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POSTCRANIAL EVIDENCE FOR THE EVOLUTION OF THE BLACK WILDEBEEST, *CONNOCHAETES GNOU*: AN EXPLORATORY STUDY

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ABSTRACT

Black wildebeest fossils from the interior of South Africa and the Cape coastal zone are compared to modern specimens in order to trace the pattern of morphological change and the distribution of the species through time. Measurements taken on selected postcranial skeletal elements, i.e. the axis and metapodials, suggest that the evolution of the black wildebeest was marked by a general reduction in body size. It appears that the evolution of *Connochaetes gnou* from a blue wildebeest-like (*C. taurinus*) ancestor is best documented in areas to the south of the Vaal River. Although the geographic range of the two temporal subspecies of *C. gnou* (*C. gnou laticornutus* and *C. gnou antiquus*) included the Cape ecozone, the reduction in body size appears to have beeen accelerated in the Cape coastal zone where in the Last Glacial *sensu lato* there was a regionally distinct population. This population, of smaller body size than extant populations, became extinct at the end of the Last Glacial with the onset of higher sea levels.

KEY WORDS:*Connochaetes gnou,* fossil history, biogeography

INTRODUCTION

The large mammal faunas of the Ethiopian faunal region are characterized by a certain degree of endemism, which is manifested at family level in some instances, but more pronounced in the subregions at generic and specific levels (Bigalke 1968). In the southern African sub-region, the tendency towards endemism appears to have increased from Miocene times into the Late Pleistocene (Hendey 1974, 1984; Klein 1984). A striking feature of southern African temperate grasslands, or highveld, is the association of the black wildebeest (*Connochaetes gnou*), blesbuck (*Damaliscus dorcas*) and springbuck (*Antidorcas marsupialis*). These species are all endemic to southern Africa, but have ecological counterparts of closely related species further to the north and in East Africa, in the blue wildebeest (*Connochaetes taurinus*), topi/tsessebe (*Damaliscus lunatus*) and gazelles (*Gazella* spp) respectively. Although the blesbuck and springbuck are found virtually unchanged since at least the beginning of the Late Pleistocene in southern Africa (Brink 1987; Brink and Deacon 1982), it appears that the black wildebeest did not reach its present form until much later.

In this paper I address the question of the origin of the black wildebeest and the nature of morphological and size changes that characterized the evolution of the species in time and in space. This study is exploratory as it forms part of a wider study of inland and coastal late Quaternary mammalian faunas and a full description of all relevant fossil material is not given here. The focus is on particular sites (Figure 1) and on those skeletal elements that would show changes in wildebeest body size.

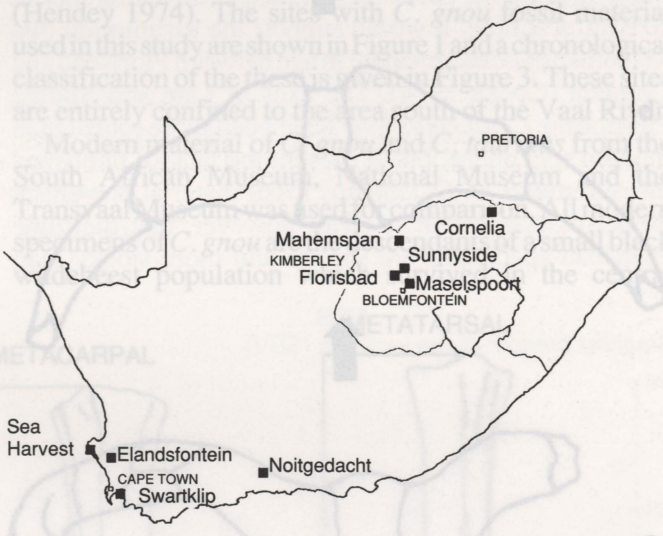

Figure 1: A locality map of sites (■) with black wildebeest material used in this study.

BACKGROUND

In spite of differences in horn shape and size the black wildbeest is very closely related to the blue wildebeest and they can interbreed successfully (Fabricius *et al.* 1988). In the recent past, before the ecological disruption of the interior of southern Africa by farming (Von Richter 1971), the two species experienced a small measure of range overlap in the Orange Free State and the southern Transvaal (Skead 1980), but no crossbreeding was documented. At least two temporal subspecies of *C. gnou*

are recognized at present on the basis of horncore shape, the Middle Pleistocene (Cornelian) form *C. gnou laticornutus* (Van Hoepen, 1932) and the end-Middle Pleistocene/Late Pleistocene (Florisian) *C. gnou antiquus* Broom, 1913 (Figure 2). The Middle Pleistocene specimens from Cornelia and Elandsfontein have horncores very similar to *C. taurinus*, but differ in having incipient basal bosses. The horncores also curve less downward and are not as recurved as in *C. taurinus* (see also Gentry 1978; Gentry and Gentry 1978; Van Hoepen 1932). The Florisian form of the black wildebeest is intermediate in form between the modern *C. gnou* and the Middle Pleistocene specimens from Cornelia and Elandsfontein (Gentry and Gentry 1978; Brink 1987).

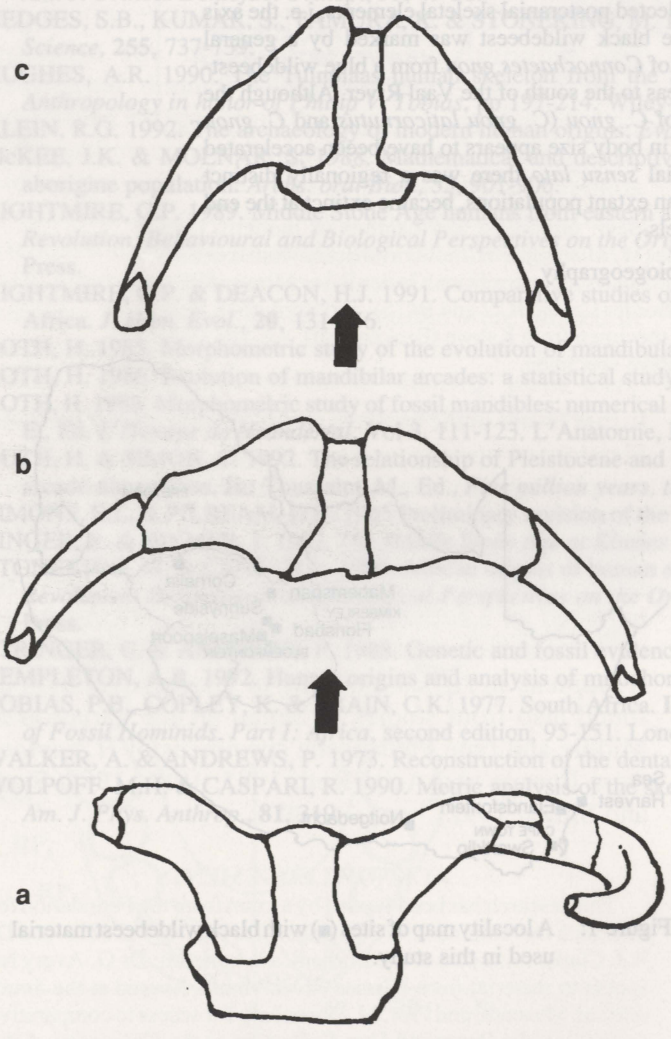

Figure 2: A chronological series of *C. gnou* horncores: a) Middle Pleistocene horncore from Cornelia, b) end Middle Pleistocene/early Late Pleistocene horncore from Florisbad and c) modern black wildbeest horncore.

The fossil history of *C. taurinus* has been mainly documented by Gentry (1978) and Gentry and Gentry (1978) on Plio-Pleistocene cranial material from East Africa and by Vrba (1976, 1979) on cranial material from similar-aged deposits in southern Africa. *C. taurinus olduvaiensis* was present in East Africa about 2 million years ago in a form that closely resembles the extant *C. taurinus*, differing only in that the horncores were less posteriorly inserted and less downwardly curved (Gentry and Gentry 1978). According to Gentry (1978) an ancestral species *Oreonagor tournoueri* had less divergent horncores and is found in the mid-Pliocene of Algeria. It appears that *C. taurinus* experienced relatively little change through time from the beginning of the Pleistocene, ca. 2 million years, to the present. In contrast, *C. gnou* underwent marked changes from the Middle Pleistocene onwards. Gentry (1978) and Gentry and Gentry (1978) also recognize a possible ancestral species of *C. gnou*, *C. africanus* (Hopwood), based on a partial skull from Olduvai Bed II.

To summarize, the black wildebeest evolved from a blue wildebeest-like ancestor (Figure 2) (Gentry 1978). Vrba (1979) agrees with this and considers the modern black wildebeest to be more specialized, with more derived attributes than the blue wildebeest. Therefore, the extant blue wildebeest would be morphologically closer to a common ancestor of both species than the extant black wildebeest. The conservative nature of *C. taurinus* as a species is clearly reflected by its long fossil history, dating from the beginning of the Pleistocene (Gentry 1978). Apart from changes in horn shape through time, which is relatively well documented (Broom 1913; Van Hoepen 1932; Gentry and Gentry 1978), very little is known of the changes that affected the postcranial skeleton of *C. gnou* in the course of its evolution. The method of using postcranial remains in the study of past animal life is common in archaeozoology (*vide* Boessneck *et al.* 1964, Plug and Peters1991; Peters and Brink 1992).

METHODS AND MATERIAL

The most obvious differences in body proportions between the two species are a shortening of the neck and shortening of the limbs, reflecting a generally smaller bodysize in the black wildebeest. If these differences reflect an evolutionary process in which the black wildebeest became smaller through time it should be evident in relevant black wildebeest fossil material. In order to explore this I have focussed on complete metacarpals, metatarsals and axes with intact dentes to outline changes in body size and body proportions.

The most diagnostic cervical elements in bovids are the atlas and the axis. These elements are also most sensitive to weight stress as seen in extant springbuck populations (Boessneck *et al.* 1964; Peters and Brink 1992). For the present exploratory purpose I have decided to focus only on the axis, as it appears to survive better than the atlas in fossil contexts.

With the increase in horn weight in bovids the neck and forelimbs would have to carry greater loads. The increase in load has an accumulating effect in bovids so that the more distally situated bones of the front limbs experience greater stress than those more proximally situated. This effect is enhanced by the absence of supporting muscles in the distal parts of limbs (Scott 1985), which is a

characteristic of all specialized ungulates. The mediolateral widening of the distal metacarpal is a characteristic of the black wildebeest, but a similar phenomenon is found in domestic draught animals, where metapodials and phalanges are buttressed by additional bone formation on the medial and lateral sides of bones (A. von den Driesch, personal communication). The distal width of the metacarpal is, therefore, an approximation of horn size and, consequently, of sexual dimorphism. The length of the metacarpal is a function of shoulder height and, therefore, of body size (Scott 1985). The length and smallest width of the shaft of the metatarsal is considered to reflect body height and stoutness. The complete state of the skeletal elements used in this study allowed for easy identification to either species in the fossil material. The need for relatively complete specimens means that the fossil sample available for study is limited and for the most part not large enough for statistical analysis.

Fossil samples from the inland region include the Middle Pleistocene collection from Cornelia, the assemblage from Mahemspan, considered to be slightly older than that of Florisbad, but more recent than Cornelia (*vide* Cooke 1974; 1979), the Florisbad Spring collection of end-Middle Pleistocene/Late Pleistocene age (Brink 1987; Scott and Brink in press), the Sunnyside Pan collection, which is probably of similar age to the Florisbad Spring collection and the Maselspoort asssemblage which has a radiocarbon date of 3770 ± 50 years BP (Pta-5879). The Cornelia and Florisbad Spring collections are the type assemblages respectively of the Cornelian Land Mammal Age and the Florisian Land Mammal Age (Hendey 1974; Brink 1987).

From the Cape Ecozone I have used fossil samples from Elandsfontein, a mixed assemblage with Middle and Late Pleistocene elements (Hendey 1974; Klein and

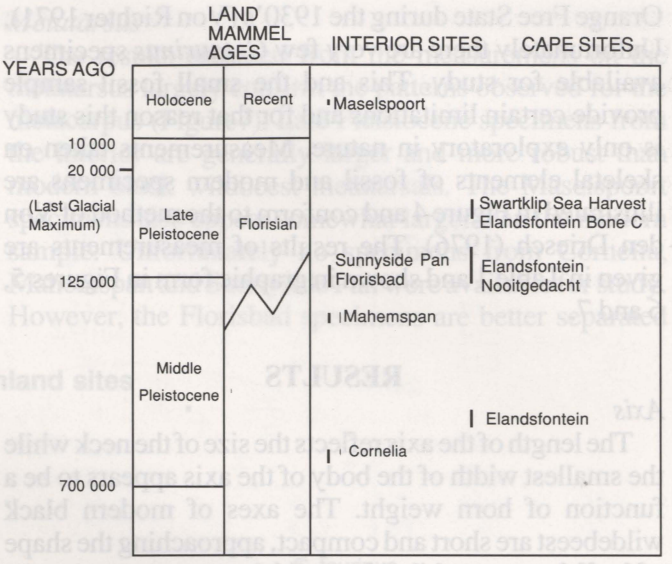

Figure 3. A chronological classification of sites with *C. gnou* material.

Cruz-Uribe 1991; personal observation), Nooitgedacht 1, a Late Pleistocene carnivore accumulated assemblage from the Cango Valley (Deacon *et al.* 1984.), Swartklip, a Last Glacial assemblage (Klein 1975) and Sea Harvest, a Late Pleistocene carnivore accumulated assemblage (Hendey 1974). The sites with *C. gnou* fossil material used in this study are shown in Figure 1 and a chronological classification of the these is given in Figure 3. These sites are entirely confined to the area south of the Vaal River.

Modern material of *C. gnou* and *C. taurinus* from the South African Museum, National Museum and the Transvaal Museum was used for comparison. All modern specimens of *C. gnou* are the descendants of a small black wildebeest population which survived in the central

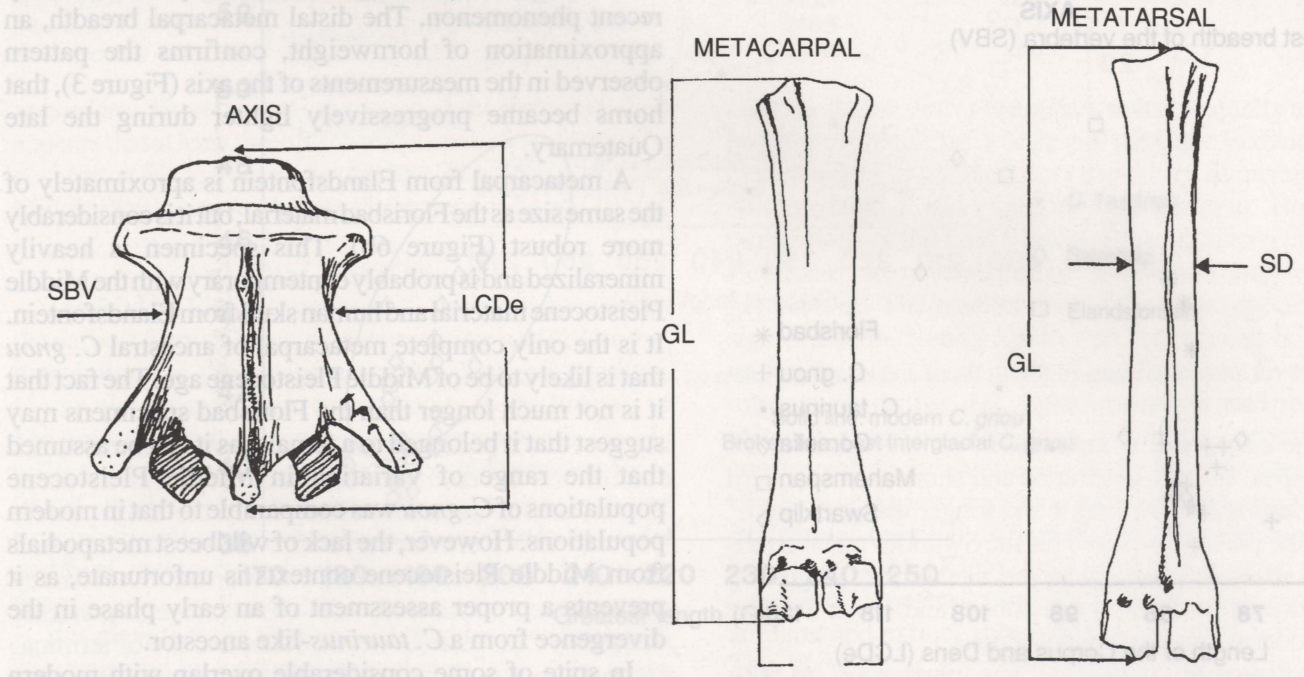

Figure 4: An illustration of measurements taken on axes, metacarpals and metatarsals. The measurements conform to the method of Von den Driesch (1976).

Orange Free State during the 1930's (Von Richter 1971). Unfortunately there are very few *C. taurinus* specimens available for study. This and the small fossil sample provide certain limitations and for that reason this study is only exploratory in nature. Measurements taken on skeletal elements of fossil and modern specimens are illustrated in Figure 4 and conform to the method of Von den Driesch (1976). The results of measurements are given in Table 1 and shown in graphic form in Figures 5, 6 and 7.

RESULTS

Axis

The length of the axis reflects the size of the neck while the smallest width of the body of the axis appears to be a function of horn weight. The axes of modern black wildebeest are short and compact, approaching the shape of buffalo axes, while blue wildebeest axes tend to be more elongated and less wide across the body of the vertebra (SBV) due to a longer neck and proportionally lighter horns. In spite of having only three blue wildebeest axes for comparison, it is clear that both the Cornelia and Mahemspan specimens are comparable in length to *C. taurinus*, but are considerably more robust. (Figure 5). The Mahemspan specimens are somewhat smaller than those of Cornelia, but not less robust. If this difference in size reflects time, it would support the assumption that Mahemspan is intermediate in age between Florisbad and Cornelia (Cooke 1974). The axes of Late and Middle Pleistocene *C. taurinus* may have been more robust than modern specimens, but at present the lack of published measurements on *C. taurinus* fossil material prevents a proper assessment. It is clear, however, that the three Florisbad specimens are shorter and more stocky than modern *C. taurinus*. The apparent decrease in size and robustness of the fossil specimens through time suggests that ancestral black wildebeest forms probably had considerably heavier heads/horns than the modern blue wildebeest. The horncore material from Cornelia, Elandsfontein, Mahemspan and Florisbad supports this deduction.

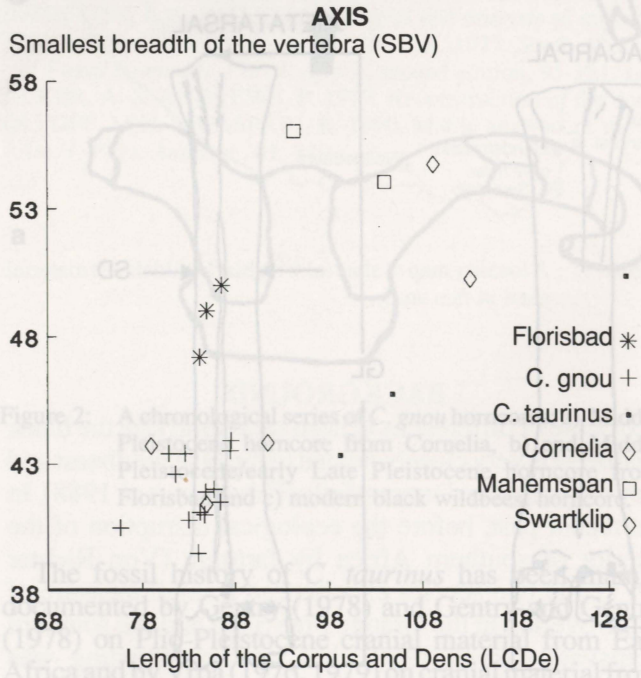

Figure 5. A plot of measurements on fossil and modern wildebeest axes.

The grouping of the Late Pleistocene material from Swartklip with the modern comparative sample is noteworthy. If the age of the Swartklip material is indeed Last Glacial *sensu lato*, as suggested by Klein (1975), then there was a marked increase in the tempo of size change from the Last Interglacial, evidenced by the Florisbad material, into the Last Glacial. Due to a lack of suitably preserved axes from Last Glacial deposits in the interior it cannot be established whether this increase in the tempo of size change also occurred in inland populations during the onset of the Last Glacial.

Metacarpus

Late Pleistocene specimens from Florisbad and Sunnyside Pan are both larger and more robust than modern black wildebeest specimens (Figure 6a). The apparent range of variation in these two fossil samples appears not to exceed that of the modern sample suggesting one sexually dimorphic population. The modern blue wildebeest sample, although small, is clearly larger and more robust than either the modern or Florisian black wildebeest specimens. The mid-Holocene sample (Maselspoort) overlaps with the largest modern specimens. This seems to support the hypothesis that the black wildebeest became smaller through time and also suggests that in populations of the interior of southern Africa the process of size decrease may not have been completed by the middle Holocene. Its present size may well be a very recent phenomenon. The distal metacarpal breadth, an approximation of hornweight, confirms the pattern observed in the measurements of the axis (Figure 3), that horns became progressively lighter during the late Quaternary.

A metacarpal from Elandsfontein is aproximately of the same size as the Florisbad material, but it is considerably more robust (Figure 6b). This specimen is heavily mineralized and is probably contemporary with the Middle Pleistocene material and human skull from Elandsfontein. It is the only complete metacarpal of ancestral *C. gnou* that is likely to be of Middle Pleistocene age. The fact that it is not much longer than the Florisbad specimens may suggest that it belonged to a female, as it can be assumed that the range of variation in Middle Pleistocene populations of *C. gnou* was comparable to that in modern populations. However, the lack of wildbeest metapodials from Middle Pleistocene contexts is unfortunate, as it prevents a proper assessment of an early phase in the divergence from a *C. taurinus*-like ancestor.

In spite of some considerable overlap with modern comparative material the Late Pleistocene material from Swartklip appears to be slightly smaller than the modern

C. gnou. This, as in the case of the axis, is noteworthy, as it confirms the impression of size decrease through time. However, the fossil and comparative samples are larger in this case and the measurements suggest that a distinct population existed in the Cape Ecozone during the Last Glacial. From the proportions of the metacarpals it appears that these animals were generally smaller than modern black wildebeest and had smaller horns. The few horncore pieces preserved in the Swartklip collection support this conclusion.

Metatarsus

The results obtained from the measuremens on the metatarsus largely confirm the patterns observed for the metacarpus (Figure7). Late Pleistocene specimens from the interior are generally larger and more robust than modern black wildbeest metatarsals. The Maselspoort specimens also appear somewhat larger than the modern sample. Unfortunately no specimens from Cornelia, Mahemspan and Sunnyside Pan were available for study. However, the Florisbad specimens are better separated

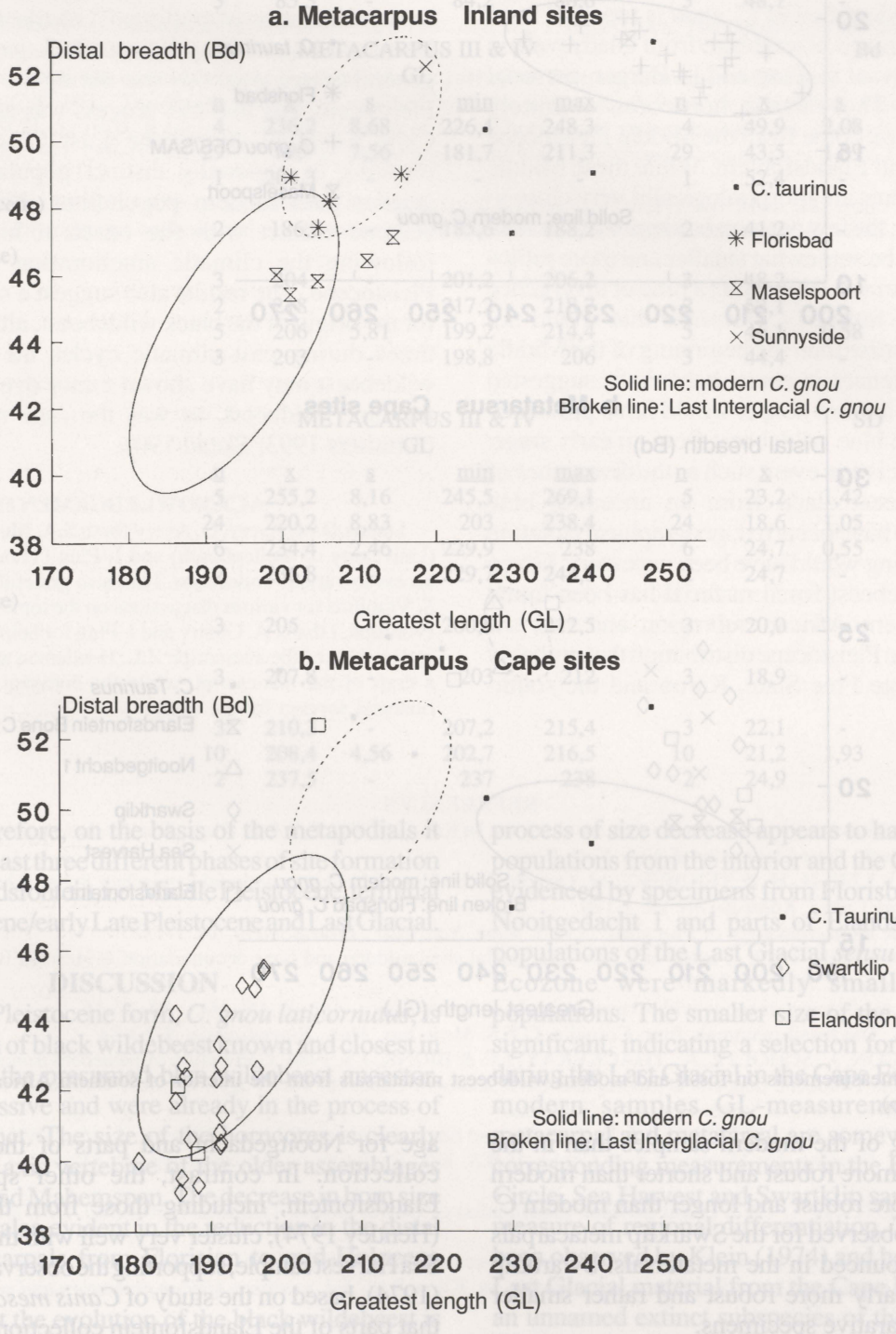

Figure 6: A plot of measurements on fossil and modern wildebeest metacarpals from the interior of southern Africa (a) and the Cape Ecozone (b).

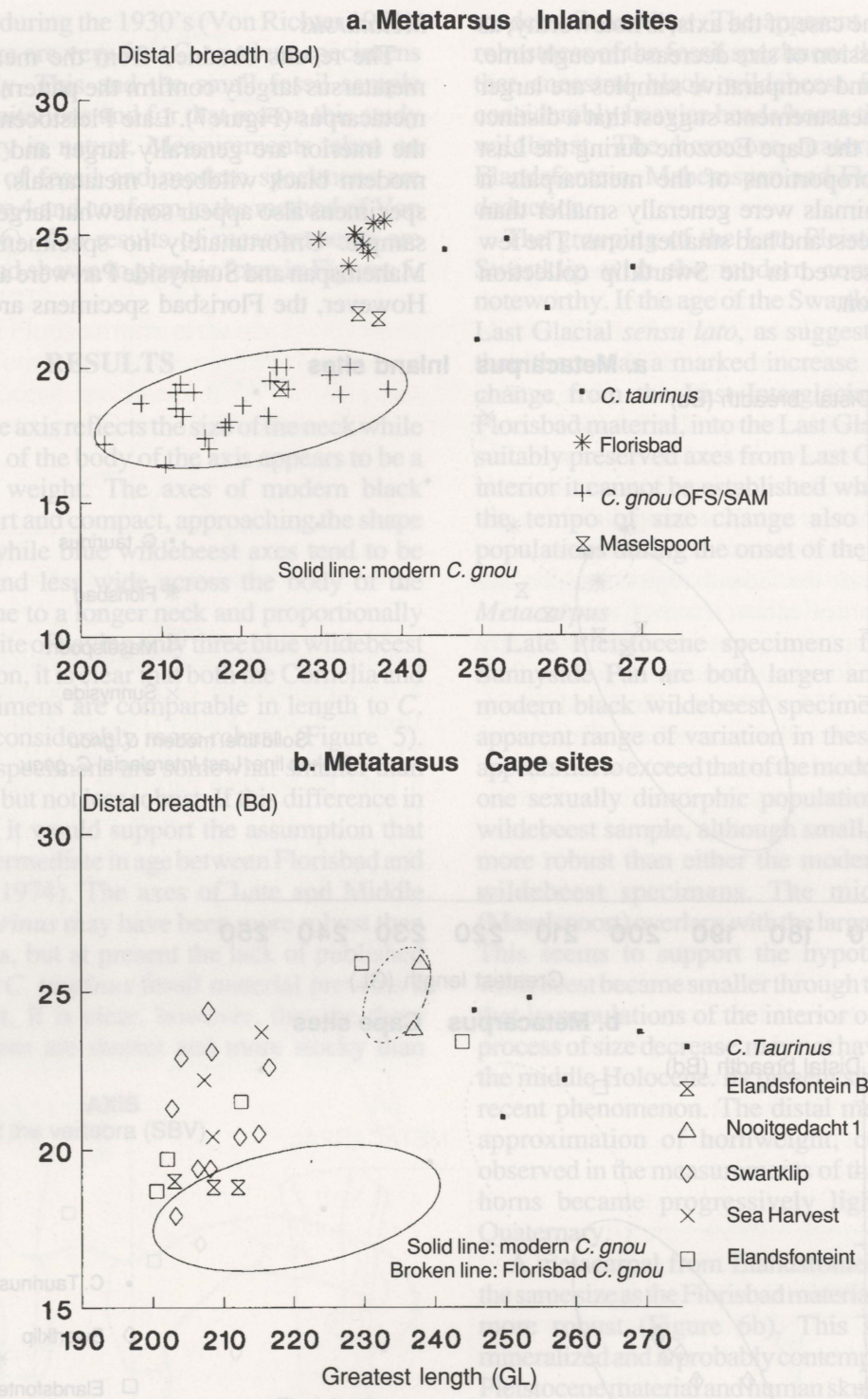

Figure 7: A plot of measurements on fossil and modern wildebeest metatarsals from the interior of southern Africa (a) and the Cape Ecozone (b).

from the clustering of the modern samples than in the metacarpus, being more robust and shorter than modern *C. taurinus* and more robust and longer than modern *C. gnou*. The pattern observed for the Swarklip metacarpals is even more pronounced in the metatarsals. Swartklip metatarsals are clearly more robust and rather smaller than modern comparative specimens.

A noteworthy feature is the clustering of both Nooitgedacht specimens and two of the Elandsfontein specimens with Florisbad, suggesting a Last Interglacial age for Nooitgedacht and parts of the Elandsfontein collection. In contrast, the other specimens from Elandsfontein, including those from the Bone Circle (Hendey 1974), cluster very well with the Swartklip and Sea Harvest sample, supporting the observations of Hendey (1974), based on the study of *Canis mesomelas* material, that parts of the Elandsfontein collection are of terminal Pleistocene age. Thus it appears that some specimens from Elandsfontein, Elandsfontein Bone Circle and Sea Harvest are of a similar age as Swarklip, i.e. Last Glacial

TABLE 1

Standard statistics for measurements on fossil and modern wildebeest axes, metacarpals and metatarsals according to sample size (n), mean (x), standard deviation (s), minimum values (min.) and maximum values (max.).

	AXIS LCDe					SBV				
	n	x	s	min	max	n	x	s	min.	max.
C. Taurinus	3	111,3	-	99,2	130	3	46,4	-	43,3	50,3
C. gnou	13	83,8	3,06	75,7	87,6	13	42	1,28	39,5	43,9
Cornelia	2	111,3	-	109,3	113,2	2	52,5	-	50,2	54,7
Mahemspan	2	99,2	-	94,3	104	2	55	-	50,2	54,7
Florisbad	3	85,3	-	84,2	86,6	3	48,7	-	47,2	50
	METACARPUS III & IV GL					Bd				
	n	x	s	min	max	n	x	s	min.	max.
C. Taurinus	4	236,2	8,68	226,4	248,3	4	49,9	2,08	47,2	52,9
C. gnou	29	195	7,56	181,7	211,3	29	43,5	1,89	40	47,3
Elandsfontein (Middle Pleistocene)	1	204,3	-	-	-	1	52,4	-	-	-
Elandsfontein (Late Pleistocene)	2	186,2	-	185,6	188,2	2	41,2	-	40,2	42,1
Florisbad	3	204	-	201,2	206,2	3	48,2	-	47,4	48,9
Sunnyside	2	218	-	217,2	218,7	2	52,1	-	52	52,2
Maselspoort	5	206	5,81	199,2	214,4	5	46,1	0,58	45,4	47,1
Deelpan	3	203	-	198,8	206	3	44,4	-	42,6	46,9
	METACARPUS III & IV GL					SD				
	n	x	s	min	max	n	x	s	min.	max.
C. Taurinus	5	255,2	8,16	245,5	269,1	5	23,2	1,42	21	24,8
C. gnou	24	220,2	8,83	203	238,4	24	18,6	1,05	16,4	20
Florisbad	6	234,4	2,46	229,9	238	6	24,7	0,55	23,8	25,5
Elandsfontein (Late Pleistocene)	2	236,8	-	229,7	243,8	2	24,7	-	23,4	25,9
Elandsfontein (Last Glacial)	3	205	-	200,5	212,5	3	20,0	-	18,7	21,5
Elandsfontein (Bone Cycle)	3	207,8	-	203	212	3	18,9	-	18,8	19
Sea Harvest	3	210,3	-	207,2	215,4	3	22,1	-	20,4	23,7
Swartklip	10	208,4	4,56	202,7	216,5	10	21,2	1,93	17,9	24,4
Nooitgedacht	2	237,5	-	237	238	2	24,9	-	23,8	25,9

sensu lato. Therefore, on the basis of the metapodials it appears that at least three different phases of site formation occurred at Elandsfontein, i.e. Middle Pleistocene, terminal Middle Pleistocene/early Late Pleistocene and Last Glacial.

DISCUSSION

The Middle Pleistocene form, *C. gnou laticornutus*, is the earliest form of black wildebeest known and closest in morphology to the presumed blue wildebeest ancestor. Horns were massive and were already in the process of becoming distinct. The size of the horncores is clearly reflected in the axis vertebrae of the older assemblages from Cornelia and Mahemspan. The decrease in horn size through time is also evident in the reduction in the distal width of metacarpals from Florisian to mid-Holocene times.

It is clear that the evolution of the black wildebeest is characterized by a general reduction in body size. In the interior of southern Africa this process had not been completed by the mid-Holocene. Until the Florisian the process of size decrease appears to have equally affected populations from the interior and the Cape Ecozone, as is evidenced by specimens from Florisbad, Sunnyside Pan, Nooitgedacht 1 and parts of Elandsfontein. However, populations of the Last Glacial *sensu lato* from the Cape Ecozone were markedly smaller than modern populations. The smaller size of the Cape specimens is significant, indicating a selection for reduced body size during the Last Glacial in the Cape Ecozone. Even in the modern samples GL-measurements in both the metacarpal and metatarsal are somewhat larger than the corresponding measurements in the Elandsfontein Bone Circle, Sea Harvest and Swartklip samples, suggesting a measure of regional differentiation. This difference has been observed by Klein (1974) and he suggested that the Last Glacial material from the Cape Ecozone represents an unnamed extinct subspecies of the black wildebeest. The process of regional differentiation might have continued had it not been interrupted by the post-glacial rise of sea level, which drowned much of the open habitat

previously available to plains-living ungulates in the Cape Ecozone.

Gentry and Gentry (1978) and Gentry (1978) hold that a population ancestral to *C. gnou* and represented by the species *C. africanus*, existed to the north of its present range in Africa at the beginning of the Pleistocene. The type and only specimen assigned to *C. africanus*, consists of a skull of which the basal parts of the horncores are preserved. No other Pleistocene fossil remains of *C. gnou* have been described from north of the Vaal River at present (Gentry and Gentry 1978; Vrba 1977, 1981), although material identified as *C. gnou* is reported from a chronologically mixed assemblage from Gladysvale in the southern Transvaal (I. Plug and L. Berger, personal communication). The earliest horncores definitely assignable to *C. gnou* come from the Middle Pleistocene sites of Cornelia and Elandsfontein. While these Middle Pleistocene horncores are morphologically very close to modern *C. taurinus*, the few postcranial elements available for study appear to be somewhat smaller and more robust than modern *C. taurinus*, suggesting a time of divergence from the ancestral form of *C. taurinus* that would not have been much earlier than the beginning of the Middle Pleistocene. Differences in social behaviour, suggested by the differences in horn shape, would have prevented crossbreeding with blue wildebeest from an early stage. However, for a speciation event such as the divergence of the black wildebeest clade from an ancestral blue wildebeest clade to have occurred, geographical isolation at the time of splitting would have been necessary. Given that no black wildebeest fossil material has been found outside the Southern African subregion and that the species has a Middle Pleistocene distribution that probably included the Orange Free State, Karoo and the south-western Cape, it can be argued that the black wildebeest is indeed a southern endemic species. For this reason and because of the Early Pleistocene age of *C. africanus* (Gentry & Gentry 1978) it may be unlikely that *C. africanus*, if it is valid taxon, would have been ancestral to *C. gnou*. However, better Middle Pleistocene samples of both species of wildebeest are needed to further address this question.

CONCLUSION

The present study shows that there is much potential in the consideration of postcranial elements in the study of bovid evolution. It appears that *C. gnou* underwent a general decrease in body size during the Middle and Late Pleistocene and that this process was accelerated in the Cape Ecozone during the Last Glacial *sensu lato*, resulting in regionally distinct populations that were smaller than modern populations. These populations became extinct with the onset of higher sea levels following the climatic amelioration in the terminal Pleistocene. The results also suggest a southern location for the origin of the black wildebeest, although at various times during past climatic cycles the range of black wildebeest may have shown minor overlap with that of the blue wildbeest, as was the case in historic times (Smithers 1993; Skead 190).

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