Late Quaternary Extinction of Ungulates in Sub-Saharan Africa: a Reductionist's Approach

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Comparative osteomorphology and statistical analysis of postcranial limb bone measurements of modern African wildebeest (*Connochaetes*), eland (*Taurotragus*) and African buffalo (*Syncerus*) have been applied to reassess the systematic affiliations between these bovids and related extinct Pleistocene forms. The fossil samples come from the sites of Elandsfontein (Cape Province) and Florisbad (Orange Free State) in South Africa. On the basis of differences in skull morphology and size of the appendicular skeleton between fossil and modern black wildebeest (*Connochaetes gnou*), the subspecies name *antiquus*, proposed earlier to designate the Pleistocene form, can be retained. The same taxonomic level is accepted for the large Pleistocene eland, which could be named *Taurotragus oryx antiquus*. The long horned or giant buffalo, *Pelorovis antiquus*, can be included in the polymorphous *Syncerus caffer* stock and could therefore be called *Syncerus caffer antiquus*. The ecology of Pleistocene and modern *Connochaetes, Taurotragus* and *Syncerus* is discussed. A relationship between herbivore body size and climate, as Bergmann's Rule predicts, could not be demonstrated. This study furthermore questions the significance of body size and horn core morphology for Pleistocene ungulate taxonomy and suggests that the number of known (late) Quaternary species extinctions in sub-Saharan Africa may be overrated. Phyletic change is considered an alternative possibility and agonistic behaviour invoked as one of the mechanisms to explain the evolutionary shift from the Pleistocene populations of *Connochaetes, Taurotragus* and *Syncerus* to modern black wildebeest, eland and African buffalo in sub-Saharan Africa.

Keywords: AFRICA, ARCHAEOZOOLOGY, UNGULATES, OSTEOMETRY, QUATERNARY EXTINCTIONS, PHYLETIC CHANGE, AGONISTIC BEHAVIOUR.

Introduction

In what follows we reassess the systematic affiliations in living and fossil African buffaloes (*Syncerus, Pelorovis*), eland (*Taurotragus*) and wildebeest (*Connochaetes*) on the basis of the comparative morphology of the cranial and postcranial skeleton and size variation within the appendicular skeleton.

In current systematics, living African buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), and black wildebeest (*Connochaetes gnou*) are considered biological species, each representing groups of potentially interbreeding populations. Fossils of related bovids may be linked to the living populations through the concept of evolutionary species or chronospecies. The latter comprises the ancestor–descendant succession of subsequent populations, which, at each time level, can be regarded as biological species.

In the case of African buffalo, eland and black wildebeest, we argue that the Pleistocene (or *antiquus*)

forms can be included in the same chronospecies as the modern ones, with which they would be linked through gradual phyletic change. The disappearance of certain Pleistocene forms would hence not illustrate true species extinctions, but represent cases of evolutionary change within genetic continuous lines of the ungulates considered.

The comparative specimens have been measured in the institutions cited in the acknowledgements. The fossil material comes from two Pleistocene sites in South Africa: Elandsfontein and Florisbad.

The Site of Elandsfontein

The site of Elandsfontein (33°05'S, 18°15'E) lies roughly 100 km NNW of Cape Town. On the basis of stratigraphical position and contents, the Elandsfontein fauna and artefacts can be divided into two major components, Elandsfontein Main and Elandsfontein Bone Circle. The Elandsfontein Main bones occur on one or several palaeosurfaces and are currently exposed by deflation. Bones in anatomical association appear to be common and many of the animals probably lie at or near the place where they died. The Elandsfontein Main bones come from a mixture of "natural" carcass sites near water holes, possibly Early Stone Age (Acheulean) butchery sites, and hyaena and porcupine lairs. Most probably, the Elandsfontein Main assemblage dates from sometime between the beginnings of the Brunhes Normal Palaeomagnetic Epoch roughly 700,000 years ago and the beginning of the Last Interglacial about 130,000 years ago. To a large extent, sampling was done by handpicking, but some small scale excavations and systematic collecting also took place. The fossils, now housed in the South African Museum, come from approximately 50 species of large mammals, of which several are extinct (Hendey, 1974; Klein, 1983, 1986, 1988).

The second, later component of the Elandsfontein fauna, or Elandsfontein Bone Circle, is taxonomically far more modern. Elandsfontein Bone Circle dates from the Last Glaciation, between 115,000 and 10,000 years ago (Klein, 1986, 1988). As far as we could ascertain, all the fossils analysed came from the Elandsfontein Main levels.

The Site of Florisbad

The site of Florisbad (32°46'S, 26°04'E) has two different contexts. The spring sand columns were sampled in the earlier phases of excavations, and the materials obtained constitute the Old Collection, containing more than 25 mammal species, of which at least four are extinct. Most likely, this assemblage results from killings by large carnivores around an ancient spring. A second, smaller sample comes from an archaeological excavation of a Middle Stone Age horizon, marginal to the spring vents. Although limited in diversity,

the fauna is essentially similar to that of the Old Collection, except that larger herbivores such as Cape horse (*Equus capensis*), giant buffalo (*Pelorovis antiquus*) and giant hartebeest (*Megalotragus priscus*) are lacking (Brink, 1987: 85). The dating of the Florisbad faunas is somewhat problematic, but they are probably not younger than early Last Interglacial, i.e. 125,000 years ago (Brink, 1987: 13). The fossil specimens we measured all belong to the Old Collection.

The African Buffaloes *Syncerus caffer* and *Pelorovis antiquus*

Living African buffaloes show a greater range of morphological variation than do any other mammal in Africa (Grubb, 1972) and, at first, zoologists considered forest-buffaloes (shoulder heights of 100–120 cm) and savanna-buffaloes (150–165 mm) (Haltenorth & Diller, 1977: 109) to represent separate species. For living *Syncerus*, size variation can be illustrated by measurements on horns (Grubb, 1972) and postcranial skeletal elements (Peters, 1986, 1988).

Fossil African buffaloes have been assigned to four genera that may represent two sequential ancestor–descendant lineages: *Ugandax–Syncerus* and *Simatherium–Pelorovis* (Gentry, 1978: 548–549; Vrba, 1987: 34). These two lineages would have diverged in the late Miocene. The separation is based on skull and tooth characteristics, and on horn core size and morphology. One of the most fascinating fossil buffaloes is the giant or long horned buffalo, *Pelorovis antiquus*. In southern Africa, the animal is known from sites of the Cornelian (1,000,000 to 400,000 BP) and the Florisian (400,000? to 10,000 BP) Land Mammal Ages. Its presence after 10,000 BP in South Africa is uncertain. In East Africa, there is no evidence for the giant buffalo after the beginning of the Holocene. In North Africa, bone finds and rock art indicate that *Pelorovis antiquus* disappeared between 4000 and 3000 BP (Gentry, 1967, 1978; Klein, 1976, 1980, 1984a, 1988; Vrba, 1987; Peters, 1990; Gautier & Muzzolini, 1991; Marean & Gifford-Gonzalez, 1991).

With the exception of the work by Thomas (1888), Pomel (1893) and Lönnberg (1933), few studies deal with the postcranial skeleton of giant buffalo and no in-depth osteological comparison between the appendicular skeleton of Pleistocene giant buffalo and extant African buffalo is available. One of the reasons is no doubt that complete *Pelorovis* bones are seldom encountered. In this respect the Elandsfontein assemblage offered a unique opportunity to examine the variation within an extensive sample of giant buffalo remains. The first conclusion of our comparison is that, as far as is ascertainable, the morphology of the appendicular skeleton of *Pelorovis antiquus* is very similar to that of *Syncerus caffer* as described in Peters (1986, 1988). Minor differences exist but they seem to be related mainly to the larger size of the giant buffalo.
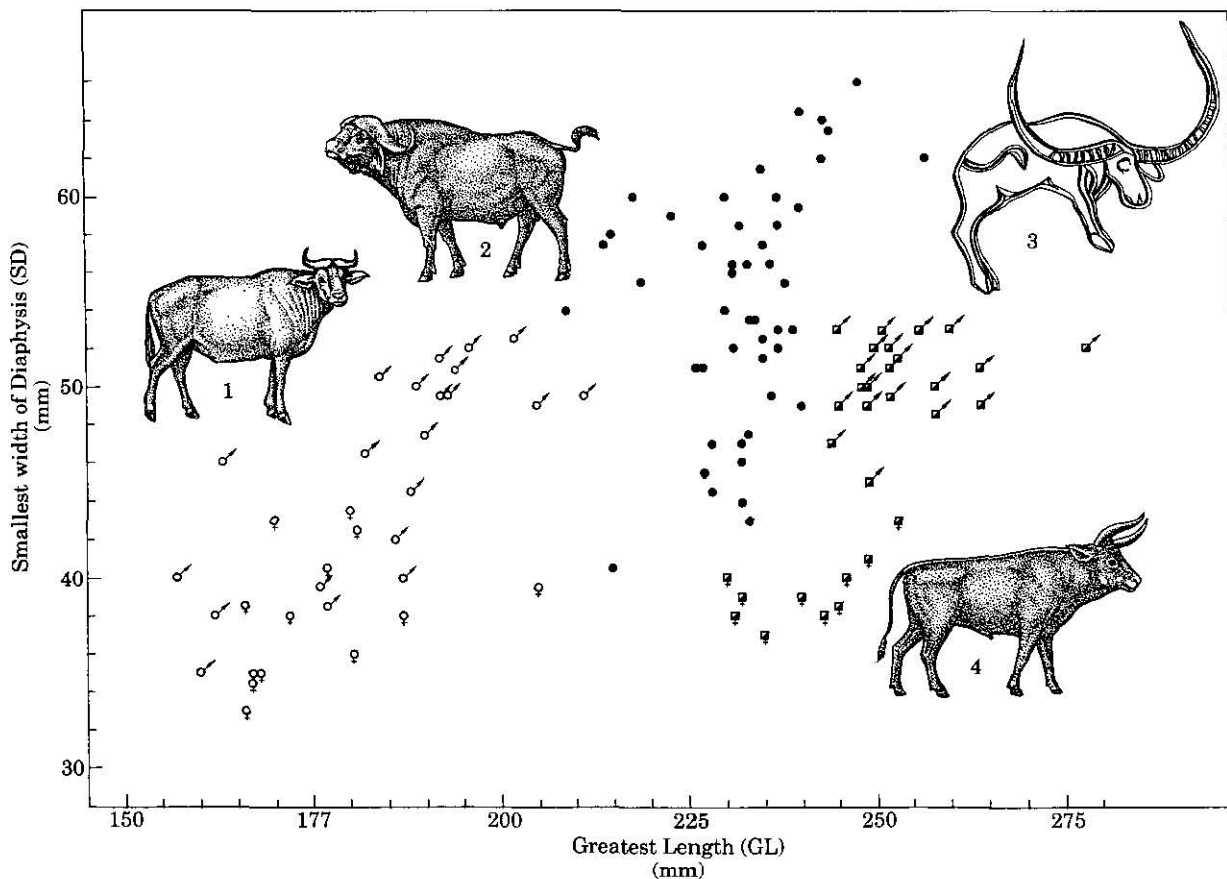
Figure 1. Metacarpal Greatest Length versus Smallest width of Diaphysis in historic and fossil *Syncerus caffer* measured by the authors, and extinct *Bos primigenius* measured by Degerbøl (1970). (○) Historic *Syncerus caffer*, with subspecies *nanus* (1), *brachyceros* and *caffer* (2); (●) Fossil *Syncerus caffer* subsp. *antiquus* = "*Pelorovis antiquus*" (3); (◼) Fossil *Bos primigenius* (4).

For example, the heaviness of the head due to the large horns is reflected in the more pronounced tuberosities and muscle attachments on many skeletal elements and in the thicker compact substance of the long bones in the forelimb. In a few instances, a somewhat different morphology has been noted, e.g. many humeri of *Pelorovis antiquus* exhibit a more developed *epicondylus medialis* in comparison with *Syncerus caffer*, but the feature is more often observed on humeri of more robust and probably male animals. The observed differences can therefore be explained in terms of individual and size-related variation. If the giant buffalo represented a separate genus and species, one would expect more distinctive morphological differences from African buffalo. In fact, at Elandsfontein, the morphological differences of *Pelorovis antiquus* from modern *Syncerus caffer* may be exaggerated, because the fossils are mainly from older males and exhibit considerable pathological modifications (Peters, in prep.). The dominance of males in the fossil samples can be demonstrated with Bayesian statistics, whereby the sexual dimorphism in metacarpi of recent African buffaloes, expressed by the ratio Greatest Length to Smallest width of Diaphysis, is used to predict the

probability of a fossil metacarpus being derived from male or female individuals. If a 70% chance is accepted as the lower limit to assign the specimens, a ratio of c. three males to two females characterizes the Elandsfontein sample (see the Appendix). That postcranial features can separate closely related species is illustrated by the comparative osteology of the extinct Bond's springbok, *Antidorcas bondi*, and the living springbok, *Antidorcas marsupialis* (Plug & Peters, 1991).

As to the size differences between giant buffalo and modern *Syncerus*, Churcher (1983: 19) states that *Pelorovis* buffaloes "differ from *Syncerus* . . . in their longer metapodials". Gautier & Muzzolini (1991) point to the fact that all the bones of *Pelorovis antiquus* are longer than those of *Syncerus caffer*. The large *Pelorovis* sample from Elandsfontein corroborates this view (Peters, in prep.). Moreover, these measurements and those available for modern *Syncerus* (Peters, 1986, and unpublished data) show a size cline from the smallest (*Syncerus caffer nanus*) through the largest living African buffalo subspecies (*Syncerus caffer caffer*) to the giant buffalo, as shown for the metacarpus (Figure 1). A two-tailed Student's *t*-test on the mean of
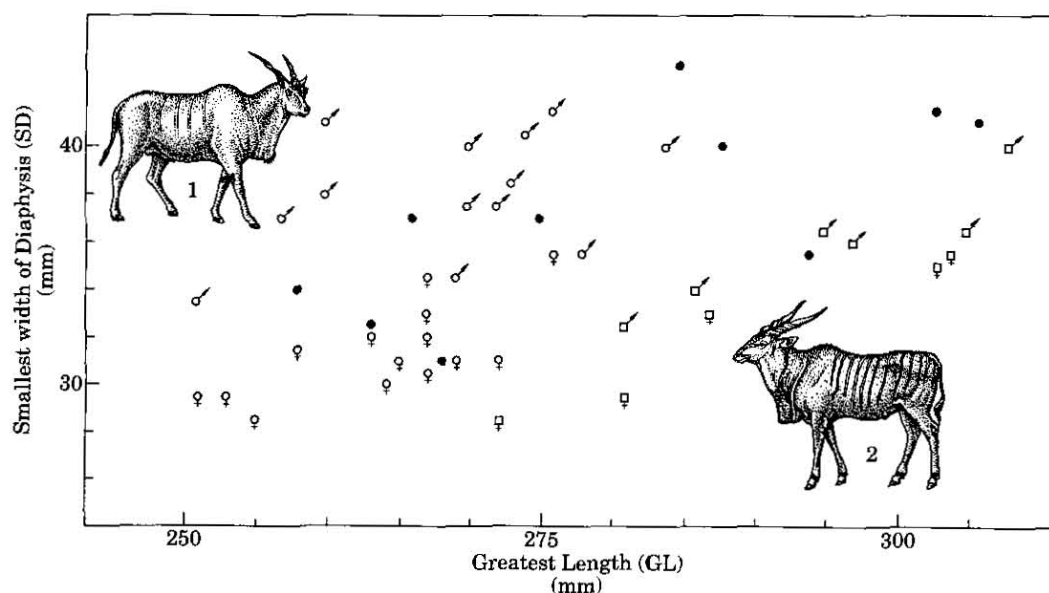
Figure 2. Metacarpal Greatest Length versus Smallest width of Diaphysis in historic and fossil *Taurotragus* measured by the authors. (○) Historic *Taurotragus oryx* (1); (●) Fossil *Taurotragus oryx* subsp. *antiquus*; (□) Historic *Taurotragus derbianus* (2).

the ratio between length and shaft width furthermore illustrates that the proportions of the Elandsfontein giant buffalo metacarpi did not differ significantly from those of modern African buffalo ($P=0.83$; see the Appendix). The same observation has been made for other bones 'of the appendicular skeleton (Peters, in prep.). Consequently, *Pelorovis* and *Syncerus* must be more closely related than is expressed by their current position in bovid systematics. In the scatter-diagram of Figure 1, the metacarpi of aurochs (*Bos primigenius*) have been included as a control group, to show that the metacarpal ratio can be used to distinguish between genera (see the Appendix). Within a single genus, even species can be separated that way, e.g. in living *Taurotragus* (Figure 2).

Gautier & Muzzolini (1991) have already drawn attention to the fact that the postcranial skeletons of giant buffalo and African buffalo are very similar. They also pointed out that North African rock art mainly figures adult *Pelorovis* bulls in which the horns cover the forehead as in *Syncerus* and argue that the giant buffalo exhibit a sexual dimorphism of the horns comparable with that of modern African buffalo: females would have more rounded horns not expanding over the forehead, while in males the horns would be more flattened and cover the forehead. The authors also have difficulties accepting the two lineages proposed by Gentry (1978: 548–549), because the ancestor of *Pelorovis antiquus*, *P. olduwayensis*, appears to be a very aberrant form. Mainly on the basis of these considerations, they hypothesize that *P. antiquus* belongs to the genus *Syncerus* and that it may not form a separate species, but that it is part of the very polymorphous *caffer*-group.

Summing up, the horns of both *antiquus* and *caffer* buffaloes do apparently exhibit fewer morphological differences than accepted up to now, whereas the postcranial skeleton differs mainly in size, the few osteological features found being no doubt related to size or sex. Giant buffaloes could hence be included in *Syncerus caffer* as a chrono-subspecies: *Syncerus caffer antiquus*.

The Eland, *Taurotragus oryx*

Fossil remains from eland in South African deposits are assigned to the Cornelian and Florisian Land Mammal Ages (Klein, 1984a; table 3). The presence of eland during the preceding Late Makapanian Land Mammal Age (?1,800,000–?1,000,000 BP) is for the moment uncertain. Gentry (1978: 543) and Brink (1987: 42) refer the fossils from both Elandsfontein and Florisbad to the living eland, *Taurotragus oryx*, although in the abundant Elandsfontein sample, Gentry (1978) observed that the insertion of the horn cores may not be at quite such a low angle as in the extant forms of the species.

As to the limb bones from Elandsfontein Main, we found that their morphology is very similar to that of modern *Taurotragus oryx*. However, many fossil bones are decidedly larger than these of the living eland, as illustrated by a scatter-diagram (Figure 2). This diagram combines the Greatest Length (GL) and the Smallest width of Diaphysis (SD) values of metacarpi from modern *Taurotragus oryx* (widely distributed south of Uganda and Kenya) and recent Derby or Giant eland, *T. derbianus* (from parts of West and
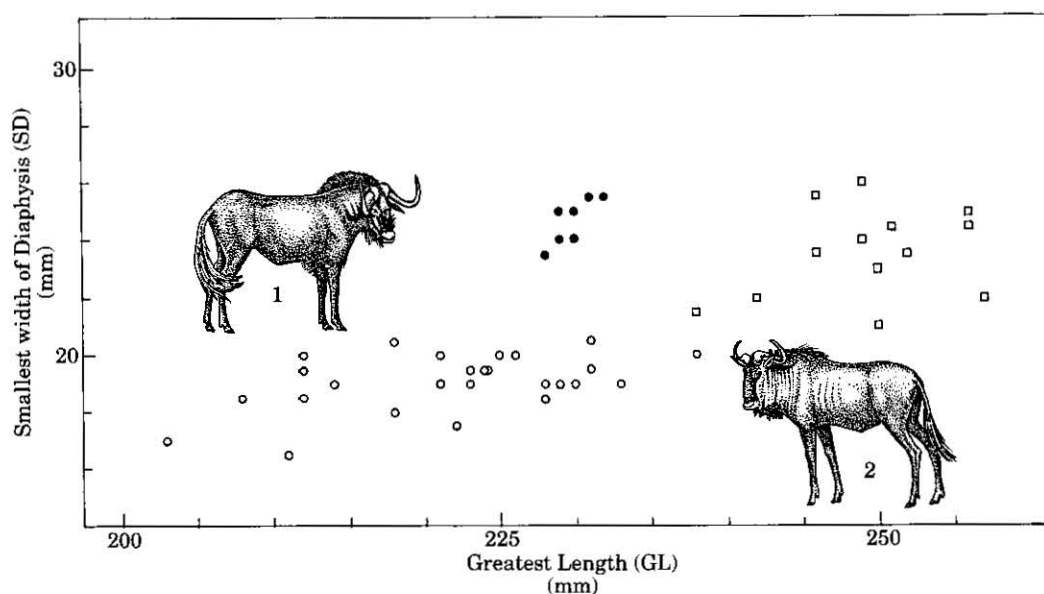
Figure 3. Metatarsal Greatest Length versus Smallest width of Diaphysis in historic and fossil *Connochaetes* measured by the authors. (○) Historic *Connochaetes gnou* (1); (●) Fossil *Connochaetes gnou* subsp. *antiquus*; (□) Historic *Connochaetes taurinus* (2).

Central Africa and eastwards to the Sudan), with fossils from Elandsfontein and Florisbad. The lengths of five fossil eland metacarpi fall within the size range of those of modern *Taurotragus oryx*, another five are clearly bigger. Their lengths compare well with those of metacarpi of *T. derbianus*, but their proportions fit the metacarpi of *T. oryx*. A two-tailed Student's *t*-test for the mean of the metacarpus ratio GL/SD confirms the identification as *T. oryx* ($P=0.47$; see the Appendix). Provided that the lengths of recent and fossil metacarpi reflect the size difference between recent and fossil eland, it can be estimated that the shoulder height of the fossil population exceeded that of recent *T. oryx* by about 10%. According to Smithers (1983: 697), the shoulder height of the latter varies between 1·5 (females) and 1·7 m (males); therefore the shoulder height of the Elandsfontein and Florisbad eland may have varied between 1·6 and 1·9 m.

The observed differences in skull morphology and size of fossil eland do not warrant the erection of a new species, as already accepted by Gentry (1978) and Brink (1987). These differences, however, allow one to put a subspecific label on the South African Pleistocene eland, for which one might propose *Taurotragus oryx antiquus*.

The Black Wildebeest, *Connochaetes gnou*

Remains of black wildebeest have been found in a number of South African sites of the Cornelian and Florisian Land Mammal Ages (e.g. Klein, 1984*a*: 132, Brink, 1987: 44). The Pleistocene black wildebeest was originally described by Broom (1913: 14) as an extinct

species, *Connochaetes antiquus*, on the basis of a right horn core from Florisbad. Later it became clear that Pleistocene black wildebeest exhibit appreciable variation in skull and horn core morphology. Brink (1987: 48), for example, records that the Florisbad horn cores have a different shape and usually less pronounced bosses than modern specimens. These changes reflect an ongoing evolutionary process, and the Pleistocene black wildebeest is now considered a subspecies of modern wildebeest, hence *Connochaetes gnou antiquus* (Gentry, 1978: 555; Brink, 1994, in press).

The Florisbad Old Collection yielded seven complete metatarsi of black wildebeest. Their Greatest Length and Smallest width of Diaphysis are compared with those of metatarsi from modern black wildebeest (Figure 3). To illustrate the size difference between black and blue wildebeest, *Connochaetes taurinus*, the measurements of 13 metatarsi of the second species are included. The scatter-diagram shows that the metatarsi of Late Pleistocene wildebeest differ proportionally from their homologues in modern *Connochaetes gnou*. A two-tailed Student's *t*-test on the mean of the GL/SD ratio in metatarsi even suggests that Pleistocene black wildebeest might be a distinct species ($P<10^{-6}$; see the Appendix). However, towards the middle of this century, black wildebeest were brought to the point of extinction due to overexploitation and agricultural development. Their survival has been ensured by protection on farms and in reserves (Smithers, 1983: 601). In 1965, only 1700–1800 animals were left in the entire South African Subregion (Brand, 1965). This stock has been used for introduction and reintroduction and the institutions we visited acquired specimens for their

comparative collections only after re-stocking took place. Our modern sample may therefore not be entirely representative, because of its restricted gene pool. This could account for the differences in size and proportions between modern and fossil *C. gnou* metatarsi. On the other hand, evolutionary change may represent a valuable alternative (Brink, 1994, in press).

Palaeocology of the Extinct Subspecies of Buffalo, Eland and Wildebeest

As seen, the three Pleistocene bovids considered here differ from their present day relatives in their absolute size (*Syncerus, Taurotragus, Connochaetes*) and in limb bone proportions (*Connochaetes*). Conceivably, these Pleistocene forms may represent distinct ecotypes, i.e. groups adapted genetically to a particular habitat but interbreeding freely with other ecotypes of the same species. The kind of environment the fossil subspecies inhabited is not well known, but a comparison of the habitat requirements of living populations with palaeosynecological data inferred from Pleistocene faunas with abundant taxa, together with information on global and regional temperatures in the past, may help to characterize the environment they preferred (e.g. Brink & Lee-Thorp, 1992).

Living buffalo

The habitat requirements of the living savanna buffalo include a plentiful supply of shade, water and suitable grasses as found in a variety of types of woodland. The animals do not frequent wide open areas of grassland far from trees, the shade of which they need during the hotter hours of the day. Buffalo are predominantly grazers, but include in their food a small percentage of browse (Sinclair, 1977: 10; Smithers, 1983: 664).

Living eland

According to Smithers (1983: 680), present day *T. oryx* are as at home in arid semi-desert scrub associations as in montane grassland, but they generally avoid more extensive, open and short grass plains. As the animals are predominantly browsers, they require trees or bushes to provide for this component of their food. Whereas in the Southern African Subregion browse forms the major part of their diet, the food of eland in Tanzania consists of more than 70% grass (Lamprey, 1963). Eland will drink when water is available, but they are by no means dependent on water and in some parts of their range they obtain nearly all their moisture from their food (Smithers, 1983: 682).

Living black wildebeest

Connochaetes gnou is today a species of the open plains, formerly associated with the Karroo in the central, northern and northeastern part of Cape Province and with the grasslands of Orange Free State and Transvaal. Black wildebeest are predominantly grazers, but during the cold winter months they will browse on karroid bushes. They show a distinct preference for grazing where the grass is short (Smithers, 1983: 602–603).

Habitat preferences of the fossil populations

As far as the habitat of *Syncerus caffer antiquus* is concerned, Klein (1980: 268–269) notes that its long horns indicate a preference for very open habitats, but Vrba (1987: 40–42) assumes that the animals lived in environments varying from a wood-grass mosaic, with a high prevalence of open grassland, to predominantly open woodland. Faunal studies in sub-Saharan Africa confirm a preference for open landscapes (e.g. Klein, 1980, 1983; Brink, 1987; Peters, 1990; Marean & Gifford-Gonzalez, 1991). *Antiquus* buffaloes from Middle and Upper Pleistocene sites in South Africa are often associated with remains of typical grazers including the extinct Cape zebra (*Equus capensis*), the extinct giant hartebeest (*Megalotragus priscus*), black wildebeest (*C. gnou antiquus*) and the extinct Bond's springbok (*Antidorcas bondi*) (Klein, 1980, 1983, 1984a; Brink, 1987, 1988). That cover in the form of trees and bushes was an essential feature in the habitat of *S. caffer antiquus* is illustrated by the species composition at Elandsfontein (Klein, 1983), Klasies River Mouth (Klein, 1976) and Florisbad (Brink, 1987). There, intermediate feeders (grazers/browsers) such as eland (*T. oryx*), and browsers such as black rhinoceros (*Diceros bicornis*) or greater kudu (*Tragelaphus strepsiceros*) are also present. From the foregoing, it can be concluded that the *antiquus* subspecies of buffalo, eland and black wildebeest inhabited landscapes largely comparable with the ones their living relatives prefer.

As indicated by the palaeontological and archaeozoological record of the Late Quaternary in the Sahara, *Syncerus caffer antiquus* possibly was more tolerant of aridity than the living savanna buffalo forms. As a whole, the Late Pleistocene in the Sahara seems to have been an arid period followed by several humid oscillations during the Holocene. Recent estimates suggest about 50–200 mm of precipitation for the Holocene optima (e.g. Maley, 1977; Gautier & Van Neer, 1982; Muzzolini, 1986; Peters, 1987; Neumann, 1989). During the Upper Pleistocene hyperarid interval, large mammals were absent from the Sahara, with the possible exception of typical desert-adapted species such as addax (*Addax nasomaculatus*), oryx (*Oryx dammah*) and dorcas gazelle (*Gazella dorcas*). With improving environmental conditions, other species recolonized the Sahara: elephant (*Loxodonta africana*), white and black rhinoceros (*Ceratotherium simum, Diceros bicornis*), giraffe (*Giraffa camelopardalis*), roan antelope (*Hippotragus equinus*), hartebeest

(*Alcelaphus buselaphus*) and other antelopes. As to *Syncerus*, there is no evidence whatsoever that the Central Sahara was inhabited by one of the savanna buffalo subspecies currently present in sub-Saharan Africa. So far, bone finds and especially rock art only indicate the presence of the giant or long horned buffalo, *S. caffer antiquus* (Muzzolini, 1986; Gautier & Muzzolini, 1991). However, at that time, savanna buffaloes were already inhabiting the northern savanna belt, and one can ask why the Sahara was not colonized by them. Pachur & Braun (1982) think that the early Holocene mean annual rainfall of up to 200 mm resulted only in the formation of small lakes and watering places scattered over the Saharan plains. This may have prevented colonization by modern savanna buffaloes. Recent *Syncerus* densities become very low at about 500 mm mean annual rainfall (Sinclair, 1977: 199–200), though buffalo might frequent areas with an annual rainfall as low as 250 mm, but then only near rivers (Stewart & Stewart, 1963).

Faunal data from Quaternary localities in eastern and southern Africa confirm that *antiquus* buffaloes were more drought tolerant than living buffaloes. In the fossil assemblages, *S. c. antiquus* are generally associated with a wide range of grazing herbivores adapted to arid or semi-arid conditions: Alcelaphinae, antilopinae, *Oryx* and *Taurotragus*. In general, *caffer* buffaloes are indicative of a more closed vegetation and moister living conditions (Klein, 1983; Vrba, 1987; Peters, 1990).

For eland and black wildebeest, the fossil record does not permit to single out aridity as a cause of separation of the Pleistocene subspecies from the present-day populations.

Temperature

Living *Syncerus* tolerate a wide range of temperatures and are found from altitudes over 4000 m, where there is frost at night, to areas in West Africa with very high ambient temperatures (Sinclair, 1977: 11). Judging from their historic distribution (Du Plessis, 1969; Skead, 1980), both eland and black wildebeest can also be considered eurythermic species.

To what extent the distribution of the palaeopopulations of buffalo, eland and black wildebeest has been influenced by temperature cannot be estimated from the available fossil record. However, for the archaeological sequence at Nelson Bay (South Africa), global and local evidence indicates that temperatures were significantly lower from 18,500 until 12,000–10,000 BP, whereas after 10,000 BP it became warmer (Avery, 1982; Klein, 1983). In this sequence, *S. c. antiquus* is last recorded towards the end of the Pleistocene, while *S. c. caffer* is recorded throughout the sequence and persists in the area until today. Thus *S. c. antiquus* was probably less tolerant toward higher temperatures than *S. c. caffer*.

On present evidence we concluded that the *antiquus* subspecies of buffalo, eland and black wildebeest inhabited open and (semi-)arid landscapes. Moreover, aridity may have been less of a problem to *S. c. antiquus* than to modern savanna buffaloes.

Herbivore Size and Climate

In various parts of the world, Quaternary climatic change is probably responsible for long-term changes in mean individual size within certain mammalian species. Some well documented cases involve fossil and living small mammals and carnivores (e.g. Kurtén, 1968; Tchernov, 1968). For Africa, information about climate-related size change in fossil mammals is still scanty. Avery (1982) investigated the variation in size of micromammals from late Quaternary sites in the southern Cape Province. Modern samples of the same species served as comparative material and illustrated that in certain micromammals body size increases with colder climate, while other species show the opposite trend. For a number of recent African carnivores, Klein (1986) demonstrated a relationship between carnassial length and latitude south, whereby mean body size increases with decreasing temperature. With the modern data in support, he estimated middle and late Quaternary temperatures on the basis of the mean carnassial length of fossil carnivores from different sites.

In African ungulates, variation in mean body size between fossil and recent populations has been observed on several occasions (Davis, 1981; Klein, 1984a, 1986; Peters, 1990). Essentially, two mechanisms can be held responsible: Bergmann's Rule and the so-called population density factor (Kurten, 1965: 62). Bergmann's Rule is based on the observation that the size of homoiothermic animals tends to increase along a temperature gradient from warm to cold temperatures. The explanation is that larger animals tend to produce more heat (body volume) and lose less (skin area), a clear advantage in cooler climates. There are exceptions to Bergmann's Rule, and according to Klein (1986: 154), herbivores are less likely to obey Bergmann's Rule than carnivores, because variation in temperature is more likely to affect herbivore food supplies. Also, the altered availability of required food plants may easily outweigh changed temperature as a selective factor on body size. Bergmann's Rule has been seriously criticized and a recent paper by Geist (1987) argues that it has no validity at all.

The necessity to keep up an adequate population density in spite of a severe limitation of habitat and/or food supply may result in a reduced mean body size. Thus selection might favour smaller individuals if a major resource becomes limited. Examining the modern ungulate fauna of Namibia, Thackeray (1980) has shown that the mean body mass of ungulates increases from arid to humid environments. Coe (1981) argues,

however, that larger herbivores may also evolve a large body size in response to selection pressures directed at avoiding competition and reducing predation. Moreover, large size may simply enable the animals to cover large areas in semi-arid environments in order to obtain sufficient pasture.

To explain a large body size in ungulate palaeopopulations, both mechanisms have been invoked. For example, Davis (1981) demonstrated that low environmental temperatures resulted in a larger size of late Pleistocene gazelles, aurochs, wild goat and wild boar, but also of fox and wolf in Israel. Gautier (1983) explained the large size of the wild herbivores of an Iron Age site in Ruanda as due to the good quality of the pasture because of the underlying volcanic soils. Klein (1984a: 141) mentions that grysbok (*Raphicerus melanotis*) may grow larger when their preferred food is more abundant, a condition which in turn results from wetter climatic conditions.

As it stands, it would seem that our knowledge about the ecology of the animals concerned is still too incomplete to explain large body sizes in the extinct buffalo, eland and black wildebeest. If we postulate an increased tolerance toward aridity in the Pleistocene subspecies, the argument used by Coe (1981) correlating foraging in dry environments with increased body size can be advanced.

Late Quaternary Extinctions in Africa: a Reductionist's Approach

Africa seems to have witnessed several total extinctions during the Late Quaternary (Klein, 1984b), including that of Thomas' camel (*Camelus thomasi*), the North African giant deer (*Megaloceros algericus*) and the giant buffalo (*S. c. antiquus*) in northern Africa, the giant buffalo in eastern Africa, and the giant buffalo, the giant hartebeest (*Megalotragus priscus*), Bond's springbok (*Antidorcas bondi*), the southern springbok (*Antidorcas australis*), the giant Cape horse (*Equus capensis*) and a giant warthog (*Metridiochoerus* sp. or *Stylochoerus* sp. according to Klein (1984b; 557)) in southern Africa. The extinction of the ungulates in eastern and southern Africa may date back to the Pleistocene/Holocene transition, i.e. 12,000–9000 years ago, that of *S. c. antiquus* in the Sahara is dated between 4000 and 3000 BP (Gautier & Muzzolini, 1991).

In bovid palaeontology, horn core morphology, dental and cranial features as well as absolute size of the skeletal elements have been used to assign fossil specimens to a profusion of genera and species. However, on the basis of the evidence presented for black wildebeest and eland, and, above all, because of the incorporation of giant buffalo into *Syncerus*, one may ask if variation in the shape of bovid horn cores and body size within a single genus or species have not been underestimated?

Some Other Ungulates

Springbok

The extinct southern springbok (*Antidorcas australis*), known from coastal sites in the Cape Province, was originally described as a subspecies of the living springbok, *A. marsupialis*, but is now accepted as a separate species (Hendey, 1974: 52). It differs from *A. marsupialis* by its smaller dentition and by its smaller and more medio-laterally compressed horn cores without any sharp bending backward and outward. However, the morphology of cores in the living springbok is quite variable. Moreover, the smaller size of its dentition implies that *A. australis* was smaller than *A. marsupialis* and we would like to compare the measurements of its postcranial skeleton with that of modern springbok. The latter shows a greater size variation than almost any other medium-sized bovid (Peters & Brink, 1992). Also, a close examination of postcranial remains of springbok from the mid-Pleistocene deposits at Swartkrans, attributed to *A. australis* by Vrba (1973: 291–297), failed to disclose any features separating the fossils from modern springbok (Plug & Peters, 1991). Until the postcranial bones of *A. australis* from other sites in the region have been compared morphologically and measured, the specific status of the southern springbok must be questioned. As to Bond's springbok (*Antidorcas bondi*), it appears to represent a genuine species. It can be separated from modern springbok (*A. marsupialis*) on the basis of cranial and dental features, its small body size, and a number of typical postcranial characteristics (Plug & Peters, 1991).

Cape horse

In general, remains of giant Cape horse (*Equus capensis*) are recognized simply because of their large size, but according to Churcher (1986), the animal is closely related to the East African extinct *Equus oldowayensis* and its descendant, Grevy's zebra (*Equus grevyi*). Extensive comparative osteological studies are lacking, and the possibility that *E. capensis* is an extinct form of a still living species has not been investigated morphometrically so far.

Warthog

In her study of the fossil pigs of Florisbad, Ewer (1957) identified two species: the extant warthog (*Phacochoerus aethiopicus*) and the recently extinct Cape warthog (*P. africanus*). Harris & White (1979) and Klein (1980) make no mention of Ewer's study of the Florisbad suids, and list the specimens as *Metridiochoerus* sp., basically because of their large size. Cooke & Wilkinson (1978: 469) and Brink (1987: 42), however, see no reason not to include the Florisbad pig in the genus *Phacochoerus*, in which case it may be a former variant of the extant warthog.

Discussion

Summing up, the number of large mammals that became extinct in sub-Saharan Africa during Upper

Pleistocene and Holocene times may be overestimated. On the basis of the postcranial evidence, the disappearance of Bond's springbok represents a genuine species extinction, whereas that of giant buffalo can be considered a phyletic replacement. Such an alternative hypothesis is also applicable to southern springbok, giant Cape horse, and giant warthog.

Late Quaternary Extinctions: Causes

Late Quaternary extinctions have precipitated an avalanche of often quite theoretical papers dealing with their causes and significance (Martin & Wright, 1967; Martin & Klein, 1984). Stated in a simple way, the main hypotheses put forward for the causes of these extinctions are climatic change, overkill by human hunters or a combination of the two. Barnosky (1989) presents such a combination as a paradigm of worldwide events in the geological record of rapid extinction affecting mammals. Such events would be due to climatic change and the invasion of one or more critical taxa. Climatic change alone would lead to a few extinctions only and to biogeographical changes due to permanent migrations. The arrival of new taxa would result in the extinction of direct native competitors or prey species or in niche partitioning. As far as we understand, both factors could induce evolutionary change since animals have to adapt to new habitats or share them differently. Large mammals would be the most vulnerable group, because their ecological requirements are great with respect to smaller mammals and because of their low population densities. Lower densities will more easily lead to population fragmentation and disappearance as a result of aleatory processes. Barnosky accepts the hypothesis that the arrival of *Homo sapiens* played a role in the diachronous extinctions of Late Quaternary megafauna in the New World, Australia, New Zealand and Madagascar. In Europe or Africa, people and their game animals coevolved and, as we understand, the effect of new weaponry or hunting techniques may have been much less deleterious than the arrival of hunters in new regions with large game. According to Klein (1984b: 562), however, progress in hunting proficiency of Late Stone Age people precipitated extinctions of game after environmental change had reduced numbers and distributions in southern Africa.

The hypothesis that the *antiquus* subspecies of buffalo, eland and wildebeest are not truly extinct corroborates the views expressed by Barnosky to a certain extent. The number of Late Quaternary extinctions in Africa would be less than accepted, because of the coevolution of people and game animals. However, we still have to explain the evolutionary shifts from *antiquus* to modern populations in the ruminants discussed here.

According to Gautier & Muzzolini (1991), the demise of *S. c. antiquus* in sub-Saharan Africa can be explained in terms of agonistic behaviour. Buffaloes evolved from a fairly small, short horned *Ugandax*-like form, probably adapted to woodland, and the living short horned forest buffalo (*Syncerus caffer nanus*) can be seen as the primitive group. Colonization of open biotope by buffaloes not only resulted in the formation of larger herds, it also generated more conflicts among the individual animals. Since social competition is generally related to reproductive success, agonistic behaviour presents an essential tool of selection among herd animals. Because agonistic encounters include a great deal of displaying, Gautier & Muzzolini postulate that selection will favour large animals with long and conspicuous horns. All-out fighting with head-to-head charges also occurred in giant buffalo, as indicated by the fact that the horns grew over the forehead. Such behaviour is also illustrated by a number of Holocene rock engravings from the Sahara. Maybe, however, long horns and large body size were disadvantageous in other respects, and renewed selection may have favoured a smaller type of savanna buffalo with less long but generally bossed horns, better adapted to violent contact. On present evidence it seems that in eastern and southern Africa the replacement of *S. c. antiquus* by its bossed relative was accomplished at the beginning of the Holocene.

In northern Africa, however, *S. c. antiquus* must have survived in some (arid?) areas, from where they spread into the Sahara with the onset of the Early Holocene climatic optimum. Whereas the remainder of the *S. c. antiquus* stock in the Sudano-sahelian belt was replaced by modern savanna buffaloes, aridity prevented the latter from extending their distribution into the semi-desert to the north. As a result of the mid-Holocene climatic deterioration, *S. c. antiquus* populations became isolated in some mountain ranges of the central Sahara. Here, they died out as a result of increasing aridity combined with the deleterious effect of man and his flocks on the vegetation (Gautier & Muzzolini, 1991).

In black wildebeest, Brink (1987: 44) noted that the frontal bosses of the horn cores of recent *C. gnou* are more pronounced than in the fossil *antiquus* subspecies from Florisbad. Again, it is possible that agonistic behaviour contributed to the decline and extinction of the Pleistocene ecotype. To what extent the difference in insertion of the horn cores between fossil and recent southern African *T. oryx* cf. (Gentry, 1978: 543) presents a selective advantage to the latter in terms of agonistic behaviour is not clear for the moment. However, the extinction of the once widespread springbok species *A. bondi* suggests that during late Quaternary times a shift in habitat utilization by the herbivore community took place; it resulted in the disappearance of the feeding niche of this highly specialized and interdependent grazer. It is

not unlikely that the postulated shift was caused by climatic change and the arrival and dispersal of new ecotypes of certain other ruminants. Consequently, the evolution to modern *T. oryx* may rather be the outcome of a response to the altered availability of environmental resources.

Conclusions

Whereas morphological features appear to be fairly constant, the metric analysis of Pleistocene and modern postcranial skeletons from buffalo, eland and black wildebeest illustrates that body size may vary considerably in these bovids. The case of African buffalo is especially interesting, since comparative osteomorphology and a statistical analysis of the proportions of the postcranial skeleton, illustrated by the metacarpus, show that the Mid–Late Pleistocene giant or long-horned buffalo *Pelorovis antiquus* belongs to the polymorphous *Syncerus caffer* group and should be regarded as a chronosubspecies, hence *Syncerus caffer antiquus*. A larger mean body size has also been observed in Pleistocene eland and black wildebeest compared with their modern relatives. Unfortunately, our knowledge concerning the ecology of these palaeopopulations is too incomplete for us to evaluate these size differences in terms of environmental and climatic parameters. A correlation, however, between body size and latitude, as Bergmann's Rule predicts, could not be established.

The fact that in these three bovids the Pleistocene ecotypes are considerably larger than their extant relatives casts serious doubt upon the specific status of other Pleistocene ungulates, such as giant Cape horse and giant warthog, which became extinct during late Quaternary times. Phyletic change rather than species extinction might account for their vanishing, but a detailed study of the postcranial skeleton is necessary to confirm this hypothesis. Research on postcranial/osteomorphology corroborates the specific status of Bond's springbok, *A. bondi*; the disappearance of this antelope towards the end of the Pleistocene therefore represents a genuine species extinction.

On present evidence we postulate that agonistic behaviour in a social context can be invoked to explain, at least partially, the evolutionary shift from *antiquus* to modern populations in buffalo, black wildebeest and perhaps eland. To what extent the development and/or dispersal of these new ecotypes can be related to Pleistocene climatic events cannot be deduced from the available fossil record. As for *Antidorcas*, since springbok species are highly specialized and interdependent grazers, the disappearance of *A. bondi* may be related to a shift in habitat utilization when, towards the beginning of the Holocene, the *antiquus* ecotypes of the Pleistocene herbivore community were replaced by their modern relatives.

Acknowledgements

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Table 1.

	Recent African buffalo: *Syncerus caffer*	Fossil Giant buffalo: *"Pelorovis antiquus"*	Control Aurochs: *Bos primigenius*
S. caffer	—	$P=0.83^*$	$P<10^{-6}$
"P. antiquus"	$P=0.83^*$	—	$P<10^{-6}$
	Eland: *Taurotragus oryx*	Eland: *T. oryx antiquus*	Derby eland: *T. derbianus*
T. oryx	—	$P=0.47^*$	$P=3.9 \times 10^{-3}$
T. o. antiquus	$P=0.47^*$	—	$P=7.6 \times 10^{-4}$
	Black wildebeest: *Connochaetes gnou*	Black wildebeest: *C. gnou antiquus*	Blue wildebeest: *C. taurinus*
C. gnou	—	$P<10^{-6}$	$P=1.9 \times 10^{-5}$
C. g. antiquus	$P<10^{-6}$	—	$P=1.5 \times 10^{-4}$

Appendix: Results of the Statistical Analysis

Two-tailed Student's t-test

The metacarpi (*Syncerus, Taurotragus*) and metatarsi (*Connochaetes*) included here have all been measured by the senior author according to the standard procedure described in von den Driesch (1976: 93). Since we are dealing with differences in sample size and with unpaired variables (Greatest Length/Smallest width of Diaphysis), a two-tailed Student's *t*-test could be applied to test the difference between the means of recent and fossil specimens. Measurements on metacarpi (*Syncerus, Taurotragus*) and metatarsi (*Connochaetes*) of a taxonomically related though different genus and/or species have been included as a control group. The results of the statistical analysis have been summarized in Table 1.

The samples marked with asterisks do not differ significantly from each other and should therefore be considered as derived from a single population. The results for black wildebeest are somewhat unexpected, but an explanation has been offered above.

Bayes statistics

In this study, Bayes statistics has been used to estimate the sex ratio within the Elandsfontein buffalo and eland populations. The proportions of the metacarpi of recent individuals of known sex are used to predict the posterior probability of the fossil metacarpi of membership in each sex. The results of this analysis are given below:

Table 2.

Syncerus caffer antiquus

Posterior probability 50%: $N=45$, $\male\male=24$, $\female\female=21$
Posterior probability 70%: $N=34$, $\male\male=21$, $\female\female=13$

Taurotragus oryx antiquus

Posterior probability 70%: $N=10$, $\male\male=7$, $\female\female=3$