

NEW SPECIES OF *PARMULARIUS* HOPWOOD AND *DAMALISCUS* SCLATER AND THOMAS (ALCELAPHINI, BOVIDAE, MAMMALIA) FROM MAKAPANGS GAT, AND COMMENTS ON FAUNAL CHRONOLOGICAL CORRELATION

by

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ABSTRACT

Two new species of Alcelaphini, based on fossils from the Makapansgat Limeworks, are described. One is an early member species of the extinct genus *Parmularius* Hopwood. The present description is the first record of a *Parmularius* from any southern African fossil site. The other new species belongs to *Damaliscus* Sclater and Thomas, and is closely related to the extinct *Damaliscus niro* (Hopwood). The phylogenetic relationships of the new species to other extant and extinct alcelaphines are discussed. Comparison with fossils of the same, and/or related, species elsewhere in Africa gives rise to comments on faunal chronological correlation.

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INTRODUCTION

Among new species described by Wells and Cooke (1956), in their extensive paper on fossil Bovidae from the Makapansgat Limeworks, are the first three named in this quote (op. cit., p. 48): "In point of numbers the Makapan fauna is dominated by four species, *Redunca darti*, *Phenacotragus vanhoepeni*, *Makapania broomi* and the wildebeest". (*P. vanhoepeni* was subsequently placed in the genus *Gazella* De Blainville by Wells, 1969.) In the more than 20 years since then, none of these three species has been recorded from any site outside the Transvaal, i.e. they remain unique to the local australopithecine-associated faunas (see Vrba, 1975). After seeing more material than was available at the time that Wells and Cooke were working, it has become clear to me that the remains of the fourth species, the "wildebeest" (loc. cit.) belong to a new species of the extinct alcelaphine genus *Parmularius*. The description which follows below is the first record of a *Parmularius* from any southern African fossil site. Although Gentry (1970b) tentatively assigned some Langebaanweg remains to *Parmularius*, he subsequently (pers. comm.) retracted his opinion. Three other species of the genus (see table 1) have to date been recorded in East African assemblages. It will be further discussed

below that the new *Parmularius* species was widely distributed in Africa.

It is no accident that the alcelaphine species, alone of the four most abundant Makapan bovid species, appears to have had a wide distribution (I agree with Gentry, 1970a, that *Makapania broomi* is an ovibovine, and not an alcelaphine as originally suggested by Wells and Cooke in 1956). Alcelaphine size and cursorial adaptation has resulted in high dispersal rates, as attested to by the trans-African distributions, apparently at any one time, of several past and present species (Vrba, 1978). This factor, together with a correlated high speciation rate (op. cit.), renders the group suitable for chronological correlation between fossil assemblages. At the base of the high alcelaphine dispersal and speciation rates lies the strong environmental specialization of this tribe for vegetationally open habitats. Alcelaphine frequencies in modern and (by fairly secure morphological extrapolation) fossil contexts serve as excellent ecological indicators (Vrba, 1974, 1975, 1976, n.d.).

Partridge has recently revised the stratigraphy of Makapansgat (as briefly outlined in Brock, McFadden and Partridge, 1977) and I refer in this paper to Members 1-5 of the Makapansgat Formation as described by him.

DESCRIPTION OF NEW SPECIES

The description of each new species is preceded by the relevant generic diagnosis. The diagnoses and horizons here given for the genera *Parmularius* and *Damaliscus* differ from those of Gentry and Gentry (1977) with respect to certain additions and several minor alterations. In a phylogenetic, or cladistic, analysis of recent and fossil Alcelaphini (Vrba, 1978) I concluded that the genera *Parmularius* and *Damaliscus* are more closely related to each other (i.e.

with a more recent common ancestry) than either is to any other published alcelaphine genus. The phylogenetic hypotheses for alcelaphine genera, and for species of the *Damaliscus-Parmularius* group, suggested in that paper (op. cit.) are reproduced in Figures 1 and 2.

Consultation with these cladograms, while reading the generic and specific diagnoses which follow below, will point out to the reader which of the diagnostic features constitute synapomorphies (i.e.

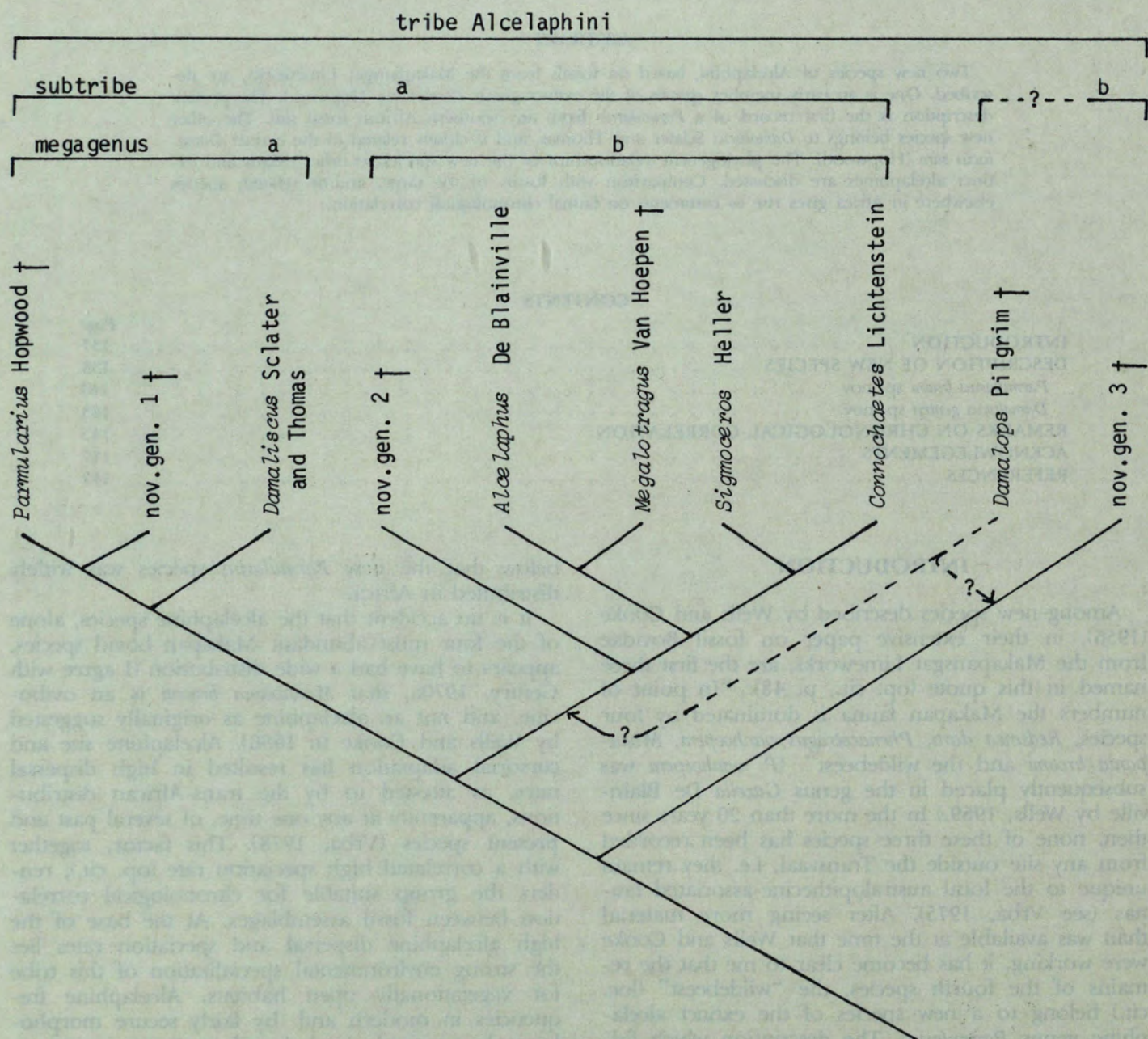


Figure 1. Phylogenetic relationships of alcelaphine genera (adapted from fig. 1 in Vrba, 1978).

nov.gen. 1 based on (Lit.) 1959.277, i.e. on nov.sp.A, from the Laetolil Beds;

nov.gen. 2 based either on a new species from the Hadar Formation, Ethiopia (specimen AL 208-7), or on a new species from the Laetolil Beds (specimen (Lit.) 1959.233).

nov.gen. 3 based on two new alcelaphine species (the only alcelaphine material) from Langebaanweg, Cape Province (material here referred to nov.gen. 1-3 is being studied by Dr. A. W. Gentry, who has kindly allowed me to refer to it prior to description).

† = extinct.

uniquely shared derived character states). Background to phylogenetic systematics may be found in Hennig (1966), Cracraft (1974), Griffiths (1972) and Nelson (1970).

Genus *Parmularius* Hopwood 1934

Type species *Parmularius altidens* Hopwood 1934

Generic diagnosis

Extinct medium-sized alcelaphines with high nar-

row skulls. Horn cores without torsion; generally not very compressed; the greatest basal horn core diameter is hardly angled to the metopic suture; horn cores inserted closely with little basal, but more distal, divergence; the presence of transverse ridges along the anterior horn core surface varies from moderately strongly marked along the entire horn core length to very weakly marked in the distal parts only; there are distinct localized basal horn core swellings situated either postero-laterally, pos-

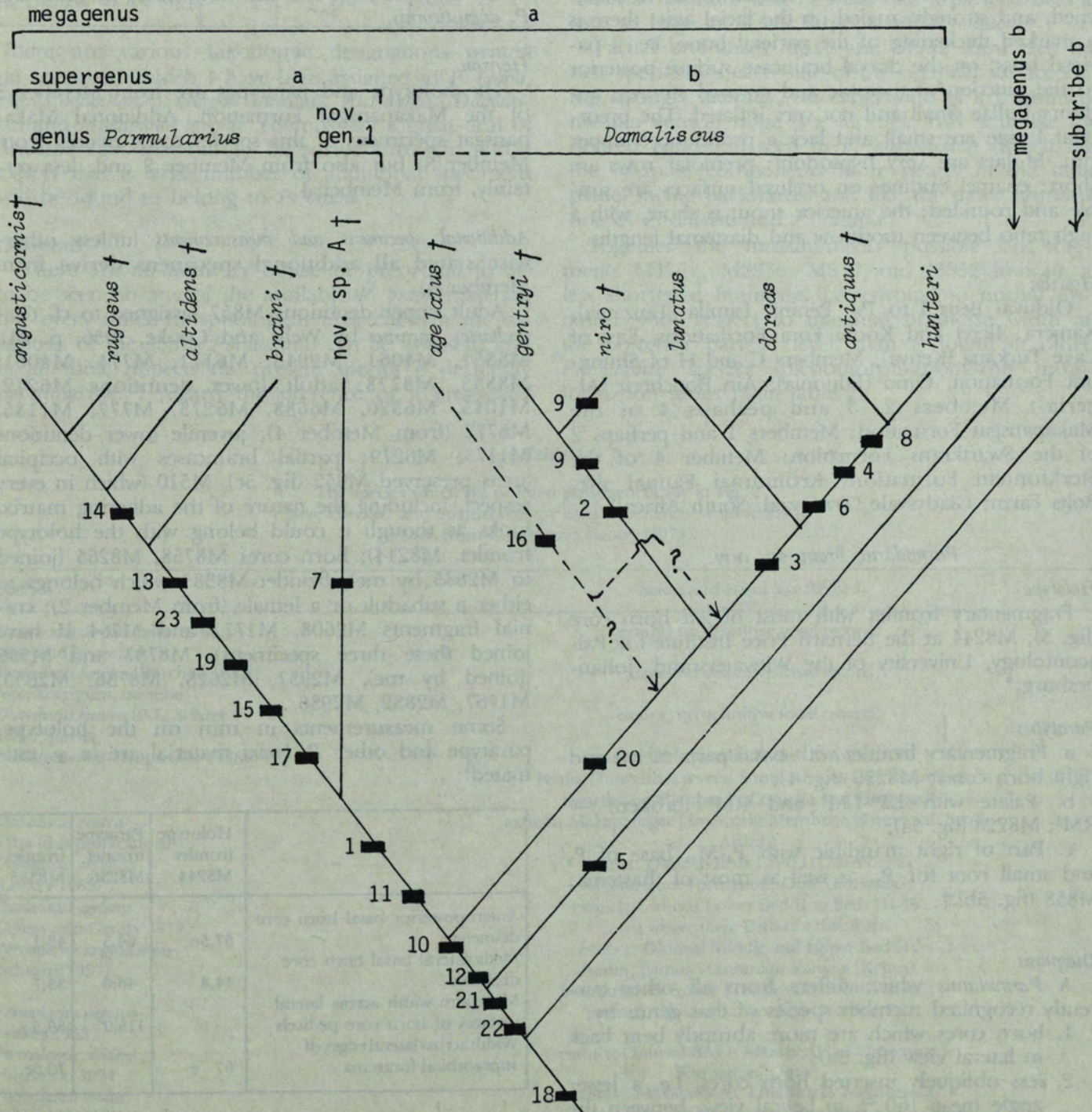


Figure 2. Phylogenetic relationships of species in the *Damaliscus-Parmularius* complex (i.e. megagenus a of fig. 1) (adapted from fig. 2 in Vrba, 1978).

■ = apomorphy, or derived character state, shared by species cluster below which it appears; apomorphies 1-23 as defined in Table 2; details of species are given in Table 1.

† = extinct.

teriorly, or postero-medially; in lateral view the horn core-pedicel boundary is oblique, being anteriorly higher than posteriorly (probably connected with the previous character of basal swelling). Horn pedicels are well defined, with near parallel sides, and are long. The basal horn core to orbit distance is long, partly resulting from pedicel length but also from elongation of the frontal anteriorly and laterally to the pedicels. The supraorbital foramina are not markedly far apart. The dorsal braincase, between coronal suture and nuchal crest, is shortened, and strongly angled on the facial axis; there is a marked thickening of the parietal bone, i.e. a parietal boss, on the dorsal braincase surface posterior to the junction of metopic and coronal sutures; auditory bullae small and not very inflated. The preorbital fossae are small and lack a pronounced upper rim. Molars are very hypsodont; premolar rows are short; enamel outlines on occlusal surfaces are simple and rounded; the anterior snout is short, with a high ratio between toothrow and diasternal lengths.

Horizon

Olduvai Beds I to IV; Peninj; Isimila (Tanzania); Kanjera; Ileret and Koobi Fora Formations, East of Lake Turkana (Kenya); Members C and H of Shungura Formation, Omo (Ethiopia); Ain Boucherit (Algeria); Members 2, 3 and perhaps 4 of the Makapansgat Formation; Members 1 and perhaps 2 of the Swartkrans Formation; Member 4 of the Sterkfontein Formation; Kromdraai Faunal site, Bolts Farm; Gladysvale (Transvaal, South Africa).

Parmularius braini sp. nov.

Holotype

Fragmentary frontlet with most of left horn core (fig. 3); M8244 at the Bernard Price Institute for Palaeontology, University of the Witwatersrand, Johannesburg.*

Paratypes

- Fragmentary frontlet with basal parts of left and right horn cores; M8236 (fig. 4);
- Palate with LP⁴-LM³ and RM¹ (broken) — RM³; M8228 (fig. 5a);
- Part of right mandible with P₄-M₃, base of P₃ and small root for P₂, as well as most of diastema; M858 (fig. 5b).†

Diagnosis

A *Parmularius* which differs from all other currently recognized member species of that genus by:

- horn cores which are more abruptly bent back in lateral view (fig. 3a);
- less obliquely inserted horn cores, i.e. a lesser angle (near 160 °), in lateral view, between the basal horn core and the face anterior to the pedicels than is found in other *Parmularius* species (near 180 °) (Fig. 3a);
- stronger basal horn core compression;

- more prominent transverse ridges on the anterior horn core surface, which extend over a greater part of the horn core length;
- supraorbital foramina which are wider apart, although they appear to be closer together than in the genus *Damaliscus* (fig. 3b).

The posteromedial positions of the basal horn core swellings in the type material (figs. 3a and 4) are shared by specimens belonging to *P. altidens*. The straight coronal suture, without forward indentation at the metopic suture, is also found in *P. rugosus* and *P. angusticornis*.

Horizon

The holotype and paratypes are from Member 3 of the Makapansgat Formation. Additional Makapansgat specimens of this species come mainly from Member 3, but also from Member 2 and, less certainly, from Member 4.

Additional specimens and measurements (unless otherwise stated all additional specimens derive from Member 3)

Adult upper dentitions M857 (assigned to cf. *Connochaetes taurinus* by Wells and Cooke, 1956, p. 24), M8351, M4061, M2943, M6171, M774, M1061, M8835, M8778; adult lower dentitions M6272, M1045, M6320, M6688, M6273, M777, M1185, M8772 (from Member 4); juvenile lower dentitions M1173, M6279; partial braincases with occipital areas preserved M952 (fig. 5c), M510 (which in every respect, including the nature of the adhering matrix, looks as though it could belong with the holotype frontlet, M8244); horn cores M8758, M8265 (joined to M2635 by me); frontlet M8385 which belongs to either a subadult or a female (from Member 2); cranial fragments M2608, M1771 and M764 (I have joined these three specimens), M8737 and M556 (joined by me), M2937, M2628, M8736, M2655, M1767, M2832, M2936.

Some measurements in mm on the holotype, paratype and other *P. braini* material are (e = estimated):

	Holotype frontlet M8244	Paratype frontlet M8236	frontlet M8385
Anteroposterior basal horn core diameter	67,5e	64,5	43,1
Mediolateral basal horn core diameter	44,8	46,0	35,7
Minimum width across lateral surfaces of horn core pedicels		116,0	89,5
Width across lateral edges of supraorbital foramina	67 e		70,5e

* All type specimens described, as well as all other Makapan fossils (catalogue numbers preceded by M) mentioned, are housed in this institution.

† This specimen was assigned to cf. *Connochaetes taurinus* Burchell by Wells and Cooke (1956, p. 24).

	Paratype palate M8228	Paratype palate M857	Paratype r. man- dible M858	l. man- dible M1045	l. man- dible M6272
LM ¹⁻³ length (maximal buccal occlusal length)	71,8				
Palatal width (across buccal surfaces of M ²⁻⁵)	89,5	93,5			
M ₁₋₃ length (maximal lingual occlusal length)			68,5	68,5	75 e
P ₂₋₄ length (as for M ₁₋₃)			26 e	26,5e	29 e

There are various taxonomic designations written on specimens which I have here assigned to *P. braini*, e.g. *Connochaetes*, *Gorgon taurinus*, *Alcelaphus*, *Damaliscus* and *Makapania broomi*. There is still a great deal of Makapansgat material to be sorted through, and I expect that a large number of additional specimens will be found to belong to *P. braini*.

Comments

There are no auditory bullae or preorbital fossae to be seen on any of the available *P. braini* material, but every other morphological area cited in the diagnosis of the genus *Parmularius* can be assessed; and in all these respects the present species is decidedly parmularine. I regard the presence of a pronounced

parietal boss as the single most diagnostic feature of this genus, because it alone among the five derived cranial character states shared by members of *Parmularius* (fig. 2) is unique among all Bovidae. The parietal boss of *P. braini*, only partially visible (as a result of damage) on the paratype M8236 (fig. 4) and cranial roofs M2936 and M1777, is best seen in specimens M2628 and M2832. Of previously described *Parmularius* species *P. altidens* has a larger boss than have either *P. angusticornis* or *P. rugosus*. The present material indicates that *P. braini* had a parietal boss at least as large as, if not larger than, *P. altidens*.

Partial braincases M510 and M952 show that the new species has each side of the occipital surface facing strongly laterally, on either side of a prominent median vertical ridge (see fig. 5c). This is unlike the derived condition seen in *P. angusticornis* (which has the occipital components more nearly in the same plane, facing backwards) and like the more primitive one of *P. altidens* and *P. rugosus*.

Together the measurements possible on fragments M1777, M2936, M510 and M952 indicate a less shortened braincase (i.e. coronal to nuchal distance), with respect to maximal braincase width at the posterior parietal level, than is found in other *Parmularius* species (plesiomorph-apomorph transformation series 14 in table 2).

Table 1

The species which are ordered phylogenetically in Fig. 2
I have checked and augmented my own experience of these fossil records from Gentry and Gentry (1977).

Species	Status and Fossil Site Record
<i>Damaliscus dorcas</i> (Pallas 1766) bles- and bontebok	extant; no definitive fossil record;
<i>Damaliscus lunatus</i> (Burchell 1832); topi, korrigum, tsessebe	extant; no definitive fossil record;
<i>Damaliscus hunteri</i> (P.L. Sclater 1889); hirola	extant; no definitive fossil record;
<i>Damaliscus niro</i> (Hopwood 1936)	extinct; Olduvai Middle Bed II to Bed IV; Peninj (Tanzania); several South African sites including Swartkrans Member 2, Cornelia and Florisbad.
<i>Damaliscus gentryi</i> Vrba (this publication)	extinct; Makapansgat Limeworks Member 5 (Transvaal, South Africa);
<i>Damaliscus antiquus</i> (Leakey 1965)	extinct; Olduvai Beds I and II; Member G of Shungura Formation, Omo (Ethiopia);
<i>Damaliscus agelaius</i> Gentry and Gentry 1977	extinct; Olduvai Lower Bed II to Beds III-IV (area where these Beds not divisible).
<i>Parmularius angusticornis</i> (Schwarz 1937)	extinct; Olduvai Middle and Upper Bed II; Peninj; Isimila (Tanzania); Kanjera (Kenya) Swartkrans Member I (Transvaal, South Africa);
<i>Parmularius rugosus</i> Leakey 1965	extinct; Olduvai Lower Bed II to Bed IV
<i>Parmularius altidens</i> Hopwood 1934	extinct; Olduvai Bed I; Member H of Shungura Formation, Omo;
<i>Parmularius braini</i> Vrba (this publication)	extinct; Makapansgat Limeworks Members 2, 3 and 4; Member C of Shungura Formation, Omo; Ileret and Koobi Fora Formations, East of Lake Turkana (Kenya); Ain Boucherit (Algeria);
nov.sp. A, based on Laetolil (Lit.) 1959.277	extinct; Laetolil Beds <i>sensu stricto</i> (M. D. Leakey <i>et al.</i> , 1976) (Tanzania)

If the joined horn core, M8265 + M2635, belongs to this species (the compression, nature of anterior transverse ridges and basal horn core hollowing make this highly likely), then *P. braini* horn cores must have varied quite a bit in the degree of back-bending in lateral view. This horn core is considerably less bent than is that of the holotype, M8244 (fig. 3a).

The paratype mandible M858 is sufficiently well preserved to allow an estimate of diastemal length. The ratio between P_3 - M_3 occlusal length and diastemal length (character 21 in table 2) would have been well over 110 %. I have measured this ratio on samples of all modern alcelaphine species and have not found a single individual of any species (other than *Connochaetes gnou* (Zimmermann) with a mean ratio of 121 %) with a ratio larger than 110 %. On the other hand this short snouted condition is definitely also found in mandibles of *P. altidens* from Olduvai Bed I and in Olduvai Bed II and Swartkrans Member I specimens which I attribute to *P. angusticornis*. I interpret this feature, and the simple, rounded, occlusal enamel morphology of the teeth, as primitive character states retained by the genus *Parmularius*, which I suspect may be found to separate it from the genus *Damaliscus* once mandibles of fossil damaliscines are better known.

Gentry and Gentry (1977) mention that about half the mandibles of Olduvai Bed I *P. altidens* lacked P_2 during life. In presumed *P. angusticornis* mandibles, which I have seen, the proportion of mandibles lacking P_2 (and its alveolus) was even greater. Of three *P. braini* mandibles from Member 3, and one from Member 4, all four had the tooth during life. This is a meagre sample, but it suggests that *P. braini* may have undergone less premolar reduction than the other *Parmularius* species.

The paratype frontlet, M8236, has a tendency to anterior horn core keels, a feature which I have not seen on other fossil and recent Alcelaphini. It is reminiscent of the condition in some caprines, an African fossil example being *Pachytragus solignaci* Robinson from the late Miocene Beglia Formation of Tunisia. I mention caprines, rather than other bovid groups, because I interpret the origin of the tribe Alcelaphini, and of the closely related Aepycerotini, as being from caprine stock.

Apart from its close relationship to other *Parmularius* species, particularly *P. altidens*, *P. braini* is most similar to the new Laetolil species based on skull (Lit.) 1959.277 (nov.sp.A in fig. 2, which I interpret as belonging to a genus separate from *Parmularius*) and to *Damaliscus niro* (Hopwood).

In what I have termed "supergenous a" (fig. 2), each temporally succeeding species branch has straighter horn cores in lateral view than the preceding one. While the strong lateral bending (character 7 in table 2) of nov.sp.A. does represent an apomorphy, stepwise reversal of the trend in *P. braini*, *P. altidens* and finally the species pair *P. angusticornis* and *P. rugosus*, would be a possible explanation. If this were

acceptable, the Laetolil species would qualify as a possible ancestor for *P. braini* (and for the genus *Parmularius*), because in every other respect it appears to be either less advanced than, or equally as primitive or advanced as, the latter. It has more uprightly inserted horn cores, which are less compressed and lacking transverse ridges and have basal swellings situated postero-laterally rather than postero-medially. The horn core to orbit distance is relatively short as in *Damaliscus*, and unlike *Parmularius*, in spite of the fact that the horn pedicels are distinctly lengthened, an apomorphy shared uniquely among alcelaphines with *Parmularius* (fig. 2). The supra-orbital foramina are probably (size independently) somewhat closer together than in *P. braini*. The braincase is less bent with respect to the facial axis, and longer and thinner, than in all *parmularines*. The occipital surfaces face at least as strongly laterally as in *P. braini*. The coronal suture is straight as in *P. braini*, while the parietal boss behind it is much less marked and more like that of *Damaliscus* species (fig.2).

Five features were cited above in the diagnosis of *P. braini*, as removing it from other *Parmularius* species. Four of these represent close approaches to the respective character states in *Damaliscus niro*: the lesser angle (than in other *parmularines*) between basal horn core and face in lateral view is as in *D. niro*; the stronger basal horn core compression is only slightly less marked; the stronger and more extensive transverse ridges on the anterior horn core surface, while not as marked nor as widely spaced as those of *D. niro*, nevertheless represent a closer approach to the latter than do their homologues in other *Parmularius* species; the wider separation of supraorbital foramina is probably (size independently) only slightly less marked than in *D. niro*. Some Olduvai Bed II horn cores, which Gentry and Gentry (1977) termed "type A" horn cores and doubtfully included in *D. niro*, are reminiscent of *P. braini*: they have a more marked change in backward curvature halfway between base and tip than other *D. niro* specimens, transverse ridges which are closer together and a small basal postero-lateral swelling. However, the elongated horn pedicels and horn core-orbit distance, as well as the pronounced parietal boss, remove *P. braini* decisively from all *D. niro* specimens on which these features can be seen. I prefer to place greater weight on these three apomorph character states, and to interpret the other resemblances as resulting from homoplasy (i.e. "resemblance not due to inheritance from a common ancestor"; Simpson, 1961). This preference is expressed in Figure 2.

Parmularius braini appears to have had a wide distribution in Africa. There are several well-preserved specimens among the fossil assemblages from East of Lake Turkana (previously Lake Rudolf), Kenya, which could belong to *P. braini*: e.g. left horn core KNM-ER270 (ER 68 FS-140), right horn core KNM-ER282 (ER 69 FS-87), frontlet KNM-ER 1596 (ER72

FS-153) and others. They differ from the Makapansgat specimens in having horn cores that are inserted more widely apart, basal horn core swellings that are situated postero-laterally rather than postero-medially, slightly less compressed basal horn cores, a lesser brain-face angle, more uprightly inserted horn cores (i.e. a smaller angle between the anterior basal horn core and the face in lateral view), and probably by a more abrupt backbending of the horn core in lateral view. With respect to the four last mentioned features, the East Turkana form appears to be less advanced than the Makapansgat one. I interpret these differences as indicating no more than subspecific differentiation. Two further fossil specimens from additional African sites probably belong to *Parmularius braini*: right horn core L.292-29 from Member C of the Shungura Formation (Omo, Ethiopia); and left horn core 1954-15-72 from Ain Boucherit (Algeria). Both specimens resemble Makapansgat *P. braini* horn cores in that the widest part of the basal transverse section is not situated anteriorly, as is the case in several *Damaliscus* species (including *D. niro*, except, according to Gentry and Gentry, 1977, some "Type A" horn cores); in the size and spacing of anterior transverse ridges; and in a comparable backward curvature in lateral view.

The specific name is after Dr. C. K. Brain in recognition of all he has done towards elucidating stratigraphical, geomorphological, taphonomic and faunal aspects of the Transvaal australopithecine cave assemblages.

Genus *Damaliscus* Sclater and Thomas 1894

Type species *Damaliscus dorcas* (Pallas 1766)

Generic diagnosis

Small to medium-sized alcelaphines with high narrow skulls. Horn core torsion may be absent, or incipient to pronounced anticlockwise*; there is a tendency for horn core tips to be directed upwards, when seen in lateral view, which increases proportionally to the degree of anticlockwise torsion; transverse ridges on anterior horn cores have a tendency to be present over the entire surface rather than just near the tips, and vary in expression from very slight to pronounced; there is little tendency to basal horn core swelling; the greatest basal horn core diameter may be slightly to strongly angled with respect to the metopic suture (angulation brought about by posterior horn core swinging laterally). Horn pedicels are well defined with near-parallel sides, but short. The basal horn core to orbit distance is short, partly resulting from the shortness of the horn pedicel but also from a lack of elongation of the frontal anteriorly and laterally to the pedicels. Supraorbital foramina are widely separated. The dorsal braincase, between coronal and nuchal crest, is shortened but longer than in *Parmularius*; the braincase is less bent with respect to the facial axis than in *Parmularius* and *Alcelaphus*. The coronal suture is straight, or only slightly indented

anteriorly at the metopic. There is a slight tendency to a parietal boss on the dorsal braincase. The surfaces of the occipital face mainly backwards, rather than laterally (i.e. they are more in one plane). The preorbital fossae are fairly large, larger than in *Parmularius*, with pronounced upper rims. The occlusal enamel configurations on dentitions have a tendency to greater complexity than those of *Parmularius*; premolar rows are fairly long in living species with P_2 's often retained.

Horizon

Olduvai Beds I to IV; Peninj (Tanzania); Member G of Shungura Formation, Omo (Ethiopia); Makapansgat Limeworks Member 5; Swartkrans Member 2; Sterkfontein Members 5 and 6 (Transvaal, South Africa); several mid-Pleistocene to later South African sites including Cornelia and Florisbad.

Damaliscus gentryi sp. nov.

Holotype

Fragmentary frontlet with basal parts of both horn cores, all surfaces extensively weathered; M8874 (figs. 6 and 7).

Diagnosis

A large *Damaliscus*, larger than *D. lunatus* and comparable in size to the larger specimens of *D. niro*. Backbending of the lower half of the horn core in lateral view is pronounced and commences almost immediately above the level of the anterior horn core-pedicel boundary, i.e. sooner than in any currently available specimens assigned to *D. niro*. In lateral view the horn core-pedicel boundary is oblique being anteriorly considerably higher than posteriorly; basal horn core swellings are absent. The frontal sinus extends far up (more than 2 cm above the anterior horn core-pedicel boundary in the holotype) into the horn core. Horn cores are more uprightly inserted than in extant *Damaliscus* species (i.e. with a lesser angle, in lateral view, between the basal horn core and the face anterior to the pedicels), as they are in *D. niro*. The horn cores diverge quite strongly and evenly from the base with a mutual angle between 40° and 50°. The mediolateral width of the horn core cross section is wider anteriorly than posteriorly, a tendency which becomes increasingly marked as one proceeds upward from the base. Horn pedicels and horn core-to-orbit distance are short, with orbital rims hardly projecting.

Horizon

The holotype was found low in Member 5 (Bed A) of the Makapansgat Formation. No additional specimens are known.

Measurements

Some measurements in mm on the holotype, M8874, are (e = estimated):

* Measured in the right horn core as seen from the base up.

Table 2
Hypothesis of apomorphy
 (all orientational terms in relation to a horizontal tooththrow)

character	state	
	plesiomorph (=primitive)	apomorph (=derived, or advanced)
<i>horn cores</i>		
1. basal swelling	absent	localized swelling present
2. surface contours	lateral and/or medial surfaces not flattened	lateral and medial surfaces flattened
3. torsion I (assessed on right core from base up)	no torsion	at least weak (i.e. involving mainly distal part) anticlockwise
4. torsion II	not pronounced	pronounced anticlockwise
5. torsion III	no torsion	at least weak clockwise
6. angle of max. basal diameter to metopic suture	$\pm < 60^\circ$	$\pm > 60^\circ$ with posterior margin swivelling laterally
7. course in lateral view I	less so	whole anterior surface strongly convex resulting from abrupt backward curvature about half way up
8. course in lateral view II	absent	tips elongated, straight, near parallel, pointing up
9. anterior transverse ridges	absent to weakly marked; where present ridges are closely spaced	strongly marked ridges spaced far apart
<i>horn pedicels</i>		
10. definition	absent to poorly defined with sloping sides	well-demarcated from horn core and rest of frontal, with near parallel sides
11. length	short	long
<i>braincase</i>		
12. parietal boss incidence I	boss absent	distinct localized "bump" or boss (a thickening of the parietal) posterior to the junction of metopic and coronal sutures
13. parietal boss II incidence	not enlarged	boss enlarged
14. brain proportion	ratio $\pm > 60\%$	length/width ratio $\pm < 60\%$ (coronal to nuchal length/max. width in midregion)
15. brain-face angulation	angle (1) $\pm > 100^\circ$; angle (2) $\pm < 130^\circ$	angle (1) between occiput-bregma line and anterior frontal $\pm \leq 100^\circ$ (and by inverse correlation an angle (2) between occiput-bregma line and occipital surface of $\pm \geq 130^\circ$)
16. dorsal parietal in lateral view	not markedly convex	marked convexity forming dome
<i>miscellaneous</i>		
17. horn core to orbit distance (assessed independently of character 11)	short	long
18. internal frontal hollowing	absent to poorly developed	extensive (i.e. past supraorbital canals and into orbital rims) with a single large smoothwalled sinus which extends into basal horn core
19. preorbital fossa	pronounced upper rim present, foss deep and extensive	loss of pronounced upper rim, and fossa less deep and extensive (or more reduced)
20. separation of supraorbital foramina	not wide apart	wide apart
21. face length	ratio $\pm > 120\%$	tooththrow/diastema ratio $\pm \leq 120\%$ (P_3 - M_3 occlusal length/min. distance between bone-tooth contacts of P_3 and C)
22. tooth morphology	basal pillars (ectostylids) present on adult lower molars; occlusal enamel pattern less rounded and more angular	basal pillars absent; occlusal enamel pattern markedly rounded (i.e. medial lobes of upper molars and lateral lobes of lowers rounded, wide out-bowing of ribs on uppers, central cavities with anterior and posterior rounding and tendency to central constrictions)
23. premolar length	P_2 present and large	P_2 absent or very reduced

Anteroposterior basal horn core diameter	62 e
Mediolateral basal horn core diameter	48,5e
Minimum width across lateral surfaces of horn pedicels	112,0
Basal horn core separation	30 e
Width across lateral edges of supraorbital foramina	62 e

Comments

Only a few of the diagnostic features for the genus *Damaliscus* are preserved on M8874. With respect to each of these the new form is decidedly damaliscine, and seems to be very closely related to *Damaliscus niro*. Gentry and Gentry (1977), in addition to the main body of typical *D. niro* specimens, doubtfully include in the species two horn core varieties (which they called Types A and B) from the BK site in Upper Bed II, Olduvai. This species appears to have undergone a size decrease, from the large specimens of Peninj and typical Olduvai *D. niro*, through the smaller Cornelia material, to the smallest from Florisbad and other late Pleistocene South African sites. *Damaliscus gentryi* is closest in size to the larger Olduvai and Peninj specimens and, according to Gentry and Gentry's (op. cit.) measurements, decidedly larger than Olduvai Type A and B varieties. However, in the following morphological respects it appears to resemble Type A specimens rather than any typical *D. niro*: type A horn cores have a more marked change in backward curvature, less basal compression and closer spacing of transverse ridges (op. cit.). (The latter comparison rests very tentatively on faint hints of ridges present on the anterior surface of the left horn core fragment of M8874). I am hoping that further Makapansgat finds may clarify whether M8874 really belongs to a species closely related to but separate from *D. niro*, as here suggested, or merely to a subspecies of that taxon.

The specific name is after Dr. A. W. Gentry, who has contributed more than anyone else to an understanding of the phylogenetic relationships of African fossil and recent Bovidae.

REMARKS ON CHRONOLOGICAL CORRELATION

A few general remarks, on faunal chronological correlation, may serve to place into perspective the particular ones concerning Makapansgat alcelaphines. The basic limitations stated here may seem obvious. While they are probably generally tacitly understood, they seem to be only rarely incorporated into published reasoning and conclusions.

1. *Temporal ranges of species.* Species have temporal ranges, and are generally not "flash" occurrences in time (although the palaeontologist often only glimpses "flashes"). In terms of the species definition it would be nonsense to postulate anything other than that temporal ranges of one species in geographically separate areas must overlap. On the other hand, chronological matching of sepa-

rate fossil occurrences of the same species, without recognizing the error limits imposed by the total duration time of that species, is simplistic.

2. *Interpretation of morphoclines.* There is a time-honoured and ubiquitous practice among palaeontologists: states of particular morphological characters (most frequently of dentitions in the case of higher vertebrates) are ordered into a primitive-to-advanced series. Then phyletic gradualism, and consequently temporal succession, are assumed for fossils showing that series of character states. We know that comparable advances in homologous structures frequently occur in separate lineages (some writers have referred to such convergence as being "rampant"). We also know that the rates of evolutionary advance may differ in different lineages. We should further consider that, in accordance with the allopatric speciation (as distinct from the phyletic gradualist) model, the ancestral morphology may survive together with the descendant one and indeed may outlast it. The fact that a primitive-to-advanced series for one morphological character may be encountered in a closely related group *at any one time* is amply demonstrated among recent faunal elements (for instance dentitions of some modern member species of the tribe Alcelaphini, as well as of other mammalian groups, might well be interpreted erroneously as temporally successive, if found in isolation in the fossil record). From all this it follows that an assertion of reasonably precise temporal correlations, based on stages of a morphological series, is logically indefensible unless it can be demonstrated independently (of the character from which time is inferred) that the series is a true transformation series, or belongs to a single lineage. I stress "independently", because all too often both the temporal correlation, as well as the necessary underlying assumption of presence on a single lineage, are deduced in circular fashion from the same morphocline.

3. *Interpretation of overall faunal similarity.* An important palaeontological task concerns the interpretation of differences between faunal compositions of fossil assemblages. It seems to be difficult to remember (judging by literature on chronological correlation) that, once taphonomic influences have been considered, observed differences need not necessarily be attributed to time, or to time only. Thus ecological factors may in reality be responsible for observed effects that are attributed to time, and vice versa. As an example may be cited the faunal compositions of the Wankie and Kalahari Gemsbok National Parks. From census data (Vrba, n.d.) I computed faunal similarity for the large mammalian genera, by means of a formula which has in the past been used to make chronological deductions on certain Pleistocene fossil assemblages (similarity values being interpreted as inversely propor-

tional to time difference). Similarity of Kalahari to Wankie (contemporaneous and some 800 km apart) was found to be low, much lower than to some fossil assemblages. Clearly ecology is responsible in this case. Even when both time and environment are held constant, geographic separation may produce differences. For example, the apparent restriction to the Transvaal of the three most abundant bovid species of Makapansgat, mentioned in the introduction, probably results from geographical/environmental factors.

Numerous specialists, working on problems relating to the Plio-Pleistocene hominid-associated fossil record, accord importance to time differences of the order of fractions of a million years. In attempts to date South African australopithecine assemblages we still depend heavily on faunal correlation. Perhaps the brief and simple reservations expressed here will help the reader (especially the non-palaeontologist) to evaluate realistically the few remarks which follow, as well as other faunal correlations.

The facts concerning the record of *Parmularius braini* and related taxa are:

I am satisfied that specimens from Makapansgat Members 2 and 3 belong to *P. braini*. From Member 4 only a single fragmentary mandible, M8772, which could belong to this species, has so far come to light. It had a well-developed P_2 during life, and thus (in view of my previous discussion on premolar length in parmularines) is more likely to belong to *P. braini* than to another *Parmularius* species. Nonetheless I will confine these remarks to the secure Member 2 and 3 *P. braini* representations.

The more advanced, but closely related (fig. 2), *Parmularius altidens* is not recorded prior to its abundant occurrence in Olduvai Bed I, while *P. braini* is absent from this alcelaphine-rich site. The most advanced *Parmularius* species, *P. angusticornis*, occurs in Swartkrans Member 1, Olduvai Middle and Upper Bed II, Peninj, Isimila and Kanjera. From the Laetolil Beds *sensu stricto*, with an upper age limit of 3,6 m.y. (M. D. Leakey *et al.*, 1976), we have the species based on (Lit.) 1959.277 (nov.sp.A. in fig. 2). I have discussed above that all we know of this species qualifies it for ancestry of *P. braini* and of the genus *Parmularius*.

P. braini is probably present in Member C of the Shungura Formation, which covers a time range of approximately 2,6–2,4 m.y. (Brown and Nash, 1976; Brown and Shuey, 1976). In the alcelaphine sample from the Hadar Formation, Ethiopia (dated near 3 m.y. ago, Aronson *et al.*, 1977), which I saw in October 1976, *P. braini* was absent.

East of Lake Turkana, specimens belonging either to *P. braini* or to a closely related species, as well as a cranium of *P. altidens*, all derive from what is currently referred to as Collection Unit 4 (J. M. Harris, pers. comm.). Samples referred to Collection Unit 4 have been loosely temporally correlated on the basis of evolutionary change exhibited by suid species

(White and Harris, 1977), although their correlation cannot at present be demonstrated lithostratigraphically. The suid correlation tentatively implies that the temporal ranges of these samples belong to the period later than the date of the KBS tuff (and preceding that of the Koobi Fora tuff). However, the authors (op. cit.) are quite clear in pointing out that the identity of the KBS tuff can only be established in two of the numerous fossiliferous areas of East Turkana. Unfortunately the latter do not include the sources of the *Parmularius* specimens which I have seen. On the basis of radiation damage and isotopic decay series techniques several dates have been suggested for (1) The KBS tuff in type area 105; $2,61 \pm 0,26$ m.y. (Fitch and Miller, 1970; Fitch *et al.*, 1974), $1,60 \pm 0,05$ m.y. (Curtis *et al.*, 1975), $2,42 \pm 0,01$ m.y. (Fitch *et al.*, 1976); and for (2) What was previously considered to be the KBS tuff in areas other than the type area: $1,60 \pm 0,05$ m.y. in area 10 (Curtis *et al.*, 1975), $1,82 \pm 0,04$ m.y. in area 131 (op. cit.), $2,44 \pm 0,08$ m.y. in area 131 (Hurford *et al.*, 1976). Palaeomagnetic results appear to be compatible with both earlier and later alternatives (Hillhouse *et al.*, 1977).

From all this, on the basis of occurrence of *P. braini* alone, I would have extracted a tentative hypothesis that the time ranges of *P. braini*, and of Makapansgat Members 2 and 3, may belong between 2–3 m.y. ago with the latter part of that time range preferable to the earlier. Among the East Turkana dating alternatives quoted above the earlier are more apposite to the present case than the later ones.

The first dating estimates, which are more rigorously based than solely on faunal correlation, for Makapansgat (or indeed for any South African australopithecine breccia) come from Brock, McFadden and Partridge (1977). In the interpretation of their preliminary palaeomagnetic results (op. cit.) they suggest that the upwards transition from reversed to normal polarity low in Member 2 is likely to have an age of either 3,32, 2,94, or 2,80 m.y., using Cox's (1969) time scale. On the basis of additional research they prefer the 3,32 m.y. alternative (reported at the May 1977 conference of the South African Society for Quaternary Research), and further suggest that the Kaena and Mammoth events within the Gauss normal epoch might be represented in Member 4. According to this interpretation most of Member 2 and all of Member 3 are bracketed between 3,32 and 3,06 m.y. or between 3,32 and 2,90 m.y.

If one rejects a later alternative in the interpretation of these palaeomagnetic results, a temporal distribution for *P. braini*, roughly spanning the time gap between the Laetolil and *P. altidens* members of the same lineage (fig. 2), must be considered. A second implication would be that the temporal distributions of the fossil finds of *P. braini* (not of the species itself) in East and South Africa are disjunct. Neither of these implications presents any difficulty: temporal ranges of near 1,5 m.y. are on record for

several alcelaphine species (Vrba, 1978, fig. 4). Concerning the second point one must remember that probably less than 10 % of the 2–4 m.y. time span is sampled in present Southern African fossil assemblages: the entire 2–3 m.y. "slice", from the point of view of identifiable alcelaphine remains (here I except Sterkfontein Member 4, formerly the Type Site, and Taung with their poor bovid remains), may be lacking.

The *Damaliscus* specimen M8874 from low in Member 5, here described as *Damaliscus gentryi*, suggests temporal correlation with the larger *D. niro* specimens of Peninj and Olduvai Bed II, or possibly with a somewhat earlier date than the base of Bed II. Such an interpretation, taken together with the estimates for Members 2–4 of Brock, McFadden and Partridge (1977), which were mentioned above, necessitates recognition of a substantial time lag between Members 4 and 5. This appears to be in

agreement with Partridge's brief description of Makapansgat stratigraphy. He writes (op. cit., p. 249) that Member 5 rests unconformably upon an eroded surface of Member 4, and that this unconformity probably represents a considerable lapse of time.

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REFERENCES

- ARONSON, J. L., SCHMIDT, T. J., WALTER, R. C., TAIEB, M., TIERCELIN, J. J., JOHANSON, D. C., NAESER, C. W. and NAIRN, A. E. M. (1977). New geochronologic and palaeomagnetic data for the hominid-bearing Hadar Formation of Ethiopia. *Nature*, **267** (5609), 323–327.
- BROCK, A., MCFADDEN, P. L. and PARTRIDGE, T. C. (1977). Preliminary palaeomagnetic results from Makapansgat and Swartkrans. *Nature*, **266** (5599), 249–250.
- BROWN, F. W., NASH, W. P. (1976). Radiometric dating and tuff mineralogy of Omo Group deposits. In: Coppens, Y., Howell, F. C., Isaac, G. L. and Leakey, R. E. F., Eds, *Earliest man and environments in the Lake Rudolf Basin*. 50–63, University of Chicago Press, Chicago and London.
- and SHUEY, R. T. (1976). Magneto-stratigraphy of the Shungura and Usno Formations, Lower Omo Valley, Ethiopia. In: Coppens, Y., Howell, F. C., Isaac, G. L. and Leakey, R. E. F., Eds, *Earliest man and environments in the Lake Rudolf Basin*. 64–78. University of Chicago Press, Chicago and London.
- COX, A. (1969). Geomagnetic Reversals. *Science*, **163**(3864), 237–245.
- CRACRAFT, J. (1974). Phylogenetic models and classification. *Syst. Zool.*, **23**, 71–90.
- CURTIS, G. H., DRAKE, R. F., CERLING, T. E., CERLING, B. L. and HAMPEL, J. H. (1975). Age of KBS Tuff in Koobi Fora Formation, East Rudolf, Kenya. *Nature*, **258**, 395–398.
- FITCH, F. J., FINDLATER, I. A., WATKINS, R. T. and MILLER, J. A. (1974). Dating of the rock succession containing hominids at East Rudolf, Kenya. *Nature*, **251**, 213–215.
- , HOOKER, P. J. and MILLER, J. A. (1976). $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the KBS Tuff in Koobi Fora Formation, East Rudolf, Kenya. *Nature*, **263**, 740–744.
- and MILLER, J. A. (1970). Radioisotopic age determinations of Lake Rudolf Artefact Site. *Nature* **226**, 226–228.
- GENTRY, A. W. (1970a). Revised classification for *Makapania broomi* Wells and Cooke (Bovidae, Mammalia) *Palaeont. afr.* **13**, 63–67.
- (1970b). The Langebaanweg Bovidae. Appendix in: Hendey, Q.B., a review of the geology and palaeontology of the Plio-Pleistocene deposit at Langebaanweg, Cape Province. *Ann. S. Afr. Mus.*, **56**, 114–117.
- and GENTRY, A. (1977) (in the press). The Bovidae (Mammalia) of Olduvai Gorge, Tanzania. *Bull. Br. Mus. Nat. Hist. (Geol.)*, **29**(4), and 30(1).
- GRIFFITHS, G. C. D. (1972). The phylogenetic classification of Diptera: Cyclorrhapa. *Ser. Entomol.* **8**, 1–340.
- HENNIG, W. (1966). Phylogenetic systematics. Univ. Illinois Press, Urbana.
- HILLHOUSE, J. W., NDOMBI, J. W. M., COX, A. and BROCK, A. (1977). Additional results on palaeomagnetic stratigraphy of the Koobi Fora Formation, east of Lake Turkana (Lake Rudolf), Kenya. *Nature*, **265**, 411–415.
- HURFORD, A. J., GLEADOW, A. J. W. and NAESER, C. W. (1976). Fission-track dating of pumice from the KBS Tuff, East Rudolf, Kenya. *Nature*, **263**, 738–740.
- LEAKEY, M. D., HAY, R. L., CURTIS, G. H., DRAKE, R. E., JACKES, M. K. and WHITE, T. D. (1976). Fossil hominids from the Laetolil Beds. *Nature*, **262**, 460–466.
- NELSON, G. J. (1970). Outline of a theory of comparative biology. *Syst. Zool.* **19**, 373–384.
- SIMPSON, G. G. (1961). Principles of animal taxonomy. Columbia University Press, New York.
- VRBA, E. S. (1974). Chronological and ecological implications of the fossil Bovidae at the Sterkfontein australopithecine site. *Nature*, **250**, 19–23.
- (1975). Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil Bovidae. *Nature*, **254**, 301–304.
- (1976). The Fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai. *Transv. Mus. Mem.*, **21**, 1–166.
- (n.d.) The significance of bovid remains as indicators of environment and predation patterns. (Proceedings of the 1976 conference on "Taphonomy and Vertebrate Palaeoecology", Wenner-Gren Foundation for Anthropological Research.)
- (1978) (in the press). Phylogenetic analysis and classification of fossil and recent Alcelaphini (Family Bovidae, Mammalia).
- WELLS, L. H. (1969). Generic position of "*Phenacotragus*" *vanhoepeni*. *S. Afr. J. Sci.*, **65**, 162.
- and COOKE, H. B. S. (1956). Fossil Bovidae from the Limeworks Quarry, Makapansgat, Potgietersrust. *Palaeont. afr.*, **4**, 1–55.
- WHITE, T. D. and HARRIS, J. M. (1977). Suid evolution and correlation of African Plio-Pleistocene hominid localities. *Science*, **198**, 13–21.



Figure 3. *Parmularius braini*. Holotype frontlet M8244.

a = left lateral view;

b = anterior view.

(scales in Figures 3–7 in centimetres)



Figure 4. *Parmularius braini*. Paratype frontlet M8236 in left lateral view.

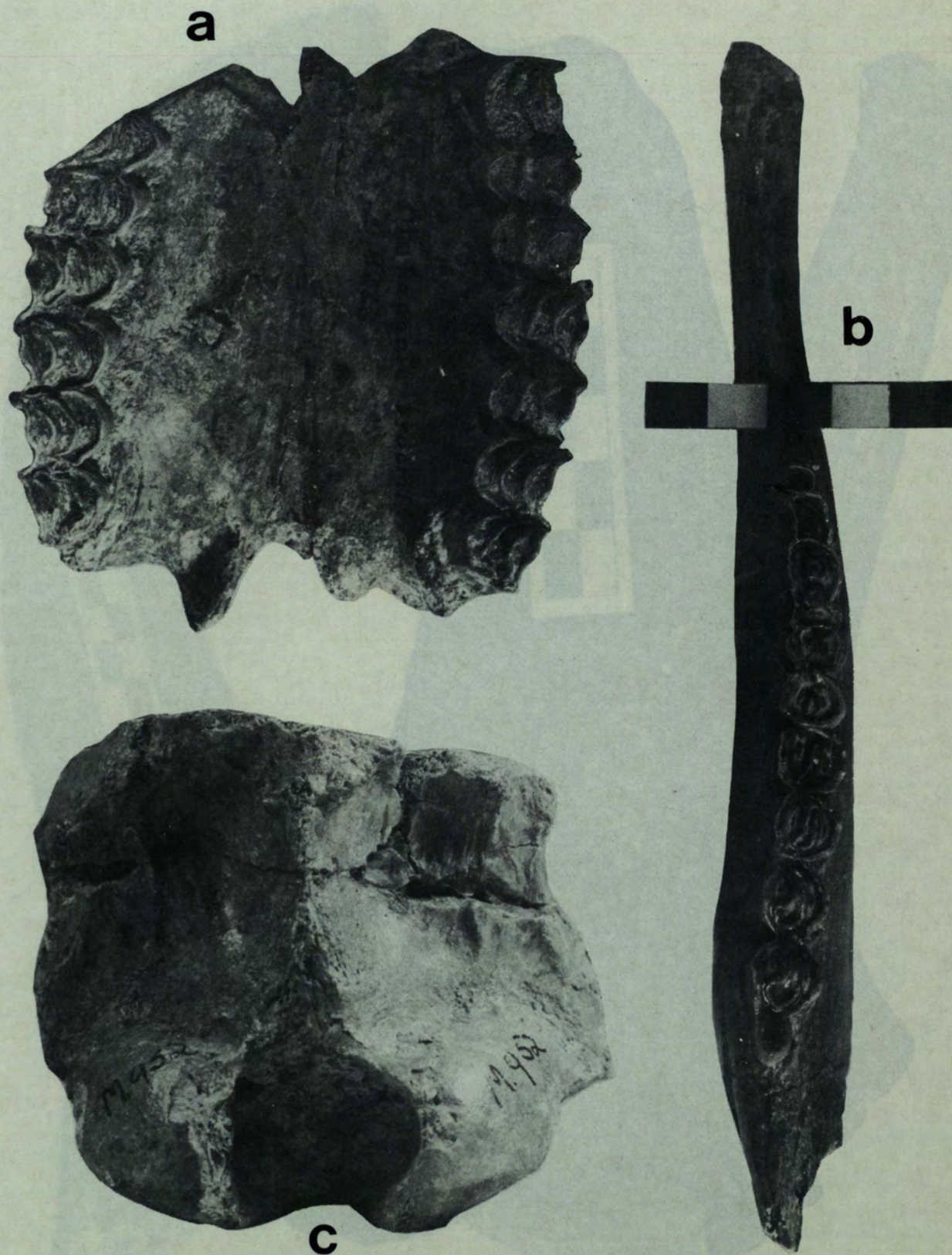


Figure 5. *Parmularius braini*.

- a = Paratype palate M8228 in occlusal view, anterior towards top of page;
 b = Paratype right mandible M858 in occlusal view; note sizes of hole for P_2 and root of P_3 ;
 c = partial cranium M952 in occipital view.



Figure 6. *Damaliscus gentryi*. Holotype frontlet M8874 in anterior view.



Figure 7. *Damaliscus gentryi*. Holotype frontlet M8874 in right lateral view.