further limited:

$$\text{STS} \quad \text{SKa} \quad \text{KA} \quad \left| \; \overbrace{\text{SE} \quad \text{SKb}} \; \right| \quad \text{D16}$$

The size of horn core base KB 3190 (Plate 37) can be seen in Vrba (1973: Fig. 1) to range with only the very largest of numerous *Antidorcas marsupialis* specimens, while corresponding well with two of the three available *A. recki* horn cores from Bolt's Farm and Elandsfontein. The small horn core of *Gazella* sp., although I have not yet been able to compare it with the Elandsfontein gazelle horn cores, may provide another link with that site. There are some horn cores that look just like those of *A. bondi* from SKb, but, as already mentioned, the percentage of extinct individuals argues tentatively for a date earlier than SKb. Perhaps the best guess, and it really is a guess, would place KB either before, with or after SE:

$$\text{STS} \quad \text{SKa} \quad \text{KA} \quad \left| \; \swarrow \overset{\text{KB}}{\overset{\downarrow}{\text{SE}}} \searrow \; \right| \quad \text{SKb} \quad \text{D16}$$

KB has three out of five species that are different, at least in appearance, to species at all other site units (the *A. recki* horn core seems different to, for instance, SE 801.1, the Incertae sedis horn core seems to have no parallel anywhere, and the only small gazelle from all site units comes from KB), including SE. Perhaps therefore it is best at present not to see it as coeval with any site unit, not even with SE. I have placed it very provisionally later than SE.

A statistical approach to all site units simultaneously, to assess their relationships in terms of their bovid species frequency content:

The distance function which formed the basis of this approach is the "Faunal Composition Difference" coefficient, or F.C.D. Its mathematical formula was given in Vrba (1974). As this is the first time to my knowledge, that this coefficient has been proposed, and used on fossil material in conjunction with a clustering method ("Weighted Pair Group Method Clustering Procedure" of Sokal and Sneath, 1963), it is perhaps desirable to go into it in a little more detail than was possible in Vrba (1974).

The F.C.D. coefficients were calculated from minimum number Tables 95 and 96. In this method not only a species' presence is taken into account, as was the case with the methods used in the section entitled "Crude estimation of sequence", but also the minimum numbers of individuals which represent it at a site unit. As the minimum number totals vary so much from site unit to site unit, the minimum number of individuals for each species must be related to the total of that site unit to have comparative value. For instance, the same species represented by 3 individuals in site unit A, and by 30 in site unit B, comes to the same thing provided the respective total minimum numbers of individuals are 9 and 90. Accordingly the minimum number of individuals for each species in a site unit was divided by the total for that site unit, to obtain the proportional or frequency presence of that species at that site unit. Such frequencies for any site unit sum to 1. For example, the first (i.e. STS) column in Table 96 would read:

$$\frac{1}{43} + \frac{7}{43} + \frac{7}{43} + \frac{1}{43} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad + \frac{8}{43} = 1$$

Then each site unit is compared with each other by doing one subtraction of frequencies for each species represented either in the one or the other, or both, site units. The absolute values (as only absolute, and not negative or positive, difference is of interest) of all differences for the two site units are then added to supply F.C.D. For example the F.C.D. calculation for STS and SKa in Table 96 would look like this:

$$\begin{array}{lcl}
\left| \frac{1}{43} - 0 \right| & = & 0.02 \\
\left| \frac{7}{43} - \frac{2}{104} \right| & = & 0.14 \\
\left| \frac{7}{43} - \frac{24}{104} \right| & = & 0.07 \\
\vdots & & \vdots \\
\left| \frac{8}{43} - 0 \right| & = & \underline{0.19} \\
 & & 1.21
\end{array}$$

Total, i.e. F.C.D. for STS and SKa = 1.21

In the theoretical case of absolute correspondence between the frequencies of two site units, F.C.D. will be 0. In the case of no demonstrable relationship whatsoever, i.e. no common species, F.C.D. will be 2.

The F.C.D.'s for all pairs of site units in Tables 95 and 96 are given in Matrix A and Matrix B (Fig. 27) respectively.

The matrices were then clustered into Dendrograms A and B, shown in Fig. 27. Unfortunately the lower the total minimum number for a site unit, the greater its tendency becomes to have disproportionately large F.C.D. values with other site units, and the later it tends to join other clusters in the dendrogram. The reader must thus be asked to disregard the position of KB, which was just included for interest sake, in both dendrograms.

Table 95 and Dendrogram A, treating Swartkrans as a unit, were included to show how the large late component draws SK towards D16. Obviously any faunal comparisons of this kind done on SK, which ignore its temporal heterogeneity, can be totally misleading.

In Dendrogram B STS is shown to be relatively isolated from those site units closest to it. SKb and D16 seem to be particularly closely associated. Both these effects are as might be expected in terms of preceding and succeeding discussion. The apparent closeness of SKa and KA may be to some extent an artificial effect. If specimens, about whose membership of the SKa assemblage there is doubt (e.g. *A. bondi, Tragelaphus* cf. *scriptus*), were to be removed to SKb, this picture might change. It is discussed in a later section why KA may belong with SE, to a later Faunal Span than does SKa.

PALAEOECOLOGY: VEGETATION COVER AND CLIMATE

This is an investigation into what, if anything, the bovid data reveals about aspects of the physical environments of site units during deposition times. It is presented in three parts:

1. Introduction and basic criteria used;
2. The past vegetation cover environments of site units, as suggested by the bovid data;
3. Possible implications concerning the Krugersdorp site hominids.

Introduction and basic criteria used: A most interesting part of any fossil faunal study, particularly where the fauna is associated with hominids, is the attempted interpretation of the environment which supported this fauna. The Bovidae are likely to be particularly instructive in this respect. All bovid species are more or less sensitive to environmental changes. Moreover, certainly in African deposits, this family generally constitutes high percentages, up to 80–90%, of fossil assemblages. Already among the later Miocene Fort Ternan faunal remains, bovids are well represented and constitute the largest part of the ruminant assemblage (Gentry, 1970a).

The Bovidae as a whole among mammals are characteristically found in more open rather than heavily wooded environments. The suitability of Africa in this respect was presumably to a large extent responsible for the explosive radiation of bovids in this continent, as attested to by their ubiquitous dominance of modern and fossil African contexts. In an investigation of the lower Pliocene *Hipparion* fauna of China from many different localities, Schlosser (1903) and Kurten (1952) found two broad faunal divisions: woodland and steppe. Bovidae were found (Kurten, 1952: Fig. 2) to predominate heavily in the steppe fauna, and Cervidae in the woodland fauna. Kurten respectively named these divisions the *dorcadoides* and *gaudryi* faunas, after the characteristic species of gazelles within them.

What criteria can be used to recognize different environments in an African context, for instance the present one where only bovids are considered? Before extrapolating directly, via taxonomy, from the extant case, let us look at some anatomical features of bovids which could be expected to correlate with different environments in both extinct and extant cases. Nothing finer than a broad distinction between more "open" and more "closed" vegetational environments, with some attendant, but even less certain, speculations on climate can be attempted here, or indeed in most faunal analyses. The anatomical features here discussed are naturally restricted to osteology, and especially to dentitions. With respect to each point made the reader must remember that a very wide net is cast, and that the many exceptions to the generalization are clearly understood.

One feature which has relevance to habitat is bovid body size. One might expect to find the largest species more often in "closed" environments, for a number of reasons:

a. While large size affords some protection against predation it is well-known that large bovids like the buffalo and eland, especially their young, are preyed upon (Pienaar, 1969). The importance of this must be acknowledged even more in the cases of fossil sites where large predators, or predators seemingly specialized on large prey, like the sabretooth cats (see below), have been found. Bush cover affords some measure of protection to such large herbivores. Inversely correlated with size is the ability to run fast to escape predation.

b. A greater availability of various food plants, and a greater variety of levels at which they may be cropped, may attract bovids, with a large body to feed, to bushier and/or wetter habitats.

c. Heat loss problems obviously become exponentially more acute with increased body size. Interesting are research findings that, while many smaller bovid species rely mainly on panting for heat loss, this would not suffice in the case of larger animals which use sweating primarily (Robertshaw, pers. comm.; Taylor, Robertshaw and Hofmann, 1967; Finch, 1972). For the larger bovids, inhabiting high temperature areas, therefore, the availability of trees for shelter would seem to be especially important.

Consequently one might expect open plains inhabitants to be more in the small to medium size range, and to be fast runners. Such cursorial features, indicative of open country, may be recognized by palaeontologists on the post-cranial skeleton (not in this case, where only cranial remains were studied). Further, one would not expect bulky horn cores on such a fast open plains inhabitant. The hollowing of horn cores in some species presumably represents an attempt at weight reduction (see also Vrba, 1971: 68).

Open plains forms are largely or entirely restricted to grazing or low vegetation browsing. Grass is often tough, especially in the dryer areas, where dust contamination plays a part. Obviously the increasing dental hypsodonty in many bovid lineages is important in this respect. Kurten (1952) distinguishes between ungulates of the Chinese Hipparion fauna as being (p. 23) "brachyodont, browsing types" or "decidedly hypsodont grazing types" (with intermediate forms), and shows (Fig. 4) how they dominate woodland and open steppe faunas respectively. He also illustrates the idea further afield. He quotes (p. 30) Schlosser and Abel as having: "pointed out that an obstacle of some kind must have existed between Pikermi and Samos, checking the westward spread of some asiatic forms". In Kurten's opinion the difference between these faunas is environmental and reflected in their dentitions: The Pikermi and Western European fauna was characterized by a great number of brachyodont, browsing types. In contrast, Maragha and Samos are dominated by hypsodont types. Although it is fairly clear from all we know that hypsodonty in bovids evolved in response to grazing environments, it is probable that some hypsodont lineages would at some stage have secondarily migrated back to more bushy closed habitats. However, such species should be in the minority, and as an overall indication of open country, a large proportion of hypsodont forms in a fossil assemblage can be regarded as reliable. The expansion of the occlusal molar surface and reduction of premolars, as grazing and possibly drought adaptations, were discussed in Vrba (1970: 289–290).

While the abovementioned features are spread to some extent throughout African bovid tribes, there can be no doubt of their concentration in the Alcelaphini and Antilopini. Concerning the modern African bovids there seems to be a general acceptance that these two tribes constitute the bulk of any open plains fauna. Numerous authors have inferred this in more or less clear terms (e.g. Pienaar, 1974, Lamprey, 1963; Dorst and Dandelot, 1970; Bigalke, 1972). Other bovid tribes range over all habitats, but on the whole are concentrated in the less open environments, like more or less dense bush, gallery forest or woodland. Of course, there are many exceptions to this, some of them notable like the hippotragine *Oryx gazella,* which is perhaps the most "drought-and-open-country-adapted" of all bovid species.

The presence of alcelaphines and antilopines in Africa, more especially South Africa (e.g. Langebaanweg and probably Makapansgat Limeworks) before the time covered by the Krugersdorp site units, is established. Nothing stood in the way of their substantial presence at any of the Krugersdorp stages, except an environment which discouraged their proliferation. Significant (in the sense of large) differences in their proportional presence at different site units are therefore likely to be a real indication of environmental differences.

The past "vegetation-cover-environments" of site units, as suggested by the bovid data: Before perusing the results obtained from the bovid data, let us look at some views about the environments of the Krugersdorp site faunas, expressed by previous authors. Brain (1958) concluded, on the basis of determinations of the sand grain angularity and chert-quartz ratios of the australopithecine breccias, that a general increase in rainfall, with minor fluctuations, occurred in the Sterkfontein valley from STS times onwards. More specifically he inferred that the primary Swartkrans breccia (here called SKa) represents "a time of small-scale climatic oscillations superimposed for the most part on present-day conditions", and that both STS and Makapansgat Limeworks had a lower rainfall than SKa, while KB had a higher one. Butzer (1971) argued that each of the breccias in question basically represents colluvial sediments compatible only with an incomplete mat of vegetation. From this he infers that "the great bulk of sediments at *each* site implies accumulation under relatively dry conditions, either with a lower (than present) rainfall, or with a less equitable distribution of rains". He concludes that "the cave breccias do not provide convincing evidence of a fluctuating climate through time, at least not contemporary with active sedimentation. This does not negate the possibility that the rates and modes of soil formation on the hillslopes, outside the caves, varied through time; but it is unlikely that such soil formation was contemporary with the periods of active erosion responsible for removing and transporting materials, and ultimate accumulation in the cave interiors".

The percentages constituted by the alcelaphines plus antilopines of the total bovid assemblages from the various Krugersdorp site units are given in Fig. 29. The fact that such percentages never sink below 51% indicates clearly that during all deposition times, here represented, there was a certain degree of open country. In fact the site units as a group distinctly fall into the more "open part" of the spectrum of known habitats. Seen from a broad perspective, then, the bovid data may be compatible with the view of Butzer (*op. cit.*) that a more or less incomplete mat of vegetation was present during all deposition times (provided the "incomplete mat" as used by him is really broadly equatable with the "open country" inferred here).

The bovid data, however, appear to distinguish differences within this overall environmental characterization. The most notable difference lies between STS on the one hand and the group formed by SKa, KA, SE and, less certainly, KB on the other. Of this latter group SKa has the percentage closest to that of STS. I have taken the lowest possible value of that percentage (i.e. when all *A. bondi* specimens and 8 *A. recki* specimens are removed to SKb, and when Gen. et. sp. indet. is considered as a neotragine species) and compared it by a χ^2 test, corrected for continuity by Yates' method, to the STS percentage. The result ($\chi^2_1 = 4.05$; $\chi^2_{1;\ (0.05)} = 3.841$) indicates that SKa, even when viewed in this extreme way, has a significantly higher proportion of alcelaphines and antilopines than has STS (the even more highly significant result of a similar test on STS and SE is discussed in Vrba, 1974).

How much may be inferred from this: It has already been argued, with respect to the general case, that such differences may justifiably be taken to indicate bush cover differences. Nonetheless, let us take a close look at the particular case of STS and SKa.

A glance at Fig. 25 shows that the frequencies of two species, *Makapania* cf. *broomi* and cf. *Hippotragus* sp. aff. *gigas*, are largely responsible for the relatively low alcelaphine-antilopine percentage of STS. The question may now well be asked: How likely is it that one or both of these species flourished (because flourish they did at STS, as attested to by their representation) in the open, predominantly grassland habitats inferred for alcelaphines and antilopines? In both cases body size, as judged by their remains, must have been comparable to that of modern species which generally prefer at least moderate bush and tree cover. Wells and Cooke (1956:31) made the point that teeth of *Makapania broomi* are more hypsodont than are those of *Tragelaphus*, which may be true of the relevant STS material as well. On the other hand I would class them as definitely less hypsodont, when height is related to occlusal surface area (see also Vrba, 1973:298) than teeth of the closest-sized alcelaphines which are present at Makapansgat, STS, SKa and KA, namely cf. *Megalotragus* sp. and the *Connochaetes*. The cf. *H.* sp. aff. *gigas* dentitions are less hypsodont, and increase in width more rapidly as they are worn down, than those of *M.* cf. *broomi*. In a general bovid context both species must be considered as having long premolar rows, although cf. *H.* sp. aff. *gigas*, if really a hippotragine, has rather a shorter one than is usual in that tribe. On the whole they are perhaps best thought of as likely inhabitants of moderately closed conditions, like open woodland, and perhaps including quite a bit of grass in their diet, as is the case with the extant buffalo (Lamprey, 1963). Nothing compels us to see them as predominantly open grassland species.

While critically examining the non-alcelaphine/antilopine content of STS, it is only consistent to do the same in the case of SKa. This assemblage too includes dentitions referred to cf. *Makapania* sp., which are smaller and more hypsodont than those of the STS *Makapania*, and in fact are under suspicion of being alcelaphine (p. 66); the specimens termed Gen. et sp. indet. are more likely to be antilopine than anything else, but have not been included in this tribe because I cannot rule out their being neotragine; *Oreotragus* cf. *major* is probably (judging by its extant relative) a species tolerant of a wide range of open and closed habitats, provided rock outcrops are present; a few dentitions of *Tragelaphus* cf. *scriptus* and *Pelea* may well belong to SKb. The large alcelaphine contingent, on the other hand, very definitely seems to be derived from primary breccia.

The STS bovid assemblage has a large average body weight (Fig. 28), which is thought to be due, at least to some extent, to the activities of a predator specialized on large prey (see below). Is it feasible to suggest, for instance, that large forms like *M.* cf. *broomi* and cf. *H.* sp. aff. *gigas* were present in the Sterkfontein valley during SKa times, but were ignored by the agencies responsible for that accumulation? In other words, could the observed difference in alcelaphine/antilopine proportions between STS and SKa be due to different predation/accumulation agencies acting on faunas of similar species composition? To some extent perhaps, but as a total explanation it must be rejected as being unrealistic and a bit far-fetched: First of all, why has the large alcelaphine *Connochaetes* such marginal representation at STS, if the predominant predator(s) was/were specialized on large prey, and if *Connochaetes* was there in similarly abundant proportions as at SKa and Makapansgat Limeworks? Secondly, the SKa predation/accumulation "mechanism" was obviously capable of including large bovids in the assemblage (see below and Fig. 28). Thirdly, if so many STS species in the larger size ranges coincide with Makapansgat Limeworks forms (Fig. 25), could not a heavier concentration of smaller species be expected to include further Makapansgat Limeworks forms like *Redunca, Oreotragus* and *"Tragelaphus" pricei,* as well as *Gazella* and alcelaphines?

Finally, although it was loosely established above that alcelaphines and antilopines were present in South Africa before and during STS times, the following objection might be raised: Does STS represent a time before a later explosive radiation of alcelaphines and antilopines in South Africa? Were they simply generally not yet present (and therefore not preserved) in large numbers? If this is true, and it may be true, why did they increase so dramatically, supplanting earlier forms, by the SKa–KA-SE stage if not in response (at least to some extent) to environmental changes? Indeed, is not the faunal change over this whole South African fossil period, marked enough to have prompted the naming of successice Faunal Stages or Spans (Wells, 1962; Cooke, 1967), suggestive of environmental change?

My conclusion is that the bovid data, with respect to STS/SKa + KA + SE as shown in Fig. 29, can be taken at its face value, viz. a proportional change in bush cover did take place. It is also suggestive that site units SKa, KA and SE, placed relatively closely together in time, on purely taxonomic considerations (preceding text and Fig. 27), should group so well in terms of environmental indications. Admittedly these two approaches overlap to some extent, but Fig. 25 shows clearly that it is often different species which make up the similar "alcelaphine-antilopine-versus-other-bovid" proportions in SKa, KA and SE. Although I have not had the opportunity to evaluate the Makapansgat Limeworks material, it is not difficult to recognize (from Wells and Cooke's, 1956, description) its close taxonomic and chronological affinity with that of STS. I suspect that its environmental indications might be similar too (see also *op. cit.*: 48).

Indications from site unit to site unit in Fig. 29, subsequent to SE, are rather weak. Although KB has only a minimum number of nine individuals the fact that at least eight of these belong either to the Alcelaphini or Antilopini strongly suggests that it too was dominated by open grassland. I have a suspicion that, if SKb could be split into earlier secondary breccial and later channel fill components, the earlier component too would have a percentage near 80% in Fig. 29, while the later SKb may fall very close to the D16 value. This would provide a more marked break between the last open phase in Fig. 29 and the subsequent apparent increase in cover. The appearance, and good representation, of *Hippotragus* cf. *niger* in this last phase is particularly suggestive of bush cover increase.

I am not suggesting that the (almost embarrassingly) smooth curve in Fig. 28 mirrors an equally smooth, simple environmental trend during the Pleistocene in the Sterkfontein valley. Neither the duration of accumulation periods of site units, nor of the intervals between them, are known. Some quite substantial environmental fluctuations may not be included in this small sampling of the whole period. However, Fig. 29 may broadly represent an overall trend in the area, and probably further afield. It is likely that during most of the Middle Pleistocene an open grassland environment predominated. The onset of this grassland phase (in the broad sense, allowing for oscillations within) succeeded a period of higher degree of bush cover, although open country was prevalent during this period too, as represented by STS and Makapansgat Limeworks.

Up to this point the terms "dry" and "wet" have been scrupulously avoided, and comparisons have been restricted to degree of vegetational cover. This is because the logical leap, from inferred vegetational density to a rainfall pattern largely or totally responsible for it, while being defensible, is not axiomatic. One could cite many examples, for instance in the Transvaal Lowveld and Highveld, where temperature differences are apparently responsible for differences in vegetation cover, although annual rainfall is similar. The most interesting analysis of the southern Cape Nelson Bay Cave fauna by Klein (1972) may be relevant in this respect. From levels dating 18,000–12,000 B.P. he records a number of alcelaphine species, which together with a springbok and giant buffalo disappeared after ca. 12,000–11,000 B.P., a time coincident with the waning of the last (= "Würm") Glacial. The inferred disappearance of grassland as a major vegetation type may however have been influenced by the concomitant rise in sea level (*op. cit.* :140). The part rainfall played in this particular faunal change is not known.

If one postulates a vegetation cover change, then either rainfall or temperature or both are likely to be responsible. It is likely that rainfall played at least some part, decreasing between STS and SKa/KA/SE, and possibly increasing towards SKb and D16. It would be begging the question, if the idea of a cover change is accepted, to suggest that rainfall was increasing from STS to SKa, and from SKa to KA times. An explanation of the bovid data in Fig. 29 invoking rainfall even minimally would thus seem to stand in contradiction to Brain's (1958) findings (see also Vrba, 1974).

Possible implications concerning the Krugersdorp site hominids: There is agreement from several sources (e.g. Wells, 1962; Cooke, 1967) that a general faunal change took place in South Africa between STS and SKa times. A purely taxonomic analysis of the Bovidae corroborates this within the Sterkfontein valley context. In the same context the Bovidae further indicate an environmental change between STS and SKa/KA/SE/KB and by (inevitably, but harmlessly, circular) corollary the environmental change, if inferred correctly, is likely to have influenced the faunal change, at least to some extent. Over the same time gap, so apparently fraught with changes, the Krugersdorp hominids seem to have changed too. It is thus not entirely idle speculation to consider whether the hominid "change" may be environmentally correlated.

What exactly this hominid "change" is, here or elsewhere, is a matter of famous controversy, which can definitely do without the recording at this point of my personal impressions. Suffice it here to delineate a basic "skeleton" on which subsequent remarks may be pinned. At one extreme are the lumpers who admit to but a single hominid lineage, with gracile and robust australopithecines (another disputed term but here employed because it is so widely used) belonging to one species, possibly in chronosubspecies. Wolpoff (1971) is an exponent who has argued this line in a most original fashion. He is of the opinion that "robust" and "gracile" forms did not have significantly different masticatory apparatusses, feeding or cultured adaptations. Applying the competitive exclusion principle to this basis, he arrives at the "single species hypothesis". The majority of hominid taxonomists and anatomists recognize a robust and a gracile species, belonging either to one genus, *Australopithecus* (e.g. Tobias, 1973) or to different genera (e.g. Robinson, 1972).

The question that may be asked now is this: Could the more open, and perhaps more arid, grassland habitat of phase SKa/KA/SE/KB be correlated with

a. the increased average robusticity favoured by the lumpers; or (extremely) alternatively

b. the appearance in the Sterkfontein valley, alongside a *Homo* species, of *Paranthropus robustus*, separated from the gracile form at STS by a long independent evolutionary history, and features such as reduced anterior teeth as compared with large molars (Robinson, 1963a and b; Wallace, 1974), and a totally different locomotory mechanism (Robinson, 1972).

In case a. the only admissible correlation would be between the grassland environment and a slightly larger body size, as no other known adaptive complexes are considered to have changed from the gracile chronosubspecies.

Case b. is more interesting. (The word "interesting" here does not imply "nearer to the truth", although my personal bias does at present lie in this direction.) Theories have been expressed which could not at the time take into account the possibility of this particular vegetation change, and which yet show interesting correspondence with it. The basic premises of Robinson's (1963a, b) dietary hypothesis would fit a grassland – robust correlation very well, although the last step (based on Brain, 1958) of his argument would not, i.e. seeing the "crushing, grinding" robust vegetarian in a (slightly) wetter and more vegetationally luxuriant environment than the gracile omnivore. If one is already operating within the framework of alternative b., perhaps one should now consider whether the robust musculature was so massive, the molars proportionally so large, *because* his "vegetables" were of the tough grassland type. The long-adapted Phase 1 hominid, or "small object" vegetarian of Jolly's (1970:23) "seed-eating hypothesis" fits perfectly in this respect.

The East African robust/gracile taxonomy and environmental data must advance much further before we will be able to see whether this "long shot" indication from the Transvaal bovids holds true in a broader context. In the lower Olduvai Beds, for instance, the arrangement certainly seems to be similar: A *Homo* and a robust form are contemporaneous with a predominantly alcelaphine-antilopine bovid fauna (Gentry, pers. comm.). It remains to be seen whether the bovid changes above member G at Omo (Gentry, pers. comm.), and from the *Mesochoerus limnetes* zone to the *Metridiochoerus andrewsi* zone at East Rudolf (Harris, pers. comm.), both apparently in the direction of more open country, are correlated in any way with hominid frequencies.

PALAEOECOLOGY: POSSIBLE PREDATION PATTERNS

What does bovid weight and age distribution reveal about accumulation agencies at the site units? This brief investigation is presented in nine parts. Brackets contain short clues to the predators (4–7) and scavengers (8) which are suspected of being predominantly responsible for the relevant accumulations.

1. Limitations;
2. Basic hypothesis;
3. Age distribution of bovids in all site units;
4. Site unit STS (mainly sabretooths);
5. Site unit SKa (mainly leopards, also sabretooths);
6. Site unit KA (mainly "lion", also sabretooths);
7. Site units KB, SKb, D16 (hominid hunters);
8. Site unit SE (scavenging hominid, *Homo* sp.?);
9. Remarks

Limitations: The whole subject of the interpretation of southern African Quaternary bone accumulations has been, and is continuing to be, the subject of comprehensive study by Brain (e.g. 1958, 1973, a, b; 1974a, b). He has pointed out on many occasions how varied the factors contributing to accumulations are. Butzer (1971: 1200) concludes that the Transvaal cave fills record, at the very least, several tens of thousands of years and, quite possibly several hundreds of thousands of years. In such a situation, perhaps more than elsewhere, the danger of simplistic interpretation is great. Furthermore the data on which such discussion can be based here is circumscribed: taxonomic, death-age structural and weight information derived only from cranial bovid material. Nevertheless a few indications are put forward in the hope that they may be further interpreted and dissected in a wider framework than I am able to consider here.

Basic hypothesis: With respect to these bovid assemblages some of the accumulation causes cited by Brain (1958: 10–12), for cave accumulations generally, are not applicable, or at least unimportant: point (a) 1 that caves may act as natural death traps; point (a) 2 that bones may be transported into caves by water; and point (b) 5 that owls contribute small mammal remains. That leaves us with a recognition of causes at two stages:

Stage 1: bovids are killed by carnivore or hominid predators (I am including hominid hunters as a subset of the set of predators throughout) in the vicinity, or die a natural death either in the vicinity or in the cave.

Stage 2: the remains of these animals are brought to the site units or caves, either by the **primary** agents, i.e. the predators themselves, in which case the cave was a predator lair or shelter; or by **secondary** agents like scavengers (e.g. hyaena, hominid) and collectors (e.g. porcupine, hominid).

Is it possible to predict characteristics of such "primary" and "secondary" assemblages, in terms of weight and age data here available (Tables 87–84)? A predatory assemblage that has not been tampered with, i.e. a primary one, is likely to include a high **proportion of juveniles** (and perhaps old individuals) for obvious reasons. In the case of secondary assemblages there is no such reason for supposing high juvenile percentages, in fact common sense points in the other direction: Both scavengers and collectors sample either from animals that died a natural death, or from predator kills, the latter being far more important than the former, In the first case the animals are more likely to be old than young. I would have thought that scavengers are more likely to find remains, worth taking home to the cave for consumption, in kills of adult animals, as juveniles may be largely or totally (from the point of edible parts) eaten by the primary predator. The hominid osteo-dontokeratic collector is surely also more likely to sample adult skeletal parts, as their firmer-knit bone structure would seem to be generally more suitable for his purposes. Porcupines seem to prefer large specimens (Brain, pers. comm.), and in so doing may of course include some of juvenile origin, but are certainly unlikely to specially select them. **Weight distribution**, too, may be expected to differ between primary and secondary assemblages. A predator, while often preying on a wide total size range, generally has a definite *preference* among the bovid species present in his/its surroundings. In effect modern predators in a particular ecological context seem to sample overwhelmingly from a few species of quite restricted size range (Pienaar, 1969). The distribution of weights of individuals in a primary assemblage can thus be expected to have a low variance (provided one predator, or predators of similar size, predominate(s) in the assemblage), i.e. the bulk of species present will belong to a more or less restricted size range. Scavengers and collectors are likely to assumulate a more random collection, less clearly defined with respect to size. These ideas are very tentative and their application is fraught with problems. Their most positive aspect lies in recognizing *predominantly* primary assemblages and separating them from the rest. An assemblage will only have strong primary features, i.e. a distinctly high juvenile percentage and a close weight spread, **if** a particular predatory pattern *predominated* during the accumulation time. The absence of such primary features, like most "absences" in palaeontological data, is an inconclusive negative result and may mean a variety of things. A brief summary of the basic approach here used is given below.

Stage 1

bovids are killed by predation in the vicinity of the cave, or die a natural death in or near the cave

Stage 2

remains of dead animals are brought into the cave to eventually constitute:

PRIMARY ASSEMBLAGES, those brought into the cave, which serves as a lair or shelter, by the primary predators	SECONDARY ASSEMBLAGES, those brought into the cave by scavengers or collectors
high percentage of juveniles	low percentage of juveniles
most individuals fall into a restricted body weight range (only where one predator or predators preying on prey of similar size predominate(s)).	the body weight distribution has a high variance

In accordance with this approach overall percentages of juveniles were calculated for each site unit (Fig. 28: A). As neither individual weights nor weight Class intervals of equal size and reliable weight frequency contents were available, no attempt was made to calculate weight spread by statistics such as variance or coefficient of variation. Such weight spread is only loosely commented upon in discussing the site units.

Age distribution of bovids in all site units: To obtain an approximate age distribution of these bovid "death-assemblages" all specimens were divided into (or estimated to belong to) three age classes, juveniles, prime adults and old adults (as defined in the explanation for Tables 87–96 in Volume II, and presented in Tables 87–94). It becomes clear, when looking at a lot of bovid dentitions, that the ages at which molar central cavities become obliterated vary widely from tribe to tribe, and (less so) from species to species within a tribe. Even intraspecifically this may be expected to vary to some extent among populations subjected to different degrees of dietary harshness. As this was the only criterion available for separating old adults, this category in each site unit is likely to contain a somewhat motley assortment. Perhaps not surprisingly, no startling indications are proffered by the obtained proportions of "old adults" in Tables 87–94. The main justification for using this criterion at all in this case, lies in the fact that it refined the minimum number evaluation within each species to some extent. The juvenile-adult separation is much better and likely to be broadly analogous from taxon to taxon.

For comparison with Fig. 28 let us look at some data on adult-juvenile proportions in modern bovid populations. In all cited cases the (at least rough) correspondence of "juveniles" as used here, and "immatures" or "subadults" as cited, was checked. Herbert (1972:35) found that in a population of waterbuck, *Kobus ellipsiprymnus,* in the Sabi-Sand Game Reserve about 33% of the population was composed of immatures or young animals, (59% adult and 8% unclassified). In age counts of *Gazella thomsoni* from the Serengeti National Park Hvidberg-Hansen and de Vos (1971: Table 4) found the average percentage of subadults to be 25% (i.e. adults make up 75%). Dasmann and Mossman (1962) did age counts on some ungulate populations in Southern Rhodesia and observed the following (p. 268): "The pattern observed for kudu, waterbuck, impala, duiker, and steenbuck was that well-situated populations consist of 40–50 percent immature animals (under 2 years of age), and 22–40 percent young-of-the-year. Among zebra, giraffe, bushbuck, wildebeest, sable, and reedbuck, the percentage of immature animals was less, varying from 25 to 40 percent". Juveniles were found to constitute 20.4% of a black-faced impala, (*Aepyceros petersi*) population (Joubert, 1971:61) from the Kaokoveld in South West Africa, and 21.2% of the total impala population (*A. melampus*) in the Mkuzi Game Reserve, Natal (Stewart and Stewart, 1966, quoted in Joubert, 1971:61).

Juveniles of the smaller species are often eaten totally, or almost totally, by predators (Pienaar, 1969; Hirst, 1968). Furthermore they obviously have a lesser chance of being preserved in fossil accumulations. One can therefore expect fossil juvenile-adult ratios to be heavily biased towards adults. With this consideration in mind juvenile percentages in STS, KA and D16 particularly, and in SKa, KB and SKb as well (Fig. 28:A), appear high in comparison with those of live populations. In fact it looks as if juveniles might have been selected in preference to adults in these cases; and it is likely that they represent primary, or predominantly primary, assemblages. SE clearly differs from the other site units in this respect.

It must be stressed that the following evaluations of individual site units represents no more than an attempt to pinpoint likely **dominant** accumulation causes. It is well-recognised that many subsidiary influences, which cannot possibly be detected by this approach, may have played a part as well.

Site unit STS: The most frequently occurring species are all of medium to large size. Weight Class I is entirely absent (Table 87). I accept this site unit as likely to be a predominantly primary assemblage. The exceptionally high average weight (Fig. 28:C) points to predators that were specialized on large prey. The possibility that the gracile australopithecine contributed to this assemblage as a hunter can probably be totally rejected, especially in view of the data on hunting remains of later, more advanced hominids in the Sterkfontein valley (see p. 158). It cannot be ruled out that *Australopithecus* contributed in the role of scavenger, but his main "contribution" is likely to have been as carnivore prey.

STS carnivore remains include *Megantereon* Croizet and Jobert, a true sabre-tooth cat, *Dinofelis* Zdansky, a false sabre-tooth cat, and a leopard (Ewer, 1955, 1956; Hendey, 1974). Pienaar (1969:122) writes that in the Kruger National Park, leopards are the most important predators of impala, reedbuck, nyala, bushbuck, duiker, steenbok, Sharpe's grysbok and klipspringer. He records that occasionally adult leopards have successfully killed full-grown waterbuck cows, subadult zebra and kudu cows. The smaller STS species, like the *Redunca, Damaliscus* sp. 1 or *Parmularius* sp., *Antidorcas* and *Tragelaphus* sp. aff. *angasi* could have fallen prey to a leopard, but the numerous individuals of *Makapania* and cf. *Hippotragus* sp. aff. *gigas* probably could not have. As individuals of smaller species are in the minority in the STS assemblage, the role of the leopard, if it did play a role, was not the dominant one. It seems likely that the major predators were the false and true sabre-tooths, and possibly other, as yet undiscovered cats of sufficient size and/or large-prey-adaptation (see also Vrba, 1974).

Ewer (1967) has pointed out that, as a result of highly efficient carnassial shear, these carnivores were well adapted to the slicing of meat. The premolars however were so reduced that the animals could not have crushed any but the smaller bones. She points out that the diversity of hyaenids encountered in the African Pleistocene may have been brought about by the fact that the contemporaneous sabre-tooths left the skeletons of they prey almost intact: "In the presence of a primary predator of this type, the niche for bone-crushing specialists stands invitingly wide open, and it would not be surprising to find that numerous evolutionary attempts to fill it were made" (*op. cit.*:120). Brain (1970:5) further elaborated on this idea: "Regrettably little is known about the behaviour of South African sabretooths and it is uncertain whether they were dominant to the associated hyaenas or whether they were forced to retreat with their prey into the seclusion of caves or trees". It is here suggested that the STS cave may have been such a sabretooth lair: Whole kills, or parts of larger kills may have been brought to the cave for peaceful consumption by the predator and its brood.

Site unit SKa: Brain (1970, 1974b) has given many convincing reasons why the predominant contribution to the SKa assemblage should have come from leopards. The sizes of the majority of bovid individuals from this site unit are in perfect agreement with this. There is however a proportion of animals too large to serve as leopard prey. The percentage of juveniles, as at STS, does not rise in these larger individuals (Fig. 28:B). Again a predator able to cope with large prey, like the eight (minimum number) fully adult *Syncerus* and cf. *Megalotragus* sp. individuals (Table 93), must have been present, although not in the major role as at STS. In the most recent, cursory breccial evaluation of Swartkrans carnivore remains, those of the "lion" all seemed to fall into SKb. Sabretooths are present in the primary breccia, and it is these cats which may be the second group of contributory predators, after the leopards at SKa. Contribution to this assemblage by a scavenging hominid again cannot be ruled out, although the data make it unlikely that such a contribution would have been the major one.

Site unit KA: Brain (1973a and pers. comm.), in comparing remains from KA and KB, noticed the following: KA specimens are far more complete than those from KB. This led him to suggest that while KA may have been a carnivore lair, the extreme fragmentation of KB bone remains may represent food remains of hominid hunters. The bovid data of KA corroborates this conclusion. Alone the huge representation of *Damaliscus* sp. 1 or *Parmularius* sp. (Fig. 25), 38% of which is constituted by juveniles, points to a predator consuming its prey in the shelter of the KA cave. Although, similar to the STS case, weight Class I contains only one individual, the average KA weight is lower than at STS (Fig. 28:C). This indicates that the predominant predatory role was filled by a species (the large lion-like KA felid described by Ewer, 1956:92?), or several species, which preferred smaller prey than did the STS predators. KA remains do however include sabretooth specimens (Ewer, 1955) as well as adult bovids in weight Class IV. As at SKa this predator may have played a secondary role, i.e. occupied KA for a shorter span during the accumulation period than did the main predator(s). As at STS and SKa, the predation pattern of KA does not indicate an increase in the juvenile percentage of the higher weight Classes (Fig. 28:B).

Site units KB, SKb, D16: The last three site units in Fig. 28 have several features in common. Like the three earlier carnivore assemblages they have high overall juvenile percentages. However they diverge sharply from STS, SKa and KA in Fig. 28: B and C: All three later assemblages are strongly dominated by species of low weight. In each case the few large-sized individuals include a distinctly higher percentage of juveniles than do the lower weight Classes. The pattern is again strongly suggestive of predation, this time by a predator specialized on small prey. The three site units have more in common: They have been placed last in the chronological sequence on taxonomic grounds. The presence of both *Homo* and stone tools is either known, or strongly inferred for reasons independent of their similarity in Fig. 28, in all three site units. The conclusion here reached is the obvious one: KB, SKb and D16 each represent (predominantly, if not entirely) the food remains of hominid hunters. It is important to stress that, while scavenging probably did play a part, Fig. 28: A, B and C are unanimous in stressing an overriding **hunting** pattern.

Site unit SE: Stone tools were first discovered at SE by Brain in 1958, and have since been found in SE breccia and in surrounding Sterkfontein dumps in their hundreds. Tobias (1965) felt that unlike STS, the SE assemblage includes at least a trace of a hominid more advanced than *Australopithecus*. It seems very likely that the Sterkfontein cave during SE times was an occupation site of a *Homo* species. Yet the pattern at SE, as revealed in Fig. 28, is quite different from those presented by the inferred hominid hunting remains from KB, SKb and D16. In fact, its markedly low juvenile percentage and the broad, platykurtic distribution of only 23 individuals throughout all weight Classes, suggest that SE represents the only markedly non-primary assemblage among those considered in this study. In Vrba (1974), in a preliminary investigation of Sterkfontein remains only it was suggested that "perhaps the predominant influence contributing to the phase B (i.e. SE) bovid assemblages was the advanced hominid, who in spite of his tools may have been confined to small to medium-sized prey". Now that data on all site units is available this statement can be amended and expanded: The SE tool-maker appears to have been a *scavenger*. The extensively fragmented SE bovid remains are probably the discards of meals that were scavenged from carnivore kills. In such a situation one would not expect a high percentage of juveniles as argued above, nor a need for increased sampling of juveniles in higher weight Classes (Fig. 28: B), while the average weight of what is consumed may still be as high as that of a primary assemblage of carnivore remains (Fig. 28: C).

Remarks: The pattern presented by the bovid remains is amazingly (and in my opinion logically) consistent with their chronological succession. In the earlier three assemblages there is strong evidence of carnivore occupation of the Krugersdorp caves, and such parameters as were here used agree consistently from site unit to site unit. Thereafter the only evidence available to us indicates (at least predominant) hominid occupation of caves in the same places that were previously dominated by carnivores. Were carnivores dominant to earlier hominids, but ousted by their more advanced descendants, in the competitive search for shelter in the Sterkfontein calley? Certainly the site units here investigated can be divided into an earlier carnivore occupation phase and a later hominid occupation phase. Within the latter, the hominid quest for animal protein first led to scavenging, and only later to hunting. If the present interpretation of bovid remains were correct, it would lend exciting support to the conclusion of a number of authors (arrived at from quite different approaches) that tools were being fashioned **before** attainment of the hunting adaptation.

SE tools, serving in the procurement of vegetable foods and preparation of scavenged meat, may have been the hominid pre-adaptation for the hunting which is evident in the later site units.

If there really was a hominid species, distinct from and more advanced than the robust australopithecine, present during SKa times, and not just in a later Swartkrans context (from this vantage point I can only note the large degree of uncertainty generally attaching to this possibility), one might expect him to have been doing some scavenging too. If he was present at SKa in this capacity, his contribution (or that of any other scavanging hominid) to the assemblage was certainly marginal and quite "swamped" by the evidence of carnivore activity.

I should like to stress again the uncertainty attaching to any patterns derived from the small KB bovid assemblage, even if they do fit in as perfectly with those of chronologically adjacent site units as they appear to in Figs. 28 and 29.

BOVID FAUNAL CORRELATION WITH OTHER AFRICAN ASSEMBLAGES

Indications of taxonomic similarities between Krugersdorp and other African assemblages, some of them dated, are tentatively put forward. The discussion begins with the later site units and progresses towards the earlier ones. The start of discussion about each assemblage is heralded by a bold typing of the respective site unit name. Conclusions are (briefly) as follows:

D16: probably less than 50,000–100,000 years, Florisbad span;
later SKb: probably less than 50,000–100,000 years, Florisbad span;
earlier SKb: late Cornelia span;
KB: Cornelia span;
SE: probably less than 0.7 m.y., Cornelia span;
KA: more or less between 0.7 and 1 m.y., with possible overlap of these limits, early Cornelia span;
SKa: between 1–1.8 m.y., Swartkrans span;
STS: probably from about 1.7 m.y. to earlier than 2 m.y., Sterkfontein span.

Some general remarks about faunal spans are appended at the end of this section.

As was pointed out (p. 123), the fragmentary nature of the bovid material from the Sterkfontein valley site units precludes secure specific identification in almost all cases. Investigations of bovids in other African assemblages have shown that a particular species, as known to date, may include several chronologically and/or geographically separated morphological types. Even where a reasonable certainty exists that the species names in Table 96 are correct, indications about which morphological types are involved are mostly weak to absent. It is clear, therefore, that no very firm correlations with other sites can be expected to emerge from these bovid data. Such indications (quite possibly spurious) which are available are recorded below. In this section an effort has been made to concentrate solely on the information derived from fossil bovids, and to disregard all cultural, non-bovid faunal, and other published evidence.

Several southern African bovid assemblages are generally regarded as having Middle Stone Age cultural associations and belonging to the Florisbad (Florisbad-Vlakkraal) Faunal span. These include some Rhodesian caves (Cooke, 1950), Florisbad (Lyle 1931, Cooke, 1955), the Cave of Hearths and Kalkbank (Cooke, 1962), Vlakkraal (Wells, Cooke and Malan, 1942), Wonderwerk (Malan and Cooke, 1940), Witkrans 2 (Cooke, pers. comm.), Driefontein near Cradock in the Cape Province (Wells, 1970), Swartklip (Hendey and Hendey, 1968) and Melkbos (Hendey, 1968). The paucity of extinct species in this faunal span has often been remarked upon (e.g. Wells, 1969b:93). The only extinct bovid "hangers-on" among the predominantly "indistinguishable-from-recent" assemblages cited here seem to be:

1. the large bovine *Pelorovis antiquus* (p. 57);
2. alcelaphines, belonging to one or more species, that are larger than the extinct blue wildebeest;
3. *Antidorcas bondi*;
4. *Damaliscus niro.*

The only **D. 16 bovid material**, that can be distinguished from recent forms, belongs to *A. bondi* and to a damaliscine larger than *D. dorcas,* which is suspected on morphological grounds to be *D. niro*. The absence of the larger categories mentioned above, i.e. 1 and 2, must be expected as the accumulating agent(s) of D16 concentrated heavily on smaller animals (p. 158). There is thus good reason for thinking of D16 as belonging to the Florisbad span. The same considerations apply to the **later (loose channel) component of SKb.** The partial cf. *Damaliscus niro* horn core, SK 2862, which looks as though it came out of loose channel fill, is quite indistinguishable from *D. niro* horn cores at Florisbad. Its measurements compare well with those given in Wells (1970) for the Driefontein *D.* cf. *niro.* This size correspondence is important as *D. niro,* in the later part of its evolutionary history at least, seems to have undergone a size decrease. Horncores of this species from Cornelia, and from Olduvai Beds III and IV, as well as from Peninj (Gentry, 1965), are larger than those from South African Florisbad span sites.*

The earlier (secondary breccia) component of SKb includes several additional "distinguishable-from-recent" forms. Both the kudu and *Pelea* include at least some specimens which are larger than the respective recent species. There is an *Oreotragus* cf. *major* horn core, the cf. *Raphicerus* sp. horn cores which are larger than recent material of this genus, and the *Beatragus* sp. horn core. The latter two provide a link with Elandsfontein. It is probable that the earlier SKb component was deposited during the later part of the faunal span preceding the Florisbad span, i.e. the Cornelia (or Vaal-Cornelia) span.

KB, SE and KA may also belong to the latter. While the Florisbad span occupies a more or less restricted part of the late Upper Pleistocene, for which radiocarbon age estimates are available, the Cornelia span is more vaguely thought of as belonging either to the upper Mid-Pleistocene or early Upper Pleistocene (Wells, 1967:99). South African sites that have yielded bovid assemblages belonging to this span include Cornelia (Van Hoepen, 1932, 1947; Cooke, pers. comm.), the Vaal River "Younger Gravels" (Cooke, 1949; Wells, 1964) and Elandsfontein (Hopefield) (Hendey, 1974; Gentry pers. comm.). Wells (1969:93) writes that the "very considerable number of species surviving from the Cornelia to the Florisbad assemblage suggests that the transition reflects the passage of time rather than a dramatic or near-catastrophic environmental change". He does however point out some extinct species, including the bovid example *Gazella wellsi* = *Antidorcas recki,* which are characteristically still present in the Cornelia span, while being absent from Florisbad span assemblages (*Antidorcas* type A remains at KB, SE and KA, incidentally, have been more or less certainly referred to *A. recki*).

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* The position with respect to earlier *D. niro* specimens seems to be somewhat more confused. I have seen larger and smaller specimens from Bed II Olduvai.

Site unit KB has yielded a horn core referred to *Gazella* sp.. This may represent the same small extinct form (the latest surviving *Gazella* in southern Africa) that has so far been found in South Africa only at Elandsfontein, in the Cornelia span. It is also known from the East African assemblages of Olduvai Middle and Upper Bed II, and Bed IV, Peninj and Kanam West (Gentry, pers. comm.). A KB *A. recki* horn core base resembles in its robusticity *A. recki* horn cores from Elandsfontein and Bolt's Farm. The *Incertae sedis* horn core may belong to a *Rabaticeras,* in which case its lack of compression would place it closer to *Rabaticeras* as known from Elandsfontein, Rabat in Morocco, and Olduvai III–IV than to the SKa representative of that genus. These slender indications point the way to a tentative inclusion of KB in the Cornelia span, somewhere (chronologically) close to Elandsfontein.

The SE assemblage remains enigmatic even if one discounts the single *Makapania* tooth fragment as being misplaced from STS. It is not clear whether the small damaliscine dentitions, referred to *D.* cf. *dorcas,* really belong to the blesbok or whether they represent an extinct precursor species, such as appears to be present at Elandsfontein and Cornelia.* Although it is difficult to decide at what point in time the modern blesbok appeared in South Africa, it seems likely to have happened after Cornelia and (at least most of) Elandsfontein. If the SE assemblage really includes *D. dorcas* it would point to a late Cornelia span date at the earliest. The SE Type A *Antidorcas* material is similarly inconclusive. The dentitions appear to be definitely more advanced, with respect to molar morphology and premolar reduction, than any *Antidorcas* material at Olduvai, up to the end of Middle Bed II, which I was able to see (I have not yet seen any such material from

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* It has been remarked on before (p. 129), that the appearance of these small damaliscine dentitions in the Krugersdorp series separates SE and later site units from the earlier ones. Interesting in this connection is Gentry's (pers. comm.) suggestion that the later Olduvai assemblages, from about the Bed III–IV junction upwards (which he sees as overlapping in time with Elandsfontein), may mark the first appearance of smaller *Damaliscus* species at Olduvai.

Upper Bed II, Beds III or IV). This would suggest a date at least later than 1 million years for SE (if the Jaramillo palaeomagnetic Event is taken to coincide approximately with the junction of Middle and Upper Bed II; Dalrymple, 1972; Isaac, Pilbeam and Walker, 1972). An attempt to distinguish earlier and later *Antidorcas* Type A dentition and horn core morphologies within South African assemblages is complicated by the presence of (at least) two species, *A. marsupialis* and *A. australis*, which are *both* likely to have arisen from *A. recki* (see Vrba, 1973: Fig. 18). The SE material, if still *A. recki* at all, seems to be either on an *A. recki – A. marsupialis* lineage or on an *A. recki – A. australis* lineage, and it is rather a pity that one cannot be sure which it is: If the former alternative is the correct one, SE is likely to postdate Elandsfontein. Hendey (1974:53) finds it likely that *A. australis* was present in both earlier and later contexts at Elandsfontein. This would mean that *A. australis* and the *A. recki* (presumably evolving towards *A. marsupialis*) were probably contemporaneous for at least some part of the Elandsfontein succession. This would mean, in morphological terms, that among Type A *Antidorcas* horn cores, slender and straight ones were contemporaneous with (increasingly?) more robust and curved ones; among dentitions reduced premolar rows were contemporaneous with such as still retained $\mathrm{PM}_{\overline{2}}$. It is therefore clearly advisable to be cautious in the interpretation of "late" and "early" antidorcine features in the Middle to Upper Pleistocene South African assemblages. Thus KB horn cores may for instance be on the *A. recki – A. marsupialis* lineage, while SE and SKb material may be on the *A. recki – A. australis* lineage. If this is true then SE antidorcine remains would be compatible with an (at least) pre-Elandsfontein date.* Also (apparently) present

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* Since the publication of Fig. 16 (Vrba, 1973) it was discovered that the SK antidorcine material, showing the typical features that prompted an *A. australis* assignation, belongs to a late Swartkrans element, i.e. from secondary SKb breccia. This has the effect that the origin of *A. australis* from an *A. recki* type, which was implied to have occurred rather early in the loosely arranged time sequence in Fig. 16, should be thought of as occurring considerably later, probably during early Cornelia span or pre-Cornelia span, times.

at SE are extinct forms like *Oreotragus* cf. *major*, medium-sized alcelaphine dentitions that appear to be decisively different to recent ones, a tooth assigned to cf. *Hippotragus* sp. aff. *gigas*. The latter, unlike STS, SKa and KA material assigned to this species, may be specifically identical with the Elandsfontein *H. gigas*, but even in its broken state is certainly unlike any recent hippotragine teeth. It is on account of the presence of such extinct forms in the small SE assemblage that I prefer to interpret the antidorcine and damaliscine material in the light of the earlier, i.e. at least pre-Elandsfontein alternative. A Cornelia span date for SE, possibly between Cornelia and Elandsfontein, therefore seems to fit the present bovid data best.

It was mentioned on p. 83 that among the Olduvai *Antidorcas* dentitions, which I have seen, those that are morphologically closest to *A. recki* from **site unit** KA come from SHK in Upper Middle Bed II. All others, from strata chronologically preceding SHK, seemed to be less advanced in terms of my interpretation of antidorcine Type A dental evolution (Vrba, 1973). Unfortunately I did not see any antidorcine dentitions from later Olduvai levels, i.e. Upper Bed II, Beds III or IV. In Vrba (1973: 290) it was noted that KA *A. recki* skull, KA 1779, has a transversely directed posterior fronto-nasal suture. In this respect KA 1779 resembles skulls of the modern springbok which I have seen, and differs from the only three Olduvai *A. recki* specimens where this feature is visible (Gentry, 1966:96). At least one of the latter, M. 21462, derives from a late Middle Bed II context, i.e. SHK. These slender morphological indications would be consistent with a KA date round about, or later than, 1 million years.

On p. 73 it was discussed why the late discovery of partial skull KA 1601 strengthens the suspicion that KA remains assigned to *Damaliscus* sp. 1 or *Parmularius* sp., do in fact belong to a *Parmularius*. The KA material has affinities to a species from the East Rudolf *Metridiochoerus andrewsi* faunal zone (ca. 1.5–1.9 million years), and to *Parmularius rugosus* from Olduvai Bed III–IV junction and Bed IV (Gentry, pers. comm.). It appears to be more advanced than the former and closer to, and probably specifically identical with, the latter. While the skull measurements of KA 1601 compare exceptionally well with those given for the *P. rugosus* holotype, M 21430, in Leakey (1965:60), the KA dentitions are smaller and closer in this respect to the East Rudolf material. An increase in tooth size **relative to** skull size would seem to be an increase in masticatory efficiency. When dealing with one lineage, therefore, a relatively larger-toothed form could be generally expected to postdate a form with smaller teeth relative to skull size. In at least one bovid lineage considered in this work (*A. recki,* p. 83) this was found to be true. If this reasoning were correct, and **if** the KA species is close to Olduvai *P. rugosus,* it might be construed to point to a KA date earlier than the Olduvai Bed III–IV junction, i.e. earlier than 0.7 million years (the start of the Brunhes Normal magnetic Epoch, Dalrymple, 1972, at the base of Bed IV, Grommé and Hay, 1971). Gentry (pers. comm.) in comparing Olduvai and Elandsfontein bovids concludes that much of the Elandsfontein time span corresponds to Olduvai Bed IV or later. From this perspective KA appears to be earlier than Elandsfontein (for instance KA 2515, assigned to cf. *Hippotragus* sp. aff. *gigas*, whether seen as being on an *H. gigas,* an eland or any other lineage, is less advanced than respective, comparative Elandsfontein material). If these chronological placements of Olduvai, Elandsfontein and KA were correct, it would provide a further indication that (at least the bulk of) KA is likely to predate Bed IV, i.e. 0.7 million years. It is tentatively suggested that most KA bovid fossils correlate well with Olduvai Upper Bed II to Bed III, and may represent a time period of ca. 0.7–1.0 million years.

The bovid evidence is rather inconclusive on the question of the relative chronology of KA and Cornelia. It is quite possible that they overlap in time and that differences between their assemblages are partly, or largely, due to the fact that KA accumulated in a cave, while Cornelia is an open site (as suggested by Wells, 1969b:94). One would be hard-pressed to state which of the respective *A. recki* assemblages, if any, is the earlier, especially as I have seen no *A. recki* horn cores in either site. It is my **impression** that styles on Cornelia upper molars are slightly more pronounced, which might be construed as being more advanced. Perhaps the scales are weighted in favour of KA being earlier by the dichotomy in small alcelaphines, often cited in this work: At KA there is a total absence of small, typically damaliscine dentitions, while this niche is apparently occupied by a *Parmularius,* last seen in South Africa (as far as we know) at this site. At Cornelia the small alcelaphine appears to be a *Damaliscus*, different from and smaller than *D. dorcas*, also present at the later Elandsfontein. The bovid material certainly does not support dissociation of KA from the Cornelia span. Rather it points to KA as being one of the earliest South African sites, perhaps the earliest, in that faunal span.

The SKa assemblage has a more archaic aspect than those in the Cornelia span: We have here the last good representation in South Africa of a large gazelle, and of strange forms like Gen. et sp. indet. and a suspected ovibovine. There is a distinct absence of "indistinguishable-from-recent" forms, which may be even more acute than Figs. 25 and 26 indicate (on present evidence we cannot be sure that a *Pelea* and a *Tragelaphus* cf. *scriptus* really existed during SKa times).

The SKa assemblage affords several tentative comparisons with East African sites. Bovine (more specifically syncerine) dentitions from Olduvai Upper Bed II and Bed III seem to be more advanced than those of SKa *Syncerus* (p. 61). The latter have quite indistinguishable counterparts in Middle Bed II. The kudu subspecies *Tragelaphus strepsiceros grandis*, which is about 10–20% larger than the extant kudu, occurs in Olduvai Middle and Upper Bed II as well as at Peninj in Tanzania (Gentry, pers. comm.). The SKa kudu remains, as those from KA and some from SKb, could belong to this large subspecies. It is interesting that, while Olduvai pre-Middle Bed II kudu remains are smaller (belonging, in fact, to a different species, *T. maryanus,* Leakey, 1965, Gentry, pers. comm.), in South Africa a large kudu, that could be *T.s.grandis,* is found at the Makapansgat Limeworks which as a whole definitely seems to predate Middle Bed II, perhaps considerably (see below). It was noted on p. 6 that the Swartkrans (SKa) *Rabaticeras* is closer to (and perhaps specifically identical with) an Olduvai skull out of the Lemuta Tuff(aged about 1.65 million years, Cox, 1969), than to later *R. arambourgi.* Below this tuff some mandibles have been found, like HWK E (level 1) 25, which seem identical in every respect to SKa

Group IIa alcelaphine specimens. The SKa skull piece SK 3812 A was tentatively assigned to cf. *Connochaetes* sp. aff. *africanus.* On pp. 15, 16 it was noted how closely this specimen resembles early *Connochaetes* from Olduvai Upper Bed I and from the *Metridiochoerus andrewsi* faunal zone of East Rudolf (ca. 1.5–1.9 million years, Maglio, 1972). From the same Olduvai and East Rudolf levels hail *Connochaetes* mandibles which are indistinguishable from SKa Group III dentitions (p. 37). The available data thus point to a Bed I – Middle Bed II (or about 1.0–1.8 million years) age for SKa. The indications towards the earlier half of this time range are perhaps stronger than those to the later half.

In my opinion no other South African bovid assemblage shows a particularly close affinity to that of SKa. (I have not seen the fossils from Bolt's Farm and Gladysvale, and am unable to comment on them in this context).

Among East African bovid assemblages there are some which seem to be indicative of an environment comparable; in including a certain degree of open grassland, to that inferred for the **STS site unit assemblage.** However, these all seem to be younger than 2 million years (e.g. Olduvai, the later Omo levels, the upper East Rudolf faunal zones). Earlier East African assemblages appear to be more or less heavily dominated (probably more so than even STS?) by the bovid tribes which are today generally indicative of a more bush-covered environment. A true comparison of STS considering sites, say through a time range from 1–4 million years ago, to see where it best fits, would thus probably be impossible at the moment. Even if I had seen all the relevant material (which I have not) the earlier East African sites may appear less taxonomically close to STS, simply because they may have accumulated under different environmental conditions. Perhaps part of the Kaiso fauna (Cooke and Coryndon, 1970) may be more suitable in this respect, but I have not seen these assemblages at all. I do not have sufficient information to be definite on this point of a lack of comparative "suitable-environment-sites", but only wish to point out that any comparison may be confined to stipulating the later limit of STS duration.

The species most characteristic of the STS assemblage, in the Krugersdorp site unit context, is *Makapania* cf. *broomi*. Gentry (1970:64) mentions that a horn core, which could belong to *Makapania*, was found below tuff G (aged about 1.93 million years) at Omo, and that it is "the only possible occurrence of the genus away from the Makapansgat Limeworks Quarry" (to this must now be added the STS occurrence and more tentatively that of a smaller *Makapania* species at SKa). He (*op. cit.*) also points out that the closely related *Megalovis latifrons* seems to occur through the whole of the European Villafranchian. The resemblance of STS *Damaliscus* sp. 1 or *Parmularius* sp. (which I strongly suspect to be a *Parmularius*), to an alcelaphine from the East Rudolf *Metridiochoerus andrewsi* faunal zone (ca. 1.5–1.9 million years), has been discussed. The scant medium to large alcelaphine material from STS could be on the same lineage, with similar time correlations, as that from SKa, whose Olduvai Bed I lower Bed II affinities were discussed above. The few available indications suggest an overlap of STS accumulation time with Bed I, and a possible extension of the earliest phase into the 2–3 million year time span.

I accept, in concert with other authors, that among South African bovid assemblages those of STS and Makapansgat Limeworks are sufficiently close to form a group, i.e. to be placed into the same faunal span. The STS assemblage is by far the poorer one, both with respect to number of specimens and their fragmentary preservation. This makes a decision, on which, if either, is likely to be the earlier one, difficult. Wells (1969b:94) writes: "There are ... many points of difference between the Sterkfontein and Limeworks assemblages, and it is difficult to determine whether these should be interpreted as ecological, regional or chronological; if the last view were taken, I suggest, contrary to the widely received opinion, that Limeworks could plausibly be regarded as earlier than Sterkfontein."

One could argue that some features of Fig. 25 support STS as being earlier. If SKa really includes *Gazella vanhoepeni*, then its heavier representation of this species matches better with that at Makapansgat Limeworks, (where *G. vanhoepeni* is one of the four dominant bovid species, Wells and Cooke, 1956), than with the marginal presence at STS. Similarly at Makapansgat Limeworks the material referred to the eland (at least some of which is identical to what has here been called cf. *Hippotragus* sp. aff. *gigas*) is only moderately well represented (*op. cit.*: 48). At STS it is one of the two most numerous species (Table 96). Placing Makapansgat Limeworks after STS would fit in better with the "petering out" of this species after STS times, suggested in Fig. 25. A *Connochaetes* is one of the four dominant species at Makapansgat Limeworks (*op. cit.*), perhaps the most dominant at SKa, but marginally present in the STS assemblage. Furthermore *Oreotragus* cf. *major,* which appears to be present in both Swartkrans and Cornelian span assemblages in Fig. 25, is found at Makapansgat but not among STS fossils. I find none of these points convincing. Firstly, as was reasoned in a previous section, smaller bovid species are likely to have been present during STS times in greater numbers than Table 96 suggests, but the STS accumulating agents appear to have concentrated on larger forms. Secondly an environmental difference between STS and SKa has been postulated. Together these two effects, if true, might account for all the points mentioned. If the large kudu of Makapansgat Limeworks, SKa, KA and possibly SKb were really absent from the STS assemblage this would be a more valid discrepancy: Both environmental and size characteristics of STS lead one to expect its presence in that assemblage, if it was in the Sterkfontein valley at that time. Also, as noted above, this form makes its first appearance at Olduvai in Middle Bed II. Its absence from the STS assemblage might be construed to mean that it was not yet"available" for accumulation. I am, however, not convinced of the absence of kudu remains from the STS assemblage: There are a considerable number of STS bovid specimens available (mostly early juvenile) which have not been removed from the breccial matrix, because they seem so extensively fragmented. They have consequently not been included in this study. All of these are large and seem to fit morphologically into either *Makapania,* cf. *H.* sp. aff. *gigas,* or a tragelaphine such as eland or kudu.

If the few *Antidorcas* Type A specimens really belong to STS, they would provide a more convincing counter-indication, namely of STS post-dating Makapansgat Limeworks: One possibility, as espoused by Wells & Cooke (1956), Wells (1969a) and Gentry (pers. comm.), would be that there is no *Antidorcas* whatsoever from Makapansgat Limeworks, only gazelles. Seen from this perspective it seems likely that the genus appeared in South Africa during the late Sterkfontein span, i.e. during STS times, being absent in earlier sites like Langebaanweg, and Makapansgat Limeworks. Alternatively, there is the tentative suggestion (Vrba, 1973:309) that the "*Gazella gracilior*" skull material, together with some antilopine dentitions with long premolar rows, may be the earliest known South African *Antidorcas* representative. Even if this were true the Makapansgat Limeworks material is definitely less advanced than *A.* cf. *recki* from STS. This can be clearly seen when comparing molar morphology and hypsodonty (e.g. similarly aged STS 1560 and M 6290), although premolars are unfortunately absent from the STS assemblage.

Among the slender indications provided by the bovid fossils, those pointing to a pre-STS date for the Makapansgat Limeworks grey breccia (from which derive the bovids here considered) seem at present to be the more convincing ones. This must be regarded as very tentative.

The results of these correlations are cautiously shown in Fig. 30. The assumption of correspondence, at a particular time, between faunas separated by thousands of kilometres is notoriously dangerous, and proven so by modern faunas. If particular assemblages of species have survived longer in southern than in eastern Africa or vice versa in the past, if for instance southern African geography has a "cul-de-sac" effect in this respect, resulting in a depressed local speciation rate, no one has yet been able to document it. Until secure dates are available from both areas there is little hope of checking this possibility. The placement in Fig. 30 of South African assemblages opposite parts of the absolute time scale, on the basis of correlation with known-age faunas, is thus clearly naive, but perhaps pardonable as the only approach available.

General remarks: In Vrba (1974) the SE bovid assemblage was thought to be close to those of Swartkrans and KA, and it was suggested that SE belongs to either the Swartkrans or Cornelia spans. This was before anyone had recognized that the greater part of the Swartkrans assemblage belongs to a substantially later period than do the *Paranthropus* – associated fossils. Now that bovids from site units STS, SKa, KA, SE, KB, SKb and D16 have all been analysed simultaneously, it is perhaps possible to be more specific: The bovid data suggest that SE and KA are later than previously realized, and may both belong to the Cornelia span. The time lapse between Faunal Phases A and B at Sterkfontein is thus even greater than was suggested in Vrba (1974). Similarly the statement (*op. cit.*) that SE "is perhaps closer to (Swartkrans than to KA) in terms of species present" is no longer relevant since SK has been split. SE is in fact closer to SKb and to KA, than to SKa.

Much justifiable pessimism has been expressed by past authors about the possibility of extending faunal divisions, whatever their names, across fossil assemblages in all of Africa. Cooke (1967) has discussed this matter comprehensively, and concludes that (p. 182): "As far as correlation (of southern Africa) with other parts of Africa is concerned, much still remains to be done, for collecting has far outstripped description of the fossil material." There exists however a general acceptance, which I share, of the likelihood that some kind of faunal patterns **will** be found to extend across Africa once sufficient data are available. Once particular successive assemblages have been studied, indications in this direction which emerge will be, and should be, put forward, although perhaps in each case based only on a small part of the "jigsaw-puzzle". Provided they are thrown tentatively into the discussion, with full recognition of their limited bases, they should not be regarded as premature, just because of the vastness of the task facing us. Perhaps in this way progress can be made towards the stage visualized by Cooke (1967:182) when "significant strides in correlation between (North, East and South Africa) will be possible, particularly if specialists on various groups of mammals can be enabled to undertake a unified study of all the faunal material of that group from all the areas".

Accordingly I wish to make some suggestions concerning African faunal patterns, and pose some questions which have arisen out of this bovid analysis of the (close on) 2 million-year-long Krugersdorp succession:

1. A few South African assemblages appear to belong to a time period of 1–2.5 million years ago. These tentatively suggest that somewhere a little less than 2 million years ago (between Makapansgat Limeworks and STS on the one hand, and SKa and succeeding assemblages on the other) certain generally more bush-adapted tribes lost ground to antilopines and alcelaphines, especially the latter, which, if not at once assuming dominance, certainly proliferated noticeably. Does a similar increase in prominence of grazing forms (they need not be the same taxa) occur at Omo above Member G (c.a. 1.9 m.y.); near the start of the *M. andrewsi* faunal zone (c.a. 1.9 m.y.) at East Rudolf; and in the lower Olduvai series (35 dates for all strata between tuffs just below the Basal Member of Bed I and the Lemuta Member of Bed II give a mean age of 1.82 m.y.; Curtis and Hay, 1972)? From various hints in the literature, personal communications from Gentry and Harris, and personal observation on material from these areas, I gather that this might be a possibility. If it were shown to be true of the bovids by the research which is being done on them, and if also found to be true with respect to other fauna, could it mirror a wide-spread overall environmental change, or merely fuller exploitation of open environments that were already there? It could just be possible that such a change in faunal tribal representation, mirroring a change in environmental exploitation, marked the boundary between a Sterkfontein span (or other similar term) and a succeeding span not only in the Sterkfontein valley, but elsewhere in Africa as well.

2. In the Krugersdorp succession there occurs a significant change, within at least the alcelaphines, at some time less than a million years ago: the advent of small *Damaliscus* forms. It has been mentioned before that a similar change has been observed among Olduvai alcelaphines round about the Bed III–IV junction (c.a. 0.7 m.y.). On its own this small faunal change would be interesting, but would not necessarily carry much weight. If accompanied by other faunal "arrivals" and changes it might signify the start of a Cornelia span here and elsewhere.

Hopefully these tentative suggestions may be tested by knowledge other than here available, and, if containing any validity whatsoever, added to.

I should also like to make one or two remarks, albeit peripheral ones, concerning suggested faunal divisions and their terminology. To my knowledge the first published suggestion to divide South African fossil assemblages into faunal "stages" came from Wells (1962). The concept was further expanded upon (Cooke, 1963, 1967; Ewer & Cooke, 1964; Wells, 1967). In his 1967 publication, Cooke argued for the use of the word "Faunal Span": "an attempt to indicate the combined concept – the duration of existence of a particular faunal assemblage." After a comprehensive analysis he convincingly pointed out that the term "span" has the advantage of being less restrictive "in its implication of a lower order of precision and lithostratigraphic control". This implication may be particularly important if faunal patterns are really found to extend across Africa, as such patterns may not lend themselves to any but the widest restrictions. In this respect I am wary of the term (mammal) "age" used by Hendey (1974): Let us assume, for instance, that an increase in open grassland forms is found to occur in the Lower Pleistocene of East and South Africa, in both cases so marked and essentially similar that it becomes desirable to express the advent of the phenomenon by a single term, **although** the (for example) South African "advent" can be shown to be somewhat later. In such a situation the term Swartkrans"span" would surely be distinctly less awkward than Swartkrans "Age". Hendey (1974:57) of course has only applied the "age" terms to a southern African context, in which cases this objection falls away. At the same time I do agree with his argument that a shorter term like "Sterkfontein fauna" would be preferable to "Sterkfontein span fauna". I am not sufficiently informed on the rules governing such terminologies to appreciate why we should not be allowed to use"Sterkfonteinian span" (i.e. why the "ian" ending should in all cases be reserved for "ages" and "stages"), and therefore a "Sterkfonteinian fauna".

Wells (1969b:94) noted that the "differences between the faunas of Swartkrans and of the Sterkfontein 'main site' (i.e. STS) ... are at least as sharp as those between Swartkrans and Kromdraai". He considers at one point in this publication whether "Kromdraai should be dissociated from Swartkrans, and either included in the Cornelia span or made the type locality of an intermediate span". The preceding discussion of chronology has shown that the bovid data corroborate this opinion. They suggest that the time lapse between KA and for instance Cornelia is shorter than between KA and SKa, and yet the latter two have generally been taken to share the same faunal span, preceding the Cornelia span. If the criterion of a presence of small *Damaliscus* for the start of the Cornelia span were indeed found to be valid, KA would of course have to be removed from this span. For the present I prefer to place KA, as well as KB, into the Cornelia span. This would leave SKa as the only occupant of the Swartkrans span (I have not seen the Gladysvale and Bolt's Farm assemblages and am unable to judge their "span placements"). The question now arises whether there are grounds for including SKa in the same span as preceding STS. Hendey (1974) has included both Kromdraai and Swartkrans with Sterkfontein and Makapansgat in the "Makapanian mammal age". This broader division may have its merits when viewing faunas from a wider perspective. From the temporally limited perspective of a student of australopithecine-associated faunas, however, I am definitely for retention of the division between Sterkfontein and Swartkrans spans: Although the time lapse between STS and SKa may not be long, there is a significant change in composition at the bovid species and tribal levels, with a probable concomitant environmental change. Furthermore there is a slim chance that this change may be more widespread than southern Africa, as argued above.

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