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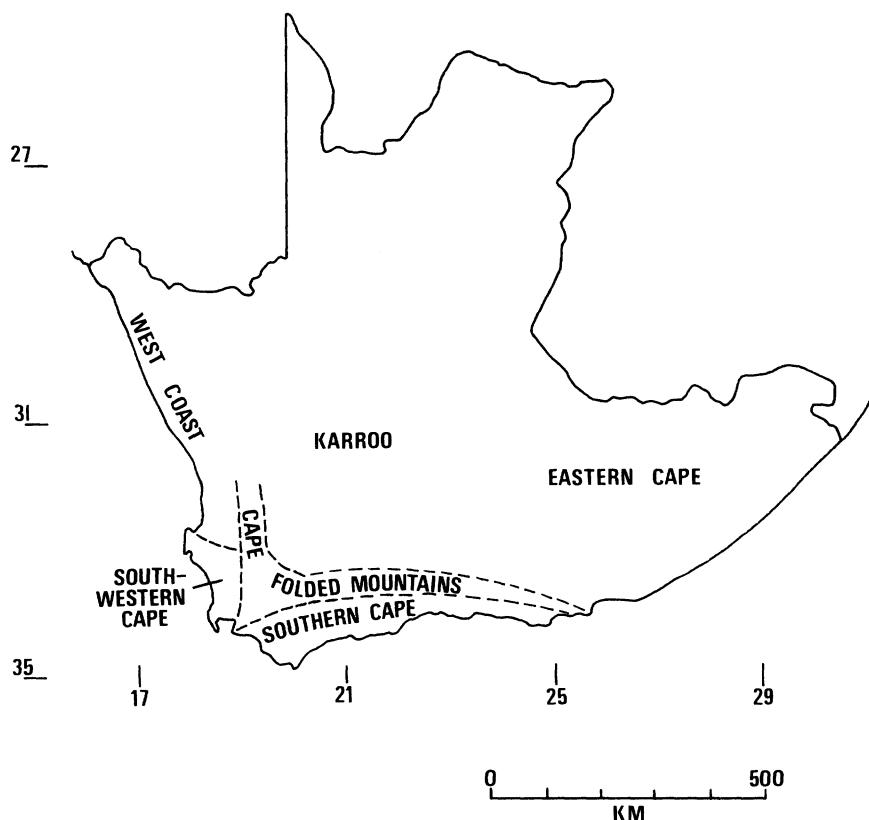
A PROVISIONAL STATEMENT ON TERMINAL PLEISTOCENE MAMMALIAN EXTINCTIONS IN THE CAPE BIOTIC ZONE (SOUTHERN CAPE PROVINCE, SOUTH AFRICA)

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Until very recently, it was widely believed that sub-Saharan Africa had escaped the wave of mammalian extinctions which swept Eurasia and especially North America at the end of the Pleistocene, roughly 12 000–10 000 years ago (Martin 1967; Kowalski 1967). While this may yet prove true for most of the subcontinent, it is now known that there were significant terminal Pleistocene mammalian extinctions in its extreme south-western corner, referred to here after Hendey (1974: 16) as the 'Cape Biotic Zone'. This is a unique area in sub-Saharan Africa, characterized by a warm-temperate (as opposed to tropical or subtropical) climate and by the distinctive Cape Macchia or fynbos vegetation. Extending from the lower course of the Great Berg River in the north-

west to Cape St. Francis in the south-east, the Cape Biotic Zone is separated from the Karoo and eastern Cape to the north and east by the arid west-coastal strip and the mountains of the Cape Folded Belt. It may be subdivided into three parts: the Cape Folded Mountains, the south-western Cape, and the southern Cape, the last two being separated by an extension of the mountains which reaches the sea at Cape Hangklip. The south-western Cape is differentiated from the southern Cape by more seasonally restricted (winter) rainfall and by a relatively impoverished mammalian fauna, lacking such creatures as velvet monkey, quagga, bushpig, bushbuck, buffalo, mountain reedbuck, blue antelope, bontebok, and blue duiker, all of which occurred historically in the



Map 1. Extent of the three subzones (Cape Folded Mountains, south-western Cape, and southern Cape) comprising the Cape Biotic Zone.

TABLE 1

The Late Pleistocene and Holocene mammalian faunas of the south-western and southern Cape as defined in the text (information from Hendey 1974 and unpublished, and Klein 1974 and unpublished). Only species which are likely to have been preyed upon by prehistoric man are included (this specifically excludes most Insectivora and Rodentia and all Chiroptera and Cetacea. All the Carnivora have been included because of difficulties in deciding which ones might or might not be relevant.) 'x' indicates a securely documented fossil or historic occurrence, '?' a possible occurrence where lack of documentation is perhaps due to the inadequacy of the record. Species listed in capital letters are those believed to have become extinct. c. 10 000 B.P.

	SOUTH-WESTERN CAPE				SOUTHERN CAPE	
	Late Pleistocene		Holocene	Late Pleistocene		Holocene
INSECTIVORA						
<i>Erinaceus</i> sp., Hedgehog	.	.	.	x	?	
PRIMATES						
<i>Papio ursinus</i> , Chacma Baboon	.	.	.	?	x	x
<i>Cercopithecus aethiops</i> , Vervet Monkey	.	.	.		?	x
<i>Homo sapiens</i> , Man	.	.	.	x	x	x
PHOLIDOTA						
<i>Manis</i> cf. <i>temmincki</i> , Pangolin	.	.	.	?		x
TUBULIDENTATA						
<i>Orycteropus afer</i> , Aardvark	.	.	.	?	x	?
CARNIVORA						
<i>Hydrurga leptonyx</i> , Leopard Seal	.	.	.	?	x	?
<i>Lobodon carcinophagus</i> , Crab-eating Seal	.	.	.	x	x	?
<i>Mirounga leonina</i> , Southern Elephant Seal	.	.	.	?	x	x
<i>Arctocephalus pusillus</i> , Cape Fur Seal	.	.	.	x	x	x
<i>A. gazella</i> , Gazelle Seal	.	.	.	?	x	x
<i>Canis mesomelas</i> , Black-backed Jackal	.	.	.	x	x	x
<i>Vulpes chama</i> , Silver Jackal	.	.	.	x	x	x
<i>Lycaon pictus</i> , Hunting Dog	.	.	.	x	x	?
<i>Otocyon megalotis</i> , Bat-eared Fox	.	.	.	?	x	?
<i>Ictonyx striatus</i> , Zorilla	.	.	.	x	x	?
<i>Mellivora capensis</i> , Ratel	.	.	.	x	x	x
<i>Aonyx capensis</i> , Clawless Otter	.	.	.	x	x	x
<i>Genetta</i> spp., Genet Cats	.	.	.	x	x	?
<i>Herpestes ichneumon</i> , Egyptian Mongoose	.	.	.	x	x	x
<i>H. pulverulentus</i> , Cape Grey Mongoose	.	.	.	x	x	x
<i>Atelax paludinosus</i> , Water Mongoose	.	.	.	x	x	x
<i>Hyaena brunnea</i> , Brown Hyena	.	.	.	x	x	x
<i>Crocuta crocuta</i> , Spotted Hyena	.	.	.	x	x	?
<i>Proteles cristatus</i> , Aardwolf	.	.	.	?	x	x
<i>Felis libyca</i> , Wild Cat	.	.	.	x	x	x
<i>Felis serval</i> , Serval	.	.	.	x	x	?
<i>Felis caracal</i> , Caracal	.	.	.	x	x	x
<i>Panthera pardus</i> , Leopard	.	.	.	x	x	x
<i>Panthera leo</i> , Lion	.	.	.	x	x	x
PROBOSCIDEA						
<i>Loxodonta africana</i> , Elephant	.	.	.	x	x	x
HYRACOIDEA						
<i>Procavia capensis</i> , Rock Hyrax	.	.	.	x	x	x
PERISSODACTYLA						
<i>Diceros bicornis</i> , Black Rhinoceros	.	.	.	x	x	x
<i>Ceratotherium simum</i> , White Rhinoceros	.	.	.	x	?	
<i>EQUUS CAPENSIS</i> , Cape 'Horse'	.	.	.	x	?	
<i>Equus</i> cf. <i>quagga</i> , Quagga	.	.	.	?	x	x
<i>Equus</i> cf. <i>zebra</i> , Mountain Zebra	.	.	.	x	x	x

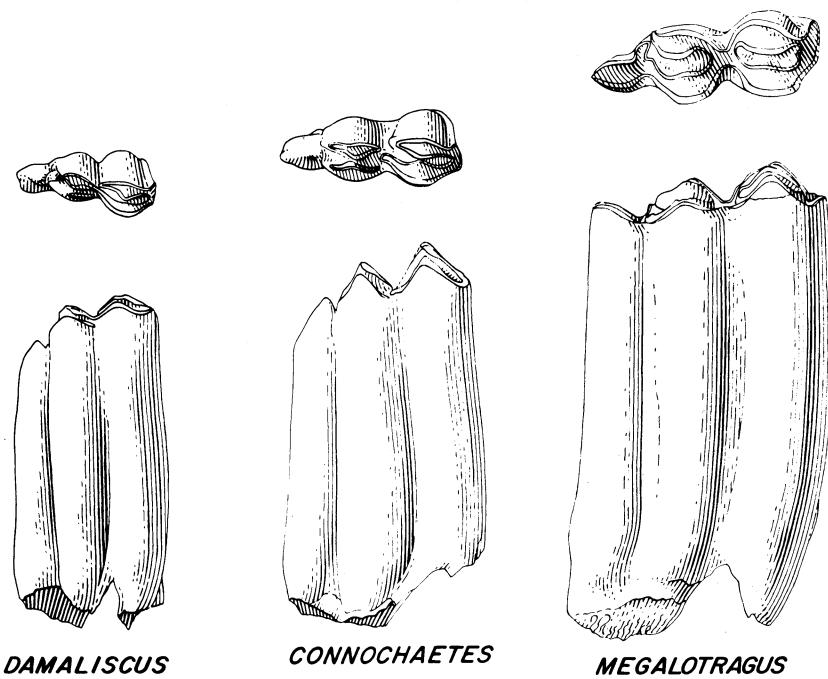
	SOUTH-WESTERN CAPE		SOUTHERN CAPE	
	Late Pleistocene	Holocene	Late Pleistocene	Holocene
ARTIODACTYLA				
<i>Potamochoerus porcus</i> , Bushpig			×	×
<i>Phacochoerus aethiopicus</i> , Cape Warthog	×		×	×
<i>Hippopotamus amphibius</i> , Hippopotamus	×	×	×	×
<i>Tragelaphus (Strepsiceros) strepsiceros</i> , Greater Kudu			×	×
<i>T. (STREPSICEROS) SP.</i> , Kudu	×		?	
<i>T. scriptus</i> , Bushbuck			×	×
<i>Taurotragus oryx</i> , Eland	×	×	×	×
<i>PELOROVIS ANTIQUUS</i> , Giant Buffalo	×		×	
<i>Syncerus caffer</i> , Cape Buffalo	×		×	×
<i>REDUNCA ARUNDINUM</i> SUBP., Southern Reedbuck	×		×	
<i>Hippotragus leucophaeus</i> , Blue Antelope	×	×	×	×
<i>Hippotragus equinus</i> , Roan Antelope			×	×
<i>DAMALISCUS</i> cf. <i>NIRO</i> , Bastard Hartebeest	×		×	
<i>Damaliscus doreas</i> , Bontebok	×		×	×
<i>MEGALOTRAGUS PRISCUS</i> , Giant Alcelaphine	×		×	
<i>CONNOCHEATES</i> sp., Wildebeest	×		×	
<i>Alcelaphus buselaphus</i> , Hartebeest		×		×
<i>Cephalophus monticola</i> , Blue Duiker			?	×
<i>Sylvicapra grimmia</i> , Grey Duiker	×	×	×	×
<i>Raphicerus campestris</i> , Steenbok	×	×	?	×
<i>R. melanotis</i> , Grysbok	×	×	×	×
<i>Ourebia ourebi</i> , Oribi				×
<i>Oreotragus oreotragus</i> , Klipspringer	×	×	×	×
<i>ANTIDORCAS AUSTRALIS</i> , Southern Springbok	×		×	
<i>Pelea capreolus</i> , Vaal Rhebuck	×	×	×	×
LAGOMORPHA				
<i>Lepus</i> spp., Hares	×		×	×
RODENTIA				
<i>Bathyergus suillus</i> , Dune Mole	×		×	×
<i>Georychus capensis</i> , Dune Mole	×		×	×
<i>Hystrix africae-australis</i> , Porcupine	×		×	×

southern Cape (see table 1).

The available evidence suggests less contrast between the two areas in the late Pleistocene, perhaps in part because of greater climatic similarity and in part because faunal interchange was facilitated by exposure of the continental shelf during periods of lowered sea-level.

The occurrence of terminal Pleistocene extinctions in the Cape Biotic Zone was first suggested by preliminary analysis of the Late Quaternary fauna excavated in 1970–1 at Nelson Bay Cave (Plettenberg Bay, southern Cape) (Klein 1972). Bones of two extinct genera—*Pelorovis* (= '*Homoioceras*', a giant buffalo) and *Megalotragus* (a giant hartebeest-like animal) (fig. 1)—were found in Nelson Bay deposits dated as recently as 12–10 000 B.P. More recent research (Klein in preparation) on the Nelson Bay fauna and on terminal Pleistocene/early Holocene faunas from other relevant sites such as Elandsbay Cave (south-western Cape), excavated by J. E.

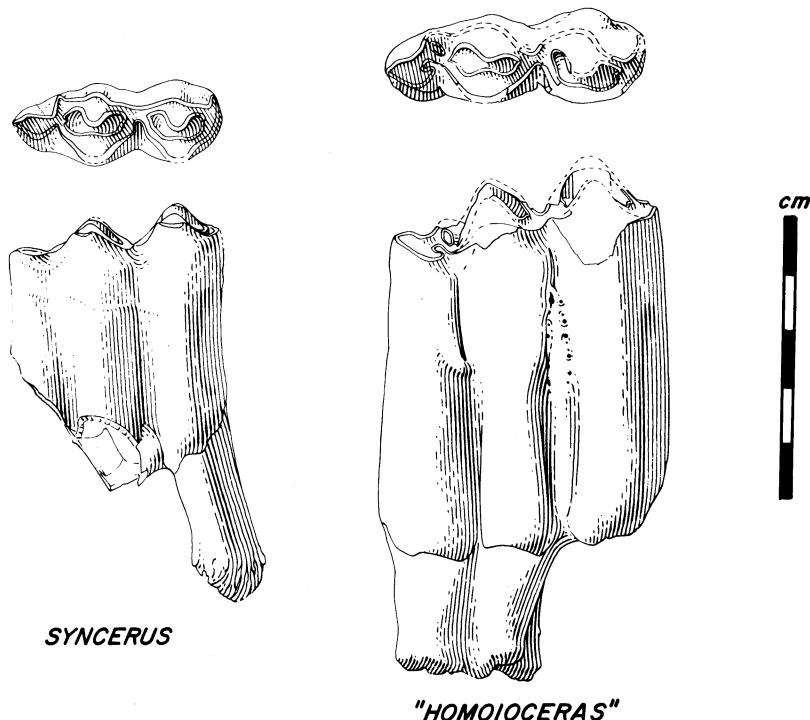
Parkington, and Byeneskranskop I Cave (southern Cape), excavated by F. R. Schweitzer, suggests that in addition to these two genera no less than five species or subspecies in surviving genera probably made their last appearance in the Cape Biotic Zone in the terminal Pleistocene. These are a wildebeest and a reedbuck at least subspecifically distinct from the extant *Connochaetes gnou* and *Redunca arundinum* respectively; a bastard hartebeest tentatively assigned to the extinct *Damaliscus niro*; a small springbok, *Antidorcas australis*; and a very large horse or zebra provisionally referred to *Equus capensis* (fig. 2). The cited taxa were important components in a fauna which is well represented in the south-western Cape at such earlier Upper Pleistocene faunal localities as Swartklip (Hendey & Hendey 1968; Klein unpublished), Melkbos (Hendey 1968; Klein unpublished), and the Sea Harvest site, Saldanha Bay (Hendey 1974; Klein unpublished) where their remains are accompanied by those of yet another extinct taxon,



DAMALISCUS

CONNOCHAETES

MEGALOTRAGUS



SYNCERUS

"HOMOIOCERAS"

Fig. 1. Lower third molars of *Megalotragus* and *Pelorovis* = '*Homoioceras*' from the terminal Pleistocene deposits of Nelson Bay Cave. Homologous teeth of *Damaliscus*, *Connochaetes*, and *Syncerus* from the same deposits are included to allow size comparisons.

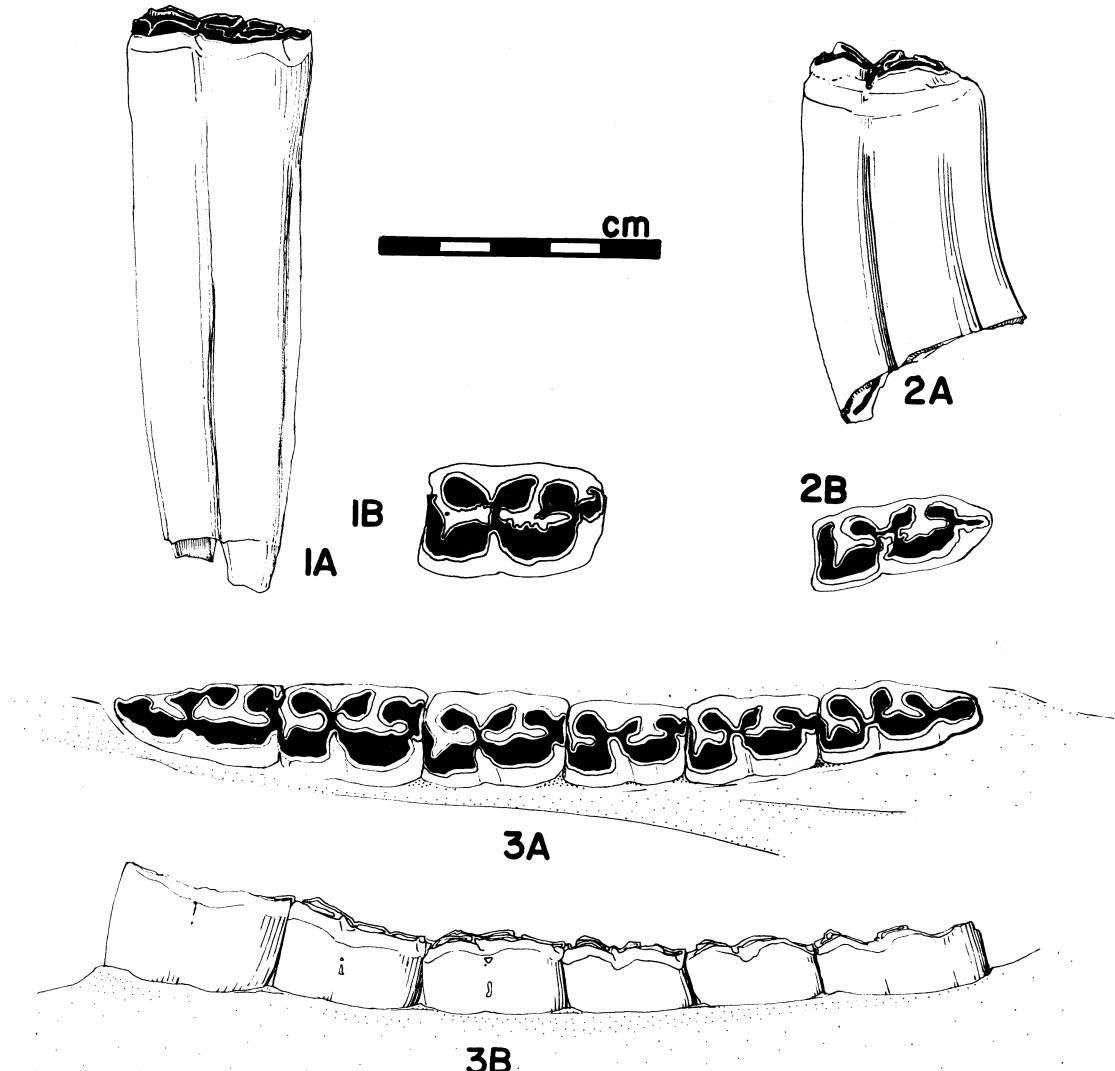


Fig. 2. 1A & B, 2A & B: Mandibular cheek teeth of *Equus* cf. *capensis* from the terminal Pleistocene deposits of Elands Bay Cave. 3A & B: Left mandibular dentition of modern *Equus burchelli* for comparison.

a small kudu subspecifically or specifically distinct from the extant *Tragelaphus strepsiceros*. Although the kudu has yet to be found in terminal Pleistocene horizons, its constant association with the other extinct taxa in somewhat earlier deposits suggests it will eventually be added to the list of terminal Pleistocene extinctions. This would then make a total of two extinct genera and six extinct species or subspecies in surviving genera.

Among the listed taxa, the evolutionary origins of the extinct wildebeest reedbuck and kudu are undocumented. It is possible that they were Cape Biotic Zone endemics, the end products of lineages differentiated from related ones to the north and east during the Mid-Pleistocene or before. The small springbok may also have been restricted to the Cape Biotic

Zone during the later Pleistocene, though evidence presented by Vrba (1973) indicates it was more widespread in earlier Pleistocene times. The remaining taxa—giant buffalo, giant ‘hartebeest’, extinct bastard hartebeest, and giant equid—may all be traced back to at least the early Pleistocene and at one time or another were widely distributed over both southern and eastern Africa. All four were important elements in earlier Upper Pleistocene faunas in the South African interior, as for example, from the site of Florisbad near Bloemfontein (Cooke 1963). The dates of their most recent occurrence outside the Cape Biotic Zone remain uncertain.

As in Eurasia and North America, terminal Pleistocene mammalian extinctions in the Cape Biotic Zone were largely without replacement so that the early

Holocene fauna appears relatively impoverished by comparison to the Late Pleistocene one (table 1). Also as in Eurasia and North America, the causes of extinction remain unclear, though the coincidence between extinctions and the relatively rapid and dramatic climatic change that characterized the end of the Pleistocene is too strong to ignore. Quaternary climatic change, documented for southern Africa in general by Van Zinderen Bakker & Butzer (1973) and more specifically for the southern Cape by Butzer & Helgren (1972), may have been especially marked in the Cape Biotic Zone because of its location in temperate (*vs.* tropical or subtropical) latitudes. Since, with the exception of the kudu, all the taxa that became extinct in the Cape Biotic Zone were grazers, it is possible to hypothesize that significant end-Pleistocene/early Holocene expansion of shrub and bush at the expense of grassland played a role in their disappearance. A reduction in grass cover and an increase in bush and forest between 12 000 and 9 000 B.P. seems well documented for the vicinity of Nelson Bay Cave (Klein 1972) and a similar end-Pleistocene/early Holocene reduction of open grassland has also been suggested for Elands Bay and Melkhoutboom Caves (Klein 1974, also Deacon 1972), located at roughly the north-western and south-eastern extremes of the Cape Biotic Zone. Grassland habitats seem never to have recovered substantially since all known Holocene faunas in the Cape Biotic Zone are as heavily dominated by browsers (whether measured in terms of species diversity or of biomass) as Upper Pleistocene ones were by grazers.

It is unknown whether similar mammalian extinctions accompanied the presumably analogous environmental changes that occurred in the Cape Biotic Zone during earlier 'glacial to interglacial' transitions. However, evidence from the apparently Last Interglacial deposits at Klasies River Mouth (southern Cape) (Wymer & Singer in preparation; Klein 1974) and Sea Harvest indicates that the taxa that disappeared from the Cape Biotic Zone at the end of the Last Glacial survived the end of the Penultimate one, roughly 125 000 years ago. Environmental change by itself is consequently insufficient to explain their final disappearance. One factor, perhaps the crucial one, that differentiated the end of the Last Glacial from the end of the previous one was the presence of significantly more effective human hunters (data from Klasies River Mouth directly support the notion that Last Interglacial and earlier Last Glacial peoples were less competent hunter-gatherers than later Last Glacial and Holocene peoples in the same habitat — Klein 1974). As a working hypothesis, by no means original, I would therefore suggest that terminal Pleistocene extinctions in the Cape Biotic Zone were brought about by environmental changes, to which at least some hominid populations responded by developing more efficient techniques for obtaining large grazers. In attempting to perpetuate their previous way of life in the face of rapid and dramatic modification of their resource base, hunting peoples may have succeeded in wiping it out altogether. Ultimately the big-game hunting way of life was replaced by new cultural adaptations based on exploitation of small, non-gregarious browsing bovids and

food plants, and, in coastal areas, on marine resources.

It is presently impossible to directly document a human role in Cape Biotic Zone mammalian extinctions, except perhaps in the case of the giant buffalo (*Pelorovis*). At the Middle Stone Age site of Klasies River Mouth (with both Last Interglacial and earlier Last Glacial deposits together probably spanning the interval from 125 000 to perhaps 60–50 000 B.P.) the giant buffalo becomes progressively less numerous relative to its close relative, the extant Cape buffalo (*Synacerus caffer*). Determination of the ages of animals at time of death (Klein unpublished) has shown that the giant buffalo is represented very largely by two age classes—near full-term foetuses or new born calves (with unworn deciduous teeth) and full adults (with complete adult dentition). Older calves, 'yearlings,' etc., are relatively rare. The Cape buffalo too is represented primarily by calves, but there are more individuals in age grades between new-born calves and full adults. Again, strictly as a working hypothesis to be tested against data obtained from other sites, I would suggest that Middle Stone Age peoples may have dealt with the formidable giant buffalo by concentrating on near-term pregnant females or perhaps even on females giving birth, thereby obtaining both mother and calf. The long-term effects of such a hunting pattern on the species would be disastrous and could well account for its reduction in numbers, if not for its ultimate extinction.

In conclusion, it is important to emphasize that research on terminal Pleistocene extinctions in the Cape Biotic Zone has only just begun and the ideas presented here will probably be modified as the relevant data are augmented and more fully analysed.

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