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NEW SPECIES AND A NEW GENUS OF HIPPOTRAGINI (BOVIDAE) FROM MAKAPANSGAT LIMEWORKS

by

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ABSTRACT

A revision of the Hippotragini from the Makapansgat Limeworks is proposed: a new species of *Hippotragus* is described, *Hippotragus cookei*, and fossils previously referred to cf. *Oryx gazella* (Wells and Cooke, 1956) and *Hippotragus gigas* (Gentry and Gentry, 1978) are assigned to this species. *H. gigas* is present in the Pleistocene Member 5, but not in the Pliocene Grey Breccia, Member 3, as had been formerly supposed. A new genus and species from Member 3, *Wellsiana torticornuta*, tentatively referred to ?Hippotragini, is described based on a frontlet that had been assigned to *Damaliscus* sp. (aff. *albifrons)* by Wells and Cooke (1956). The horncore piece previously referred to *Aepyceros* cf. *melampus* (Wells and Cooke, 1956) may belong to the same species as ?Hippotragini sp. nov. (Gentry, 1986) from the Laetolil Beds, Tanzania. The hippotragine fossils here discussed again emphasize that Makapansgat Member 3 contains a Pliocene assemblage that is more ancient than was originally thought, with particular affinities with the Laetolil Beds and also with the Pinjor Formation of the Siwaliks in India and Pakistan.

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INTRODUCTION

The hippotragine fossils discussed in this paper come from two strata at Makapansgat Limeworks:

1. The grey fossil-rich cemented marl of Wells and Cooke (1956) that is equivalent to part of Lower Phase I of Brain (1958) and to Member 3 of the Makapansgat Formation of Partridge (1979). In this stratum were found hundreds of thousands of fossils, densely packed together, including most of the remains of *Australopithecus africanus* from Makapansgat. About 90% of the large mammals from this stratum are bovids. The evidence of the Bovidae to date suggests an age near 3 million years (m.y.) for this assemblage (Vrba, 1982). This agrees with palaeomagnetic results that bracket it between 3,32 and 3,06 m.y., or between 3,32 and 2,9 m.y. ago (Brock et al., 1977).
2. The coarser brownish-red, sandy breccia of Wells and Cooke (1956) that is equivalent to the Phase II breccia of Brain (1958) and to Member 5 of the Makapansgat Formation of Partridge (1979). Bovid material of the tribe Alcelaphini from low in Member 5 has suggested temporal correlation with Olduvai Bed II (Vrba, 1977).

Recent re-evaluations of Makapansgat stratigraphy (Maguire, 1985; Schrenk, n.d.) have expressed reservations about Partridge's (1979) lithostratigraphic scheme of Members 1-5. For instance, they have pointed out that different lithologies (Members) may represent contemporaneous facies deposited in different parts of the cave, e.g. parts of Member 2, Member 3 and the lower part of Member 4. My present study cannot contribute to this debate apart from re-affirming the following: the rich bovid fossil assemblage from the Grey Breccia, Partridge's (1979) Member 3, furnishes no reason to doubt that it is a cohesive, geologically contemporaneous assemblage considerably older (being early Upper Pliocene or perhaps late Lower Pliocene) than the few bovids from the Pleistocene Member 5 assemblage. In this paper I shall refer to the earlier stratum as Makapansgat Member 3 (hereafter abbreviated as MAK3) or as the Grey Breccia; and to the later stratum as Makapansgat Member 5 (MAK5).

This contribution is a revision of the sparse remains of the antelope tribe Hippotragini found so far at Makapansgat. There are three living genera of hippotragines: *Hippotragus* Sundevall, 1846; *Oryx* Blainville, 1816; and *Addax* Rafinesque, 1815. There is one recently extinct species, *Hippotragus leucophaeus* (Pallas, 1766) the small South African bluebuck exterminated about 1799. The living species are: *Hippotragus equinus* (Desmarest, 1804) the roan antelope; *Hippotragus niger* (Harris, 1838) the sable antelope; *Oryx gazella* (Linnaeus, 1758) the gemsbuck and beisa; *Oryx leucoryx* (Pallas, 1777) the Arabian oryx; *Oryx dammah* (Cretzschmar, 1826) the scimitar-horned oryx; and *Addax nasomaculatus* (Blainville, 1816) the addax of the Sahara.

The only hippotragine species on Wells and Cooke's (1956) original list of Makapansgat Limeworks bovids is cf. *Oryx gazella*. To this species they assigned M34 a portion of left maxilla, and M8 a right lower molar (see fig. 3). They mentioned two additional worn upper third molars, without giving catalogue numbers, as belonging to this species. They implied biostratigraphic equivalence of these materials with the numerous other bovid fossils from the Grey Breccia, MAK3.

The only reference since then to Makapansgat hippotragine material comes from Gentry and Gentry (1978, p. 350), who regarded M8 and M34 as well as some horncore specimens as belonging to the large hippotragine first described from Olduvai, *Hippotragus gigas*: "*H. gigas* is also known from Makapansgat Limeworks, being represented by a right lower molar BPI M8 and two left upper molars M34 ..... Parts of horncore bases M1029 and M1775, both left, and a damaged frontlet with part of the left horncore M2795, could be this species".

A brief outline of the revisions concerning Hippotragini that I propose in this contribution is as follows (see Table 1 for summary):

TABLE 1

REASSIGNMENT OF REFERRED SPECIMENS

SPECIMEN	WELLS & COOKE 1956	GENTRY & GENTRY 1978	THIS PAPER
M34	cf. *Oryx gazella*	*Hippotragus gigas*	*H. gigas* [MAK5]
M8	cf. *Oryx gazella*	*Hippotragus gigas*	*H. cookei*
M1029[1]	—	cf. *H. gigas*	*Makapania broomi*
M1775 (M556)[2]	—	cf. *H. gigas*	*Parmularius braini*
M2795	—	cf. *H. gigas*	*Hippotragus cookei*
M781	*Damaliscus* sp.	Alcelaphini sp.	*Wellsiana torticornuta*
M654	*Aepyceros* cf. *melampus*	?*Aepyceros* sp.	Laetolil ?Hippotragini sp.nov. of Gentry 1986

[1] — fits onto M387
[2] — fits onto M8737

1. There is no *Oryx* or *Hippotragus gigas* material from MAK3.
2. Frontlet M2795 (fig. 1) is the holotype, and horncore base M1020 (fig. 2) the paratype, of a new species *Hippotragus cookei*. Dentitions referred to this new species include M8 (but not M34; fig. 3) as well as dentitions from Sterkfontein Member 4 previously discussed as ?Hippotragini (Vrba, 1976).
3. I agree with Gentry and Gentry's (1978) identification of M34 as *H. gigas*. But, unlike the *H. cookei* specimens, M34 does not derive from MAK3. Instead it comes from MAK5 according to a recent personal communication from J.W. Kitching. MAK5 has been temporally correlated with Olduvai Bed II (Vrba, 1977). That is, at Makapansgat *H. gigas* occurs in a Pleistocene context, considerably later than *H. cookei* from the Pliocene MAK3.
4. Horncore base fragment M1775, which also bears the number M556, has been joined to M8737, and assigned to the alcelaphine species *Parmularius braini* (Vrba, 1977).
5. Right horncore M1029 has been joined to M387. The composite specimen is a partial frontlet of the ovibovine species *Makapania broomi*. (I suspect that Gentry and Gentry, 1978, in mentioning M1029 as hippotragine were in fact referring to the hippotragine specimen M1020.)
6. A new genus and species of ?Hippotragini from Member 3, *Wellsiana torticornuta*, is based on frontlet M781 (fig. 4). M781 was previously referred to *Damaliscus* sp. (aff. *albifrons)* by Wells and Cooke (1956, p. 23, fig. 11), and Alcelaphini sp. by Gentry and Gentry (1978, p. 66).
7. The horncore piece M654, previously assigned to *Aepyceros* cf. *melampus* by Wells and Cooke (1956, pp. 36, 37, fig. 19) and referred to as *?Aepyceros* sp. by Gentry and Gentry (1978, p. 66), is assigned to the new Laetolil species that was discussed as ?Hippotragini sp.nov. by Gentry (1986).

DESCRIPTION OF NEW TAXA
Tribe Hippotragini
Hippotragus cookei sp.nov.

Diagnosis

An extinct species that was large in comparison with other Pliocene *Hippotragus* species, larger than the living sable antelope *Hippotragus niger*, with smaller and more compressed horncores than in the extinct *Hippotragus gigas*, and similar in these respects to the living roan antelope *Hippotragus equinus*. The horncores are more than normally divergent at the base for a *Hippotragus* species. In lateral view the angle between the posterior pedicel and horncore base on the one hand, and the anterior braincase on the other, is higher than in living *Hippotragus* species. That is, the horncore was inserted more upright relative to the braincase, similar to the condition in the extinct *Hippotragus bohlini*. The horn cores have a tendency to a flattened lateral surface. A large frontal sinus is present in the pedicels and extends into the base of the horncore, where it is more extensive laterally than medially. The superior part of the orbit juts out laterally close to the horncore base and quite strongly. The frontal surface from anterior to the horncores to the level of the coronal suture is hardly bent, indicating less bending of the anterior face on the braincase than in living species. The supraorbital foramina are closer together than in living species or in *H. gigas*.

Holotype

Fragmentary and damaged frontlet, M2795, with posterior part of base of left horncore (fig. 1a, b), housed at the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg (all Makapan fossils mentioned — catalogue numbers preceded by M — are housed in this institution). It is possible that this specimen comes from a subadult individual. The surface of the bone is weathered away in places. Most of the supraorbital canals are preserved, but only the superior part of the right supraorbital foramen survives. The coronal suture is almost straight with a slight and gentle indentation at the midline towards the horncores. The metopic suture is small, relatively uncom-



Figure 1. *Hippotragus cookei*. Holotype frontlet M2795.
a = left lateral view;
b = anterior view.
(Scale in centimetres.)

plicated and moderately raised anteriorly. Because of surface damage it is not clear whether there was a postcornual fossa or not, but it must have been very shallow if present. The left horncore base has its anteroposterior axis almost parallel to the metopic suture. There is no sign of a posterolateral keel.

Paratype

Partial basal left horncore, M1020, with a part of the orbital rim (fig. 2a, b). There is no sign of keels, transverse ridges or deep longitudinal grooving on this horncore. It has no lateral flattening at the base,



Figure 2. *Hippotragus cookei*. Paratype left horncore M1020.
a = anterior view;
b = left lateral view.
(Scale in centimetres.)

but shows such a tendency higher up. The preserved pedicel and horncore base are smoothly hollowed by the frontal sinus, more extensive laterally than medially. The preserved distal cross-section suggests that the specimen may come from a subadult individual. The orbit juts quite sharply laterally close to the horncore base. The horncore is quite strongly mediolaterally compressed.

Horizon

The holotope and paratype come from the Grey Breccia at Makapansgat Limeworks, Member 3 of Partridge (1979).

Name

The new species is named for H. Basil S. Cooke in recognition of his contributions towards the study of Makapansgat Bovidae.

Additional specimens and measurements

Left horncore pedicel, M2629, also from the Grey Breccia, probably belongs to *H. cookei*. It has extensive hollowing in the pedicel which does not extend into the horncore base.

Measurements that are possible on the fragmentary holotype and paratype include the following (all measurements in mm; e = estimate):

	M2795	M1020
anteroposterior basal horncore diameter (apd)		58e
mediolateral basal horncore diameter (mld)	44e	47e
basal horncore index (100 mld/apd)		81%
apd 20-25 mm above base		52,5
mld 20-25 mm above base	42e	42,0
horncore index 20-25 mm above base		80%
width across lateral edges of supraorbital foramina		62e
separation between basal horncores	40-50	
length of preserved piece of left horncore	70-80	134

Gentry and Gentry (1978) mentioned horncore bases M1775 and M1029 as conspecific with M2795, suggesting that all belonged to *Hippotragus gigas*. M1775 (which also bears the number M556) has since then been joined to M8737 and now seems very clearly to be assignable to the alcelaphine species *Parmularius braini* (Vrba, 1977). Right horncore M1029 has been joined to M387 as a frontlet of the ovibovine species *Makapania broomi*.

Referred dentitions

Upper molars M34 (fig. 3c) and lower molar M8 (fig. 3a) were referred by Wells and Cooke (1956) to cf. *Oryx gazella* and by Gentry and Gentry (1978) to *H. gigas*. I suggest here that their morphologies indicate that they belong to two different *Hippotragus* species. They derive from different strata at Makapansgat. M8 comes from the Grey Breccia, MAK3, as does the horncore material of *H. cookei*. M34 comes from the brownish-red breccia, MAK5, according to J.W. Kitching (pers.comm.). This latter stratum is probably of lower Pleistocene age in contrast to the Pliocene MAK3 (Vrba, 1977).

In this contribution two dental specimens from MAK3 are assigned to *Hippotragus cookei*: M8 and M597 (fig. 3a, b). M8 is a right M_2 in mid-wear, length = 30,4 mm and maximum breadth = 15,6 mm at the occlusal surface. Features of M8 include a very small basal pillar that is situated close to the tooth, a small but definite anterior goatfold, strongly developed lingual ribs, small and not very well de-

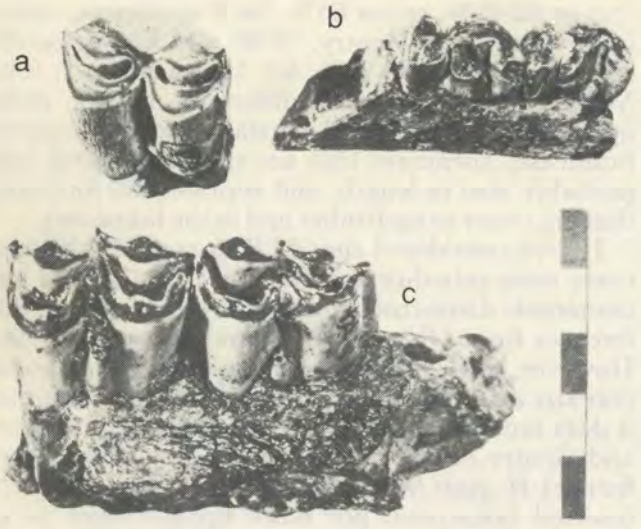


Figure 3. Hippotragine dentitions from Makapansgat.
a = *Hippotragus* cf. *cookei*. RM_2 M8 from MAK3;
b = *Hippotragus* cf. *cookei*. LP_{3-4} M597 from MAK3;
c = *Hippotragus* cf. *gigas*. LM^{2-3} M34 from MAK5.
(Scale in centimetres.)

veloped parastylid and entostylid, fairly rugose enamel especially on the buccal surfaces, and central enamel islands with central constrictions. It is brachyodont for a tooth of this wear stage and size. M597 has left P_3 and P_4; P_3 length = 19 mm e, breadth = 10 mm e; P_4 length = 20 mm e, breadth = 11 mm e; P_{3-4} length = 38,6 mm. Although the metaconids of both teeth are broken, what is left of them suggests that they were prominent and round, and far from fusion with the paraconids on both teeth. Other characters of M597 include the fact that the teeth have rugose enamel and are long relative to breadth in comparison with living *Hippotragus* species.

Conspecific dentitions are known from Sterkfontein Member 4 (ST4). They were previously described as ?Hippotragini in Vrba (1976, pp. 45, 46, tables 70, 71, plate 39). Both M8 and M597 have indistinguishable counterparts among the ST4 dentitions. There can be little doubt that the same species was present in both assemblages, and I tentatively assign the ST4 ?Hippotragini dentitions (Vrba, 1976) to *Hippotragus cookei*.

Features that cannot be studied on M8 and M597, but that are suggested as possible characteristics of *H. cookei* on the basis of the more abundant ST4 dentitions, include the following. There are no complete ST4 toothrows, but composite estimates suggest that the premolar row was surprisingly short for teeth of such primitive occlusal morphology (100 P_{2-4}/P_2-M_3 = 35%e for ST4 *H. cookei*; compared with 35%, 36% in two *Oryx gazella*, 40-41% in four roan and 35-40% in four sable antelopes). Left maxilla ST2336A shows an infra-orbital foramen quite high above the junction of P^3 and P^4, and also suggests a premolar row that was not long. This specimen, as also maxilla fragment ST1539a, has an abrupt medialward dip of the maxilla above the molars, which suggests that a preorbital fossa may have been present. The upper molars from ST4 have a tendency to slight indentations of the central cavities; and they show consistenly present, although small, basal pillars. The lengths of P_3 and P_4 of M597 are a bit longer than the corresponding means for ST4 dentitions (18,9 mm for 9 P_4, 16,8 mm for 2 P_3). This tentatively suggests that the ST4 dentitions may be more advanced in having a slightly more reduced premolar row than the MAK3 population of *H. cookei*.

It can be very difficult to distinguish the isolated dentitions of plesiomorph species of the hippotragine, tragelaphine, boselaphine and also the bovine clades. In the present context one needs to consider particularly the distinction between Hippotragini and Tragelaphini. I favour a hippotragine assignation for the conspecific dentitions from MAK3 and ST4 for the following reasons:

— the premolars have prominent, rounded, bulbous lingual cusps with completely unfused paraconid and metaconid that are characteristic of Hippotragini, but not of Tragelaphini;
— although plesiomorph tragelaphines have a tendency to basal pillars, the incidence on the dentitions here considered is probably too high for tragelaphines;
— the presence of definite goatfolds on the lower molars argues against tragelaphine and for hippotragine affinity;
— tragelaphine teeth in general have a low degree of enamel rugosity for their size. The eland is a good example of this. On the other hand the rugosity of the teeth assigned to *H. cookei* has counterparts in other hippotragines, such as *H. gigas*.
— the premolars of early tragelaphines already are relatively wide with respect to length, and in this respect the present dentitions are more reminiscent of early Hippotragini;
— the suggestion of a short premolar row, relative to molars, is at variance with tragelaphines but not with hippotragines;
— the dumbbell-shaped central cavities of lower molars, and tendency to indentations of central cavities of upper molars, suggest a plesiomorph hippotragine rather than tragelaphine;
— an infra-orbital foramen situated high above the toothrow and not anteriorly over the premolars, as in ST2336A, is characteristic of hippotragines, but not of tragelaphines that tend to have the foramen situated low and anteriorly over P^2.

The left maxillary specimen M34 (fig. 3c) from MAK5 is satisfactory as *H. gigas*, as suggested by Gentry and Gentry (1978). Its measurements are: M^2 length = 31mm e, breadth = 20,5mm ; M^3 length = 28mm e, breadth = 18mm e; M^{2-3} length = 59,0mm . There are very close morphological counterparts in the *H. gigas* assemblage from Olduvai. For instance, comparison of M34 with left M^{2-3}, BK II 1963.2226 from Upper Bed II, shows similarities in development of buccal styles, ribs between styles, basal pillars and central cavities, although the Olduvai dentition is a little smaller.

Comparisons

The horncore specimens M2795 and M1020 (figs 1, 2) may be recognized as hippotragine by the nature of the basal sinuses and the lack of keels and transverse ridges. They can be attributed to *Hippotragus* because of the upright insertion above the orbits and mediolateral compression of the horncores. Therefore I shall compare the *H. cookei* remains with those of other *Hippotragus* species.

Within the genus *Hippotragus* there are few resemblances to the two extant species. M2795 and the sable share the apomorphic feature of frontals that are raised between the horncores above the level of the top of the orbits. M1020 and the roan have in common a similar degree of compression of the horncores, and M2795 resembles the roan in the advanced features of a more prominently projecting top of the orbit and a higher degree of basal horncore divergence than are found in the sable. *H. cookei* differs from both in having an anteroposteriorly more flattened frontal between the horn pedicels, more upright basal horncore insertions, lower pedicels and closer supraorbital foramina.

Two of the earliest known hippotragine species are the one represented at Sahabi by a complete left horncore with part of the orbital rim and frontal (discussed in Gentry, 1986), and *Praedamalis deturi* (Dietrich, 1950) from the Laetolil Beds and from the Hadar formation in Tanzania (Gentry 1981, 1986). I see only commonly held plesiomorphies, and no advanced similarities between the *H. cookei* skull material and either of these two species. Differences between the Makapansgat and the Sahabi species include the fact that *H. cookei* has more extensive hollowing at the base of the horncore, is larger, and probably has less compressed horncores. Differences from *P. deturi* are as follows: *H. cookei* has an anteroposterior horncore axis that is less angled relative to the skull midline, horncore bases that are better demarcated from the pedicel (as observed on M1020 which has a less damaged surface than M2795), no concavity in the frontal posteromedially to the horncores as has *P. deturi*, and probably more extensive basal horncore hollowing and raising of the frontal between the horns, and larger size than *P. deturi*. Gentry and Gentry (78; see also Gentry, 1978) argued that the holotype of *Sivatragus bohlini* (Pilgrim, 1939) from the Pinjor Formation of the Siwaliks of India (Pilgrim, 1939, considered that it could alternatively derive from the preceding Tatrot Formation), would be suitable as an ancestor of the large extinct species *H. gigas* which is principally known from Olduvai Beds I-III in Tanzania, and Elandsfontein in South Africa. They suggested that *S. bohlini* can be placed in *Hippotragus*. The MAK3 *Hippotragus* shares with *H. gigas* some plesiomorph features such as low pedicels; and some advanced features such as a prominently jutting orbit close to the horncore base, extensive pedicel hollowing that extends into the base of the horncores, and large size among fossil *Hippotragus* species. The two taxa differ in the following respects: horncore compression in *H. cookei* (81%) is lower than in all Olduvai *H. gigas* (range 82-91%, mean 86%, for 9 specimens, taken from Gentry and Gentry, 1978) and Elandsfontein *H. gigas* (range 83-91% for 11 specimens). The MAK3 *Hippotragus* also differs in having more upright horncore insertion relative to the anterior braincase, horncores that are smaller in girth and probably also in length, and supraorbital foramina that are closer to each other and to the horncores.

I have considered that M2795 and M1020 may come from subadult animals and that age, and not taxonomic distinctness, might account for these differences from Olduvai and Elandsfontein *H. gigas*. However, while that reasoning might apply to horncore size and to spacing of the supraorbital foramina, it does not apply to the first two differences. Gentry and Gentry (1978, p. 344) record that young (and female) *H. gigas* from Olduvai have more obliquely inserted horncores, not more upright ones as in M2795. And one would expect a lower horncore compression in younger animals than in adults of the same species. Thus, I suggest that the Makapansgat *Hippotragus* belongs to a separate species, *H. cookei*, that is in some respect similar to *H. gigas*, in some respects more plesiomorph (e.g. spacing of supraorbital foramina, horncore size), and in others probably more advanced (e.g. horncore compression, the tendency to a flattened lateral surface above the horncore base, raising of the frontals between the horncores) than *H. gigas*.

H. cookei shares the following with the Siwaliks *H. bohlini*: a similar degree of horncore compression, markedly upright horncore insertions, little angulation of the frontal anterior to the horncores relative to the anterior braincase, similar morphologies of the superior orbital margin and of the gently indented coronal suture, distinct demarcation of basal horncores from pedicels, and little angulation of the anteroposterior basal horncore axis relative to the skull midline. The two forms differ in that *H. cookei* has weaker temporal ridges immediately behind the horncores, higher basal horncore separation, more elevated frontals between the horncores, and in somewhat larger size. With respect to each of these differences *H. bohlini* can be interpreted as more plesiomorphic than *H. cookei*. Thus on the limited material available no characters debar *H. bohlini* from being ancestral to *H. cookei*.

I suggest that within the *Hippotragus* clade *bohlini*, *cookei* and *gigas* belong to the same subclade that diverged during the Pliocene from the sister-clade that contains *equinus*, *niger* and *leucophaeus* — the recently extinct bluebuck.

A comparison of the Makapansgat and Sterkfontein *H.* cf. *cookei* dentitions with those of other hippotragines suggests that they are quite large relative to the M2795 and M1020 horncore material. However the *H. cookei* horncores represent the largest hippotragine species, while the large dentitions are the only hippotragine dentitions, from the MAK3 breccia. Also, M2795 and M1020 may be subadult and/or female. Thus *H.* cf. *cookei* seems a reasonable assignation for the MAK3 and ST4 teeth.

The *H.* cf. *cookei* dentitions (fig. 3a, b; Vrba, 1976,

plate 39) differ decidedly from those of all extant hippotragines and *H. leucophaeus*. The dentitions of the living *Oryx/Addax* subclade are closer to (although quite distinct from) the *H.* cf. *cookei* specimens than are those of living *Hippotragus* in the following respects: lower tooth width relative to length than in *Hippotragus*, smaller goatfolds and basal pillars, simpler central cavities on the molars, shorter premolar rows and an infraorbital foramen that is situated further posteriorly, over the P^3/P^4 junction, than in *Hippotragus*. This may simply mean that the plesiomorph morphology prevalent in early hippotragines, including members of the *Hippotragus* clade like *H. cookei*, was lost in later *Hippotragus* species but retained in oryxes and the addax.

Hippotragine dentitions from the Laetolil Beds and the Siwaliks, although much smaller, show many similarities with *H.* cf. *cookei*, particularly in their plesiomorph occlusal morphology. The premolar morphology is closely comparable to my descriptions for *H.* cf. *cookei*. The metaconids of Laetoli P_3's point backwards towards the hypoconids as in M597. Lower molars have similar small goatfolds and basal pillars, some as small as on M8 while on others they are a bit more prominent. Among the Laetolil upper dentitions some are close in their morphology to counterparts from ST4. Upper and lower premolar rows from Laetolil also seem to be somewhat reduced, as in *H.* cf. *cookei*. In short, many of these Laetolil dentitions seem to be at a similarly plesiomorph stage of occlusal evolution as, but yet taxonomically distinct from, *H.* cf. *cookei*. Comparable features are present on dental remains from the Tatrot of the Siwaliks (Pilgrim 1939, pp. 84-86), as for instance the mandible M15373 at the British Museum of Natural History. But, as Gentry and Gentry (1978, p. 352) noted: it is interesting that on P_4 of this mandible there is fusion between paraconid and metaconid, a feature not found in later, more definite Hippotragini and also absent in the present dentitions, with the exception of one or two ST4 specimens in advanced wear.

The *H.* cf. *cookei* dentitions are sufficiently different from all *H. gigas* material from Olduvai and Elandsfontein to rule out decisively the possibility of belonging to the same species. They differ from Olduvai *H. gigas* in being longer with a much less complex occlusal morphology. That is, basal pillars, goatfolds and complexity of central enamel cavities are all more pronounced, and the teeth are relatively broader, in the Olduvai dentitions. Similar differences from *H.* cf. *cookei* with respect to occlusal advancement are present on the Elandsfontein *H. gigas* material. But the latter dentitions are larger than those from Olduvai. They have coarsely rugose enamel, a feature shared with the Makapansgat and Sterkfontein dentitions. The *H.* cf. *cookei* molar rows are a little shorter, the premolars a little longer, than their counterparts from Elandsfontein. (Length $M_{1\text{-}3}$ range 87-96, 5, mean 91, for 4 *H. gigas* specimens, compared with 87e for *H.* cf. *cookei* from ST4; $P_{3\text{-}4}$ range 34,5-35,2 for 3 *H. gigas* specimens compared with range 34-38,6 for 3 *H.* cf. *cookei* specimens.) Thus, the Elandsfontein *H. gigas* has a more reduced premolar/molar ratio than *H.* cf. *cookei*, although even the latter is reduced enough to be comparable to *Oryx* and more reduced than roan and sable. ($100 \times P_{2\text{-}4}/P_2\text{-}M_3 = 33\%$ for 1 *H. gigas* compared with composite estimate 35% for ST4 *H.* cf. *cookei*, 35% and 36% in 2 *Oryx gazella*, 40-41% in 4 roan and 35-40% in 4 sable antelopes.) In most morphological respects the *H.* cf. *cookei* teeth look more plesiomorph than *H. gigas*. Yet *H.* cf. *cookei* dentitions by Pliocene Makapansgat-Sterkfontein times had already attained greater tooth length than the earliest known Pleistocene *H. gigas* from Olduvai. The mosaic of features suggests that the two forms belong to separate lineages, perhaps sisters of a sister-group, and not simply in an ancestral-descendant sequence.

On the basis of the *H. cookei* horncore material I hypothesized that, within the genus *Hippotragus*, *H. bohlini*, *H. cookei* and *H. gigas* belong to the same subclade that diverged during the Pliocene from the sister-clade that contains the living species. If the dentitions under consideration are indeed conspecific with the horncore material, the dental characters would fit well with the hypothesis of a close cladistic relationship between *H. cookei* and *H. gigas*. *H. gigas* dentitions are remarkable among *Hippotragus* species for their combination of retention of plesiomorph occlusal morphology, together with the advanced characters of reduced premolars (both features reminiscent of oryxes) and large size. The presence of these features on the MAK3 and ST4 dentitions is consistent with their belonging to a *Hippotragus* species within a *gigas*-subclade.

Tribe ?Hippotragini
Genus *Wellsiana* nov.

Type species *Wellsiana torticornuta* sp.nov.

Generic diagnosis

The type species is the only species of the genus and a diagnosis is given under the species.

Wellsiana torticornuta sp. nov.

Diagnosis

This extinct bovid was medium sized with horncores moderately short relative to the size of the frontlet. The right horncore viewed from pedicel to tip, has weak anticlockwise torsion. The horn pedicels are hollowed by frontal sinuses, with the sinuses not extending into the bases of the horncores. The horncores are quite strongly compressed at the base, and even more so towards the tip. The largest, anteroposterior diameter at the horncore base is strongly angled relative to the metopic (mid-frontal) suture. In lateral view the horncores are inserted obliquely, that is, with a relatively low angle between the basal horncores and the anterior part of the braincase. The horncores do not have keels, but there is a distinct posterolateral edge that persists, and participates in the anticlockwise torsion, towards the tip. There are no transverse ridges on the horncores. There is a rapid diminution in the circumference of the horn-

core above the base. The metopic and coronal sutures are not complicated. The coronal suture passes closely behind the base of the pedicels and is strongly indented forward between the horn pedicels. The pedicels are short, not parallel-sided, and are anterolaterally demarcated distinctly from the base of the horncore.

Holotype

Fragmentary frontlet with most of right horncore, the base of the left horncore, and a short piece of the parietal projecting backwards, M781 (fig. 4a, b). The spongy texture of the damaged distal surfaces of the horncores suggests that the holotype may have belonged to a subadult individual. This would mean that the overall skull size and the length of the horncores typical of adults of this species may have been larger than as shown on M781, and the anticlockwise torsion considerably more pronounced. The circumference of the more complete right horncore diminishes markedly above the base, which gives the appearance of a basal swelling. It does not show marked longitudinal grooves along its length. The metopic suture is not raised above the level of the frontals between the pedicels, but forms part of a smooth, U-shaped valley.



Figure 4. *Wellsiana torticornuta*. Holotype frontlet M781.
a = left lateral view;
b = anterior view.
(Scale in centimetres.)

Horizon

The holotype is from the Grey Breccia, Member 3 of the Makapansgat Formation. No other specimens have been assigned to this species.

Name

The generic name is in honour of the late Lawrence H. Wells, formerly Professor of Anatomy at the University of Cape Town, who first introduced me to the wonders of bovid fossils. The specific name refers to the torsion of the horncores (*tortus* = twisted; *cornus* = horn).

Measurements

Only a few measurements are possible on M781:

anteroposterior horncore diameter (apd) at base	44,0
mediolateral horncore diameter (mld) at base	32,7
basal horncore index (100 mld/apd)	74%
apd 75 mm above base	29,0
mld 75 mm above base	17,8
horncore index 75 mm above base	61%
maximum width across lateral surface of basal horncores	110,0
separation between horncore bases	26,3
estimated angle between basal apd and metopic plane	50-60
length of broken right horncore	94
estimated length of complete right horncore	150-170

Comments and comparisons

M781 was originally described and figured by Wells and Cooke (1956: 23, 24, fig. 11) as a new alcelaphine species, *Damaliscus* sp. (aff. *albifrons*). The main reason why I do not place M781 in the Alcelaphini is that its frontal sinuses do not extend upward into the horncore, and are not sufficiently extensive and smooth-walled posteriorly in the pedicel (see Vrba, 1979). Additional reasons include the lack of transverse ridges, the shortness of the pedicels and the rapid diminution of the horncore circumference above the base.

The Makapansgat bovid species of which M781 is superficially most reminiscent is *Redunca darti*. Characters of *R. darti* that constitute major differences from M781 include the following: the absence of sinuses in the horn pedicels, the absence of horncore torsion, the absence of rapid reduction of size above the horncore base, less horncore compression at the base and especially higher up, more divergent horncores, the presence of strong longitudinal grooving along the horncore surface and the sigmoid curvature of the horncores in lateral view. On the basis of a combination of some characters of M781 I would prefer to include it in a tribe other than Reduncini: the extent of sinuses in the horn pedicels, the distinct anticlockwise torsion that is apparent already low down on the core, the absence of a complicated and raised metopic suture and the absence of transverse ridges on the horncores. Other characters of M781 would be consistent with reduncine membership, such as the low pedicels, the strongly angled setting of the horncores and their oblique insertion relative to the braincase. It should also be borne in mind that transverse ridges are not always visible on horncores of reduncine species, and that the tribe is known to

include species with a combination of features that are aberrant relative to most other member species. An example is *Menelikia lyrocera*, first described from the Shungura Formation in Ethiopia (Arambourg, 1941), which has extensive internal hollowing of the frontals and clockwise torsion of the horns, unlike other known reduncines. Thus, in the absence of more complete skull remains and associated dentitions, I suggest only tentatively that the new species represented by M781 is not well placed in the Reduncini.

On the available evidence I prefer assignation to the tribe Hippotragini. There are three extant genera of hippotragines, *Hippotragus*, *Oryx* and *Addax*. Fossils that can be assigned to this tribe are known from various sites in southern, eastern and north Africa and from the Pinjor Formation of the Siwaliks of India and Pakistan (see overview in Gentry, 1978). I agree with Gentry (1978) that most hippotragine fossils can probably be attributed to *Hippotragus* or *Oryx*, with the possible exception of the material described by Dietrich (1950) as *Praedamalis deturi* from Laetolil in Tanzania.

The combination of features present in M781 cannot readily be placed into one of the available genera, *Hippotragus*, *Oryx*, *Addax* or *Praedamalis*; yet each of the features of M781 has counterparts in one or more extant or extinct hippotragine species:

— Transverse ridges on the horncores are typically absent in hippotragines as a whole, as they are in M781.
— Internally hollowed pedicels are characteristic of Hippotragini, being more extensive in some species, such as the extinct *Hippotragus gigas* and *H. leucophaeus*, and less well-developed, with bony instrusions, in others, for example in some skulls of extant *Oryx* and *Addax* and in *Praedamalis*. The limited sinuses of M781 are comparable to the condition in some of the latter group of hippotragines.
— The relatively strong compression of the basal horncores in M781 (index 74%) is paralleled in *Praedamalis*, *H. niger* and in some *H. leucophaeus* specimens, while other hippotragine species are characterized by rounder basal horncores (closer to an index range of 78-90%).
— Strongly inclined horncores relative to the braincase in lateral view are shared by M781 and modern skulls of *Oryx* and *Addax*, while the horncores of *Hippotragus* and *Praedamalis* are more uprightly inserted.
— Such marked horncore inclination is positively correlated in many bovids with a strongly angled horncore setting, both being advanced features or apomorphies. There seems to be an evolutionary tendency for lateral excursion of the posterior extremity of the basal horncore (thus increasing the posterior angle between the anteroposterior horncore axis and the skull midline) as horncores become more bent back towards the braincase. The morphology of M781 is much more advanced in this respect (with an angle of 50-60°) than that in *Hippotragus* species (0-20°) or *Praedamalis* (near 30°). However, in extant *Oryx gazella* I measured angles close to 90° and in some *Addax* specimens the angles were larger than 90°. Thus the condition of M781 might be seen as intermediate between those of *Hippotragus* on the one hand, and *Oryx/Addax* on the other and closer to the latter than the former.
— Anticlockwise torsion of the right horncore, that is visible in M781, is present in *Addax*. Horncore torsion is unknown in other living hippotragines.
— The low pedicels with ill-defined, sloping sides of M781 are again closer to the condition in *Addax* and *Oryx* than in *Hippotragus* species.
— The feature of M781 that is most difficult to reconcile with membership of the Hippotragini is the shortness of the horncores relative to frontlet size. The hippotragine clade is generally seen as characterized by long horncores, with the extant roan antelope, *Hippotragus equinus*, having shorter horns than other species. One factor to consider here is that long horns may not be an apomorphy of the clade Hippotragini, but rather a transformation that occurred in parallel in several sublineages. That is, one might expect to find member species that are plesiomorph in this respect. Another consideration is that, if M781 is subadult, then the discrepancy in horncore length may be much less marked. In fact, the estimated lengths of the complete horncores of M781 compare well with those of some juvenile roan skulls in the Transvaal Museum, in which second but not third permanent molars have erupted.

Comparison of M781 with all known extinct hippotragine material suggests similarities with the following: *Sivatragus bohlini* and *Sivoryx sivalensis* (Pilgrim, 1939), *Antilope sivalensis* (Lydekker, 1878), all three from the Pinjor Formation of the Siwaliks, and *Brabovus nanincisus* (Gentry, 1986) from the Laetolil Beds in Tanzania. I agree with Gentry (1978) that *Sivatragus* should be sunk in *Hippotragus* and that *Sivoryx cautleyi* and *Antilope sivalensis* are probably conspecific and should be referred to as *Oryx sivalensis*.

Similarities shared by M781 and *H. bohlini* include: hollowing of the horn pedicels, a relatively high frontlet width and similar basal separation of horn pedicels. M781 differs by greater basal horncore compression, much stronger angulation of the anteroposterior horncore axis relative to the midline, and markedly greater inclinations of the horncores relative to the anterior braincase.

Similarities shared by M781 and *Oryx sivalensis* include: hollowing of the horn pedicels, similar separation of horn pedicels, the strong angulation of the horncore settings which is only a little less pronounced in *O. sivalensis*, and the tendency to a posterolateral edge at the base of the horncore. M781 differs by greater basal horncore compression and somewhat more inclined horncores relative to the anterior braincase, although this latter difference is not so pronounced as the corresponding one from *H. bohlini*. Altogether, on the limited material available, M781 seems closer to the *Oryx* species than to the *Hippotragus* species.

A fossil bovid with even more impressive resemblances to M781, although again clearly distinct, is the skull with horncores and mandibles, no. 5376, from Laetolil. Gentry (1986) described this fossil as representing a new genus and species, *Brabovus nanincisus*. *Brabovus* and M781 share the following: basal hollowing with bony intrusions of the horn pedicels (the sinus is, however, more extensive in *Brabovus*, extending right up into the horncore), the same high degree of angulation of the horncore settings; horncores that are short relative to basal girth with a rapid diminution in horncore circumference above the base, similarly oblique insertions relative to the braincase, lack of transverse ridges on horncores, a short ill-defined pedicel and uncomplicated sutures. M781 differs in having no sign of a concave anterior horncore surface in lateral view (while *Brabovus* does have this because of the anterior orientation towards the horncore tip), the anticlockwise torsion in contrast to the absence of torsion in the Laetolil fossil, horncores that are inserted more widely apart and distally more divergent, much greater basal horncore compression (74%) than *Brabovus* (with 90%), and probably larger size.

I examined specimen no. 5376 in 1978 at Laetolil and concluded that it might be hippotragine with affinities to the new Makapansgat species represented by M781. Gentry (1986) considered whether to assign *Brabovus* to Bovini or to Hippotragini. He noted the difficulties of a bovine attribution, chief among them the high narrow skull of the fossil. Nevertheless, he decided in favour of Bovini because of four features of Laetolil specimen no. 5376: small I_1 hardly larger than the other incisors and canine, quite rugose tooth enamel, short horncores and strong brachyodonty. Of these I find the subequal incisors the most convincing resemblance to Bovini. However, possession of small I_1 is probably a plesiomorph feature in Bovidae. The distribution of incisor size (small I_1 in Bovini, Caprinae, *Panthalops*, that is, mainly in Eurasiatic bovids, enlarged I_1 mainly in African bovids; Gentry, 1986) strongly suggests that the advanced character state in this case evolved more than once, and perhaps within each monophyletic tribe of African Bovidae. That is, we might expect that in a given tribe, such as Hippotragini, lineages with relatively early divergence within the clade may retain plesiomorph features like subequal first incisors. The same argument can be applied to rugose tooth enamel, short horncores and brachyodonty. Thus while Gentry (1986) argues that *Brabovus* is a primitive bovine, one can equally well argue that it is a hippotragine that retains many plesiomorph features.

I debate this here because it is relevant to the affinities of *Wellsiana torticornuta*. I suggest the following regarding the Laetolil cranium no. 5376 and the Makapansgat form represented by M781: they could be related taxa whose cladistic derivation is situated near the base of the hippotragine clade, and which have therefore retained certain plesiomorph features such as relatively short horncores and plesiomorph dentitions, while sharing advanced features with respect to basal horn inclination and orientation. These particular advanced features may indicate that Laetolil 5376 and M781 may be associated with the base of a clade that includes the *Oryx/Addax* subclade. (It is interesting that the most plesiomorph dental occlusal morphology in modern Hippotragini is found in *Oryx* and *Addax*, particularly in the latter.) The anticlockwise torsion of *Wellsiana* may indicate membership of a clade that includes the *Addax* subclade.

?Hippotragini sp. nov.

M654 is a piece approximately 80 mm long from the middle or the basal half of a right horncore with anticlockwise torsion (seen from base to tip). Its maximum and minimum diameters are 39,5 mm and 33,8 mm respectively, with a compression index of 86%. It has prominent V-shaped transverse ridges anteriorly that are spaced about 32 mm apart. It has a posterior keel and flattening of the posterior part of the lateral surface.

Wells and Cooke (1956, pp. 36, 37, fig. 19) described and figured this specimen as *Aepyceros* cf. *melampus*, the living impala. I here want to suggest that we explore an alternative affinity of this fossil.

Gentry (1986) described ten horncores from the Laetolil Beds as ?Hippotragini sp.nov. and regarded this species as synonymous with Aepycerotinae gen. et sp. indet of Dietrich (1950). I have studied the Laetolil horncores, and consider that every feature visible on M654 agrees very well with them: considering that the specimen comes from somewhere near the middle and not the base of the horncore, its large size agrees closely with the dimensions of the Laetolil horncores (range 37,0/30,1 — 50,5/45,0 for 10 horncore bases). Other similarities are the degree of slight mediolateral compression, the tendency to a flattened posterior part of the lateral surface, the size, shape and spacing of the transverse ridges, the posterior keel and anticlockwise torsion. The problem with an assignation to *Aepyceros* is that M654 would have to belong to the largest impala ever recorded in the fossil record. Large impala horncores are known from Chiwondo in Malawi (Kaufulu et al., 1981) and from Member G in the Shungura Formation of Ethiopia. But the corresponding part of the horncore in these specimens would have been smaller than M654. In contrast to the largest impala horncores from Shungura G (dated about 2,33-1,88 my ago, Brown et al., 1985), earlier impalas from Hadar, Mursi and the earlier Shungura Members (which are closer to the deposition time of MAK3) are smaller. Thus for the present I prefer a tentative assignation of M654 to the Laetolil species and to ?Hippotragini. If this group of fossils were indeed referable to hippotragines they are likely to represent a new genus.

CONCLUSIONS

In the initial species list for the Makapansgat Limeworks Bovidae, Wells and Cooke (1956) referred ten out of 19 species more or less securely to living species, and a further three to extinct species

known elsewhere from the Late Pleistocene. The list featured only three extinct genera. The impression was one of a Pleistocene assemblage with strong affinities to living southern African forms. My recent revisions, to date restricted to the larger bovids, suggest more ancient affinities for MAK3, with a preponderance of extinct genera and an absence of extant species. On the basis of the adhering breccia several of the forms of Pleistocene affinity can be recognized to belong to MAK5 and not MAK3 (Vrba, 1977, 1982, 1987).

This change in temporal emphasis is exemplified in the revision of the Hippotragini. Thus, cf. *Oryx gazella*, *Damaliscus* sp. (aff. *albifrons)* and *Aepyceros* cf. *melampus* of Wells and Cooke (1956), all discussed with reference to modern species by these authors, are instead proposed to represent respectively: a new extinct species *Hippotragus cookei* with some Pliocene affinities; a new genus and species *Wellsiana torticornuta* that shows relationships to a form from the Laetolil Beds dated about 3,7 my; and possibly another new species and genus, at presently tentatively referred to ?Hippotragini sp.nov., that is also present in the Laetolil Beds. The new studies of the Hippotragini again point to a particular relationship with the Laetolil Beds, although these seem to be earlier than MAK3, as was previously suggested (Vrba, 1982).

Hippotragines probably diverged early in their history into the two major subclades represented by *Hippotragus* and *Praedamalis* on the one hand, and *Oryx* and *Addax* on the other. Both subclades are represented in MAK3. The new species *H. cookei* is a good *Hippotragus*. I propose that within *Hippotragus* the subclade that contains the Siwaliks *H. bohlini* and the African *H. cookei* and *H. gigas* diverged during the Pliocene from the sister-clade that contains *H. equinus, H. niger* and *H. leucophaeus*. The divergence of *Wellsiana* may be associated with the base of the *Oryx—Addax* subclade. Both these Makapansgat forms seem to have close cladistic relatives in the Siwaliks. This suggests faunal exchanges between Africa and Asia that occurred earlier, perhaps not much earlier, than MAK3 times. Thus the new studies not only suggest a change in our temporal concepts of MAK3 affinities, but also a broadening of our geographic concepts of such affinities to include Eurasia as well as Africa.

Gentry and Gentry (1978) recorded *H. gigas* from Makapansgat, Chiwondo, perhaps Shungura Members C and G (all Pliocene assemblages), Olduvai Beds I-III, Kanjera, Peninj (all Lower Pleistocene), Elandsfontein (Middle Pleistocene) and possible Florisbad (Late Pleistocene). My present study relegates the Makapansgat material referred to *H. gigas* to the Pleistocene MAK5. Furthermore, I regard the attribution to *H. gigas* of the scant and fragmentary Chiwondo and Shungura hippotragine fossils as very doubtful, an opinion also reflected to a lesser extent in Gentry and Gentry (1978). Thus I propose that *H. gigas* has a more curtailed duration than hitherto supposed, with an earliest secure record in Olduvai Bed I.

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