PALAEOENVIRONMENTAL IMPLICATIONS OF QUATERNARY LARGE MAMMALS IN THE FYNBOS REGION

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INTRODUCTION

For the purposes of this paper, a large mammal is one in which adults exceed 0,75 kg. This is an arbitrary definition, but has a practical basis. It includes species that were probably introduced to sites by people or carnivores and excludes ones that were probably introduced by owls. The difference in bone collector is important for interpreting the palaeoenvironmental implications of a fossil fauna.

In general, large mammals are relatively insensitive to environmental change, particularly compared to plants. However, the Quaternary mammals of the fynbos zone are a partial exception. At least during the late Quaternary, beginning approximately 128 000 years ago, the large mammal fauna of the fynbos region changed systematically in response to climatic events that have been established both locally and globally. My purpose here is to summarize the evidence for the change.

HISTORIC LARGE MAMMALS OF THE FYNBOS REGION

The historic mammal fauna of the fynbos region provides a benchmark against which earlier faunas may be evaluated. At least in a general way, the historic fauna may be reconstructed from its surviving remnants and from an examination of early European settlers' and travellers' accounts, as collated most systematically by Skead (1980).

In terms of its large mammals, as well as of its climate and vegetation, the fynbos region can be divided into two major subregions, separated by a spur of the Cape Fold Mountains that reaches the sea at Cape Hangklip. The two subregions may be conveniently referred to as the 'south-western Cape', in which rainfall is largely restricted to the winter months, and the 'southern Cape' (Overberg and Outeniqualand), in which it is more evenly distributed throughout the year. In both subregions, browsers tended to dominate grazers in both species diversity and absolute numbers.

In the southern Cape, the principal browsers were bushpig (Potamochoerus porcus), bushbuck (Tragelaphus scriptus), blue duiker (Cephalophus monticola), grey duiker (Sylvicapra grimmia), Cape grysbok (Raphicerus

melanotis), and black rhinoceros (Diceros bicornis). Among the grazers, only the Cape buffalo (Syncerus caffer) was common more or less throughout. Hartebeest (Alcelaphus buselaphus) was locally fairly numerous. Bontebok (Damaliscus dorcas dorcas) and blue antelope (Hippotragus leucophaeus), though entirely restricted (endemic) to this region, were rare, and the blue antelope became extinct about 1800 A.D. Roan antelope (Hippotragus equinus) occurred in small numbers in the forests of the south-east. Eland (Taurotragus oryx), steenbok (Raphicerus campestris), and elephant (Loxodonta africana) (all mixed feeders) occurred more or less throughout, though the steenbok was probably completely replaced by the grysbok in areas of dense fynbos, bush or forest. Vaalribbok (Pelea capreolus), mountain reedbuck (Redunca fulvorufula), and klipspringer (Oreotragus oreotragus) were common in suitably hilly locales, particularly in the flanking Cape mountains where they were joined by the mountain zebra (Equus zebra).

The most common non-ungulate herbivores were baboon (Papio ursinus), rock hyrax (Procavia capensis) (technically an ungulate sensu lato), porcupine (Hystrix africaeaustralis), and hares (Lepus capensis and others). On the west, a large endemic mole rat (Bathyergus suillus) was also abundant in sandy, mainly coastal areas. Among the large carnivores, lion (Panthera leo), leopard (Panthera pardus), caracal (Felis caracal), brown hyaena (Hyaena brunnea), ratel (Mellivora capensis), and black-backed jackal (Canis mesomelas) were well represented. Common smaller carnivores included the wildcat (Felis libyca), grey mongoose (Herpestes pulverulentus), Egyptian mongoose (Herpestes ichneumon), striped polecat (Ictonyx striatus), Cape fox (Vulpes chama), and bat-eared fox (Otocyon megalotis). Cape fur seal (Arctocephalus pusillus) was common in coastal waters, and rookeries even occurred on the mainland.

The fauna of the south-western Cape was similar, but notably impoverished, lacking bushpig, bushbuck, blue duiker, buffalo, mountain reedbuck, blue antelope, roan, bontebok, and perhaps other species found in the southern Cape. Grey duiker was relatively abundant and steenbok was generally more common than grysbok. As will become clear below, the southern and south-western Cape were much more similar in their large mammal faunas during Quaternary 'glacials', perhaps partly because faunal interchange was facilitated when lower sea levels exposed the continental shelf, but probably mainly because the two subregions were more similar climatically.

LATE QUATERNARY FAUNAL CHANGE

There are at least sixteen sites in the southern and south-western Cape that have provided mammal fossils dating from the last 5 000-3 000 years. In each case, neither the species represented nor their relative abundance in any way suggest an environment significantly different from the historic one.
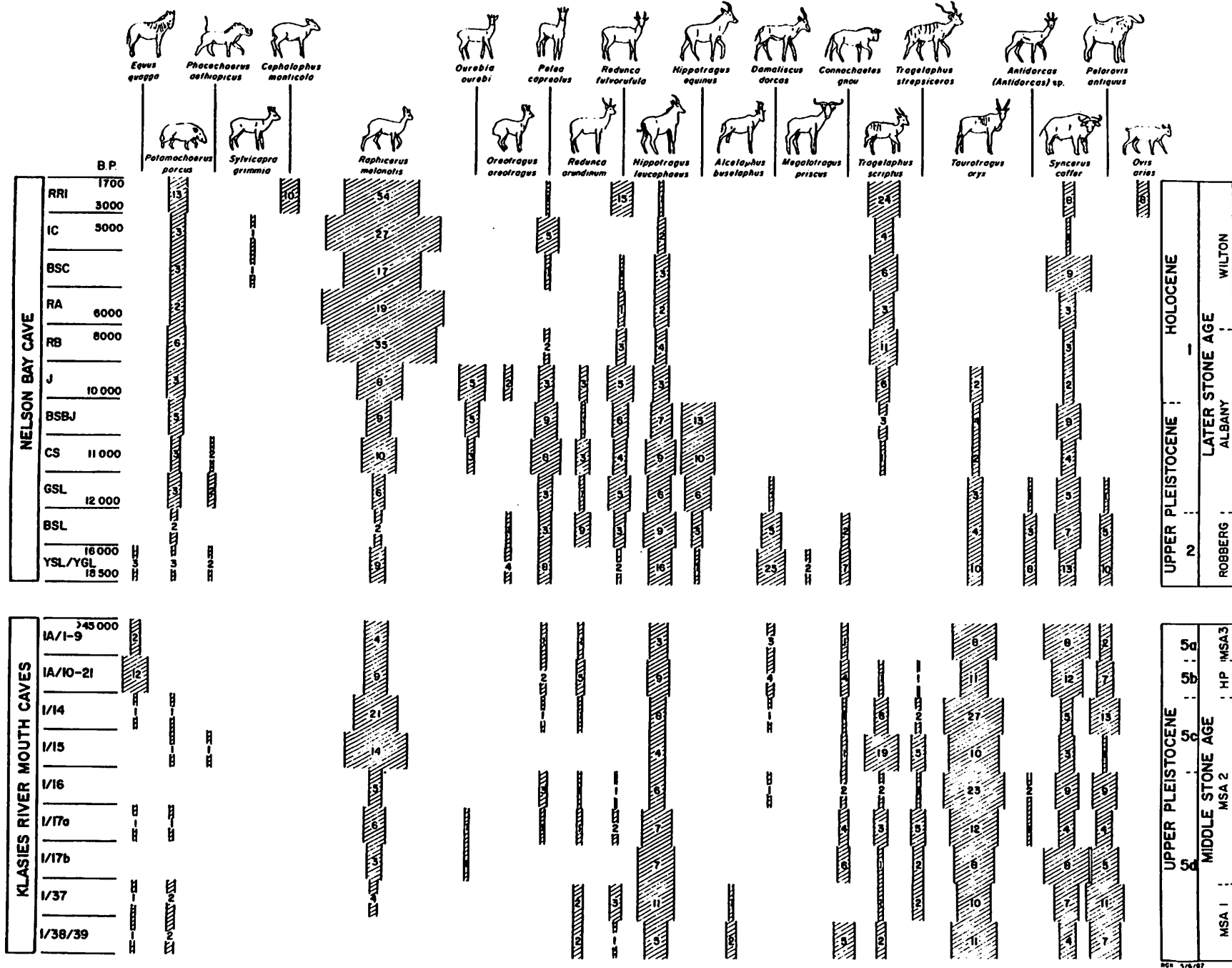
Fig. 1

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Fig. 1. The relative abundance of equid, suid and bovid species in different levels at Nelson Bay Cave (above) and in Klasies River Mouth caves 1 and 1A (below). Absolute abundance is measured by the minimum number of individuals (MNI) by which each species is represented in each level. The MNI numbers are presented inside hatched bars, while the bars are proportional to the percentage abundance of each species within each level. Levels are listed in descending order, from youngest to oldest, on the right hand side of the diagram. The numbers associated with the level designations are approximate radiocarbon ages B.P. (Before Present).

This is totally in keeping with regional and global evidence that the last 5 000-3 000 years was climatically broadly comparable to the present.

Yet earlier faunas, however, often point to a substantially different environment. The clearest example comes from Nelson Bay Cave located on the seaward edge of the Knysna Forest at Plettenberg Bay (Klein 1972). Bones were introduced to Nelson Bay primarily, if not exclusively, by Later Stone Age people. The fauna from levels dated by radiocarbon to between 18 500 and 16 000 years B.P. is comprised overwhelmingly of grazers, including quagga (Equus quagga), warthog (Phacochoerus aethiopicus), bontebok, black wildebeest (Connochaetes gnou), and springbok (Antidorcas cf. australis), none of which were recorded nearby historically. A similar fauna persisted, perhaps with interruptions, until about 12 000 years ago, when it was replaced by one in which historically dominant species (bushpig, grysbok, bushbuck, and buffalo) shared prominence with vaalribbok, mountain reedbuck and roan antelope. Only in deposits post-dating 5000 B.P. or so do the historic forms come to dominate completely (Fig. 1).

Global and local evidence for past temperatures and local (geomorphic/sedimentologic) evidence for past precipitation indicate that climate in the vicinity of Nelson Bay was cold and moist between 18 500 and 16 000 B.P., then cold and probably dry until 12 000-10 000 B.P., warm and dry from 10 000 to 5000-4000 B.P., and warm and moist (broadly like the present) after 5000-4000 B.P. (Butzer & Helgren 1972; Butzer 1973). The microfaunal bones accumulated by owls at Nelson Bay between 18 500 and 16 000 years ago confirm that local temperatures were significantly lower on average, and suggest that the vegetation nearby was more open than it was historically (Avery 1982), but do not confirm that climates were moist.

There is thus ample reason to conclude that climatic change was responsible for the faunal change observed at Nelson Bay, through the mediating influence of vegetation. From the large mammal fauna, it may be inferred that between 18 500 and 16 000 to 12 000 years ago, the surroundings of Nelson Bay were largely open grassland. In the 12 000-5000 year period,

BOOMPLAAS CAVE A

Equus capensis | *Oreotragus oreotragus* | *Redunca sp(p).* | *Hippotragus sp(p).* | *Damaliscus dorcas* | *Tragelaphus strepsiceros* | *Syncerus caffer* | *Ovis aries*

Equus sp(p). (small) | *Raphicerus spp.* | *Pelea capreolus* | *Antidorcas (Antidorcas) sp.* | *Connochaetes/ Alcelaphus* | *Megalotragus priscus* | *Taurotragus oryx* | *Pelorovis antiquus*

	B.P.												
DGL			8/5	2/1									13/4
BLD	1700 2000		8/3	3/3		5/2		6/1					
BLA	6400		6/2	3/1	2/1			1/1					
BRL	10,000	28/7	69/14	71/12	23/10	6/3		9/4	60/15	5/3	2/1	5/6	2/2
CL	12,500 14,000	107/14 9/5	7/4		7/3	5/3	2/1	12/5	218/23	1/1	1/1	35/10	8/3 2/1
GWA/HCA		9/3			3/2		2/1	26/5				4/1	2/1
LP	21,000	6/2					3/2	23/3				1/1	3/2
LPC		6/3		2/1	3/2			38/10				2/1	
YOL		13/2		6/2	11/2			14/2					
BP	32,000	8/3		6/3	8/3	7/3		68/11	6/2		2/2		
OLP	42,000	2/1		8/3	9/3	13/3	6/2	1/1	14/4	2/1		1/1	
BOL	>40,000	1/1		15/4	3/1	13/5	7/3	1/1	9/4	2/1			
OCH		2/1		39/8	62/10	36/9		2/2	2/2	14/7	4/3		6/4
LOH				3/2		10/3	2/1	1/1					

HOLOCENE — LATER STONE AGE (Robberg · 'Albany' · Wilton)

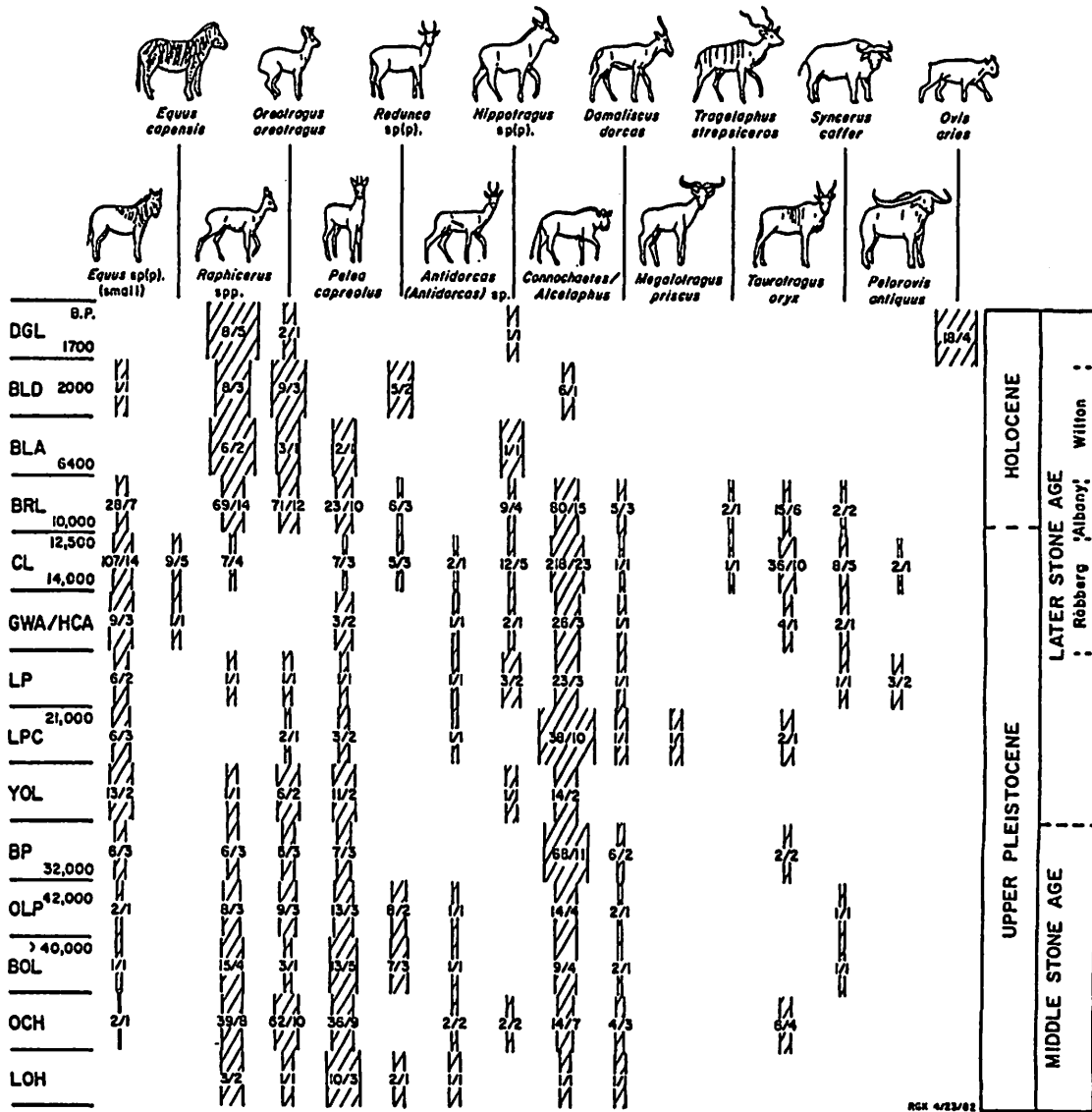UPPER PLEISTOCENE — MIDDLE STONE AGE

Fig. 2

The relative abundance of equid and bovid species in the main stratigraphic units of Boomplaas Cave A. For each unit and species "-/-" is the number of teeth or jaws/the minimum number of individuals (MNI) from which they must come. The hatched bars are proportional to the percentage of each species in each level as calculated from the MNI numbers. The figures associated with the stratigraphic units are approximate radiocarbon dates B.P. Because of the fragmentary nature of the teeth and jaws, some closely related species could not be consistently distinguished from one another. These include the grysbok (Raphicerus melanotis) and steenbok (R. campestris), the mountain reedbuck (Redunca fulvorufula) and southern reedbuck (R. arundinum), the blue antelope (Hippotragus leucophaeus) and roan antelope (H. equinus), and the black wildebeest (Connochaetes gnou) and Cape hartebeest (Alcelaphus buselaphus). Some of the isolated, late Pleistocene teeth assigned to the Connochaetes/Alcelaphus pair are very large and it is possible they come from the blue wildebeest (Connochaetes taurinus).

this was probably replaced by bushier vegetation with an important grass component. Only after 5000 B.P. or so did the present more or less complete bush and forest cover of the area become established. Both a pollen sequence developed by Martin (1968) at Groenvlei near Knysna and the changing geomorphic/pedologic environment (Butzer & Helgren 1972) may be read to support the kind of vegetational change the Nelson Bay fauna suggests for the 5000-4000 B.P. interval.

Broadly the same kind of vegetational change -- from a mosaic in which grasses were extremely prominent, if not dominant, to one in which they were progressively replaced by bush, forest or fynbos after 12 000-10 000 B.P. -- is implied by faunal changes at other Later Stone Age sites with deposits of appropriate age. These include Byneskranskop 1 (Schweitzer & Wilson 1982), Buffelskloof (Opperman 1978) and Boomplaas (Deacon 1979) within the fynbos zone proper, and Elands Bay Cave (Parkington 1979, 1981) and Melkhoutboom Cave (Deacon 1976) just beyond its north-western and south-eastern margins respectively.

The case of Boomplaas near Oudtshoorn is particularly clear, given the large samples involved (Fig. 2). The fauna from Boomplaas levels dated to between 22 000 and 12 000 B.P. is heavily dominated by equids (quagga, mountain zebra, or both) and alcelaphine antelope (wildebeest, hartebeest, or both). As at Nelson Bay, the indigenous ungulate species that dominated the local fauna historically -- grysbok, steenbok, klipspringer, and mountain reedbuck -- only dominate the fossil fauna after 6-5000 B.P. or so. In the period between perhaps 12 000 and 6-5000 B.P. the historically dominant species and the large grazers that dominated before 12 000 B.P. are about equally represented, suggesting a vegetation in which grasses were less common than before 12 000 B.P., but more common than after 6-5000 B.P. Taxonomic identifications of charcoals from the Boomplaas deposits confirm that the vegetation between 12-10 000 and 6-5000 B.P. was different from the vegetation both before and after (Deacon 1979), as do microfaunal bones accumulated by owls (Avery 1982).

At Boomplaas, the bottom-most units are believed to date from the 'last interglacial', and it is interesting that the fauna from these units is broadly similar in species composition and relative species abundance to the fauna from the topmost units, dating from the present interglacial or Holocene. This is true not only with respect to the frequencies of equids and bovids (Fig. 2), but also with regard to the frequencies of other species, especially baboon and hyrax (Fig. 3). It is tempting to conclude that the overall pattern of faunal change at Boomplaas reflects cyclical environmental change from 'interglacial' to 'glacial' and then back to 'interglacial' conditions, and this may well be true. However, there is evidence that many of the bones from the bottom of the sequence were collected by leopards, while the ones in the middle and top were collected by people. If so, this, rather than a similarity in environment, could explain
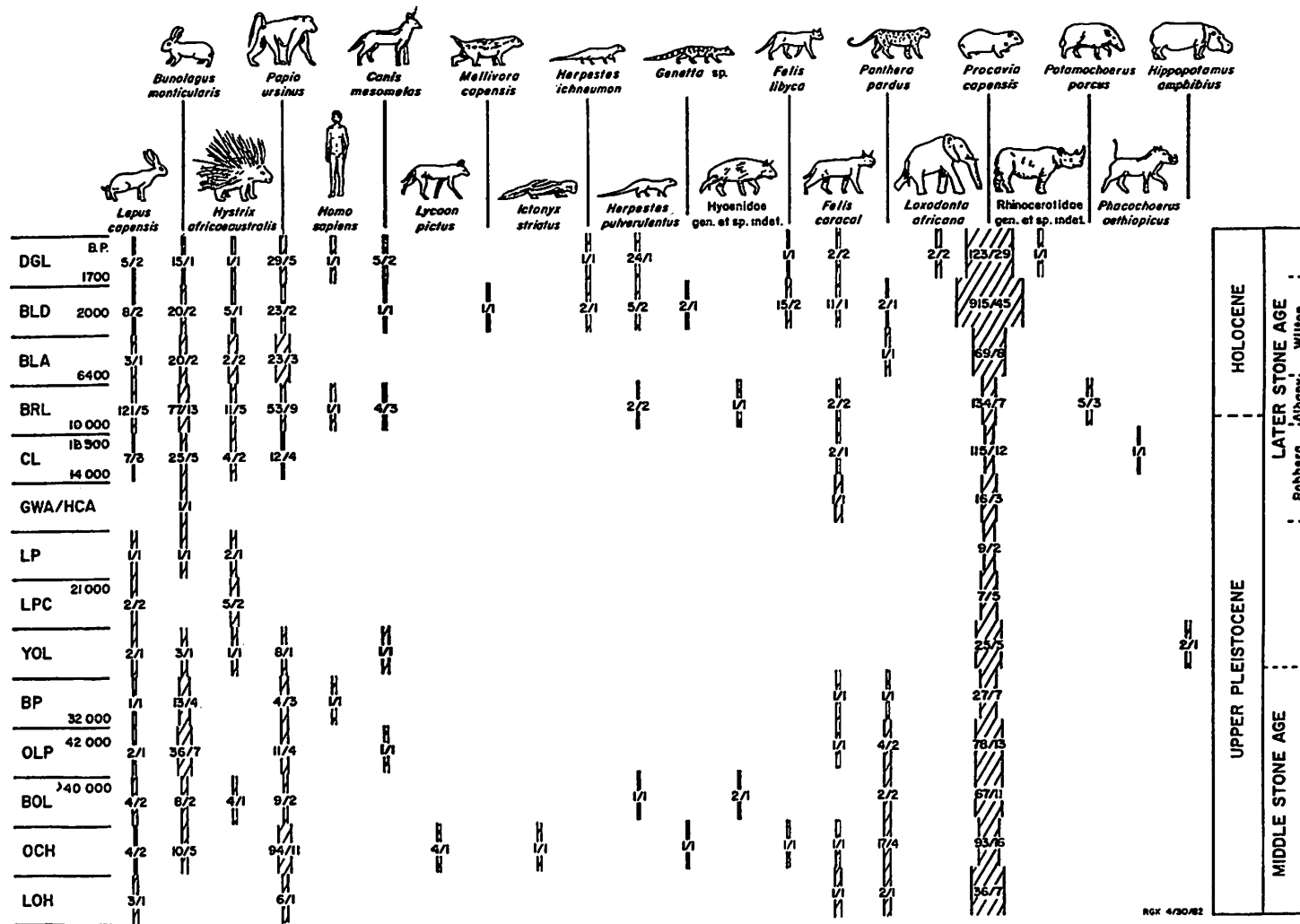
BOOMPLAAS CAVE A

Bunolagus monticularis | Papio ursinus | Canis mesomelas | Mellivora capensis | Herpestes ichneumon | Genetta sp. | Felis libyca | Panthera pardus | Procavia capensis | Potamochoerus porcus | Hippopotamus amphibius

Lepus capensis | Hystrix africaeaustralis | Homo sapiens | Lycaon pictus | Ictonyx striatus | Herpestes pulverulentus | Hyaenidae gen. et sp. indet. | Felis caracal | Loxodonta africana | Rhinocerotidae gen. et sp. indet. | Phacochoerus aethiopicus

	B.P.																	
DGL		5/2	15/1	1/1	29/5	1/1	5/2			1/1	24/1		1/1	2/2		2/2	123/29	1/1
	1700																	
BLD	2000	8/2	20/2	5/1	23/2	1/1		1/1		2/1	5/2	2/1	15/2	11/1	2/1		915/45	
BLA	6400	3/1	20/2	2/2	23/3									1/1			69/8	
BRL	10 000	121/5	77/13	11/5	53/9	1/1	4/3			2/2		1/1	2/2				134/7	5/3
	13 900													2/1			115/12	1/1
CL	14 000	7/3	25/5	4/2	12/4													
GWA/HCA																	16/3	
LP		1/1	1/1	2/1													9/2	
	21 000																	
LPC		2/2		5/2													7/5	
YOL		2/1	3/1	1/1	8/1	1/1											25/5	2/1
BP	32 000	1/1	13/4		4/3	1/1							1/1	1/1			27/7	
OLP	42 000	2/1	36/7		11/4	1/1							1/1	4/2			78/13	
BOL	>40 000	4/2	8/2	4/1	9/2						1/1		2/1		2/2		67/11	
OCH		4/2	10/5		94/11			4/1	1/1		1/1		1/1	17/4			93/15	
LOH		3/1			6/1								1/1	2/1			36/7	

HOLOCENE | LATER STONE AGE Wilton, Albany, Robberg

UPPER PLEISTOCENE

MIDDLE STONE AGE

RGK 4/30/82

Fig. 3   The relative abundance of species besides equids and bovids in the main strati-
graphic units of Boomplaas Cave A.   For each unit and species, "-/-" is the
number of bones/the minimum number of individuals from which they must come.
Other features of the diagram are the same as for Fig. 2.

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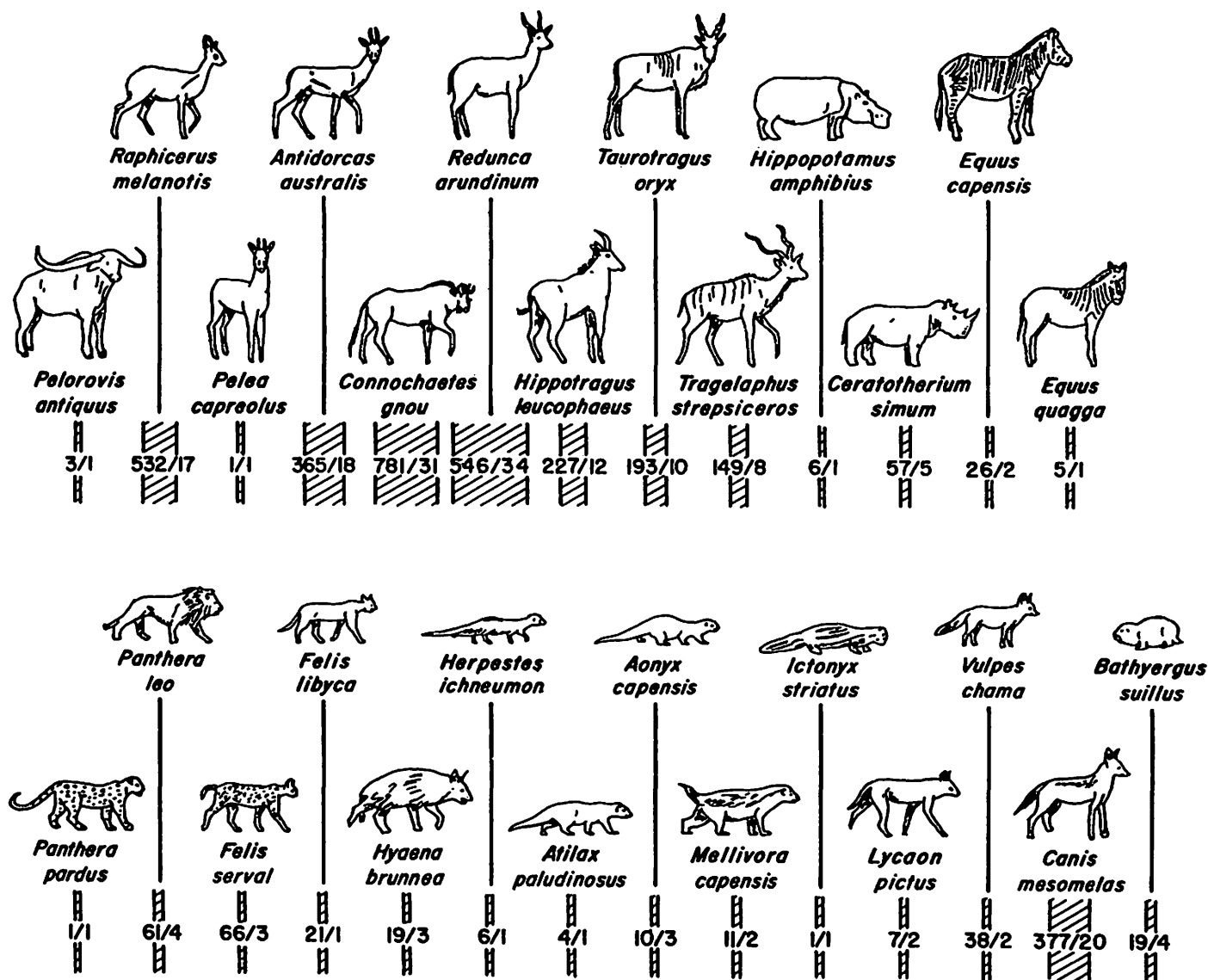the abundance of hyraxes, baboons, and small ungulates at both the bottom and top.

The term 'last interglacial' as used here is synonymous with deep-sea oxygen-isotope stage 5, spanning the interval from approximately 128 000 years ago to about 75 000 years ago. The deep-sea record indicates that stage 5 was by no means uniformly warm, however (Shackleton & Opdyke 1973, 1976). It was interrupted by two pronounced cold intervals centred at about 109 000 and 92 000 B.P. These are known as substages 5d and 5b respectively. The preceding, intervening, and succeeding warm phases are known (from oldest to youngest) as 5e, 5c and 5a. Only 5e (from perhaps 128 000 to 118 000 B.P.) was as warm or warmer than the present interglacial (Holocene), and some specialists think that 5d to 5a are better regarded as the opening phases of the last glacial.

In addition to Boomplaas, other sites in the fynbos region that contain faunas dating from the time span of isotope stage 5 are the Klasies River Mouth caves near Humansdorp (Klein 1975b; Singer & Wymer 1982), Lake Pleasant (Groenvlei) near Knysna (Butzer & Helgren 1972), the Herolds Bay midden/bone occurrence (Brink & Deacon 1982), Linkerhandsgat-East near Stanford (Cooke 1955; Klein unpub.), Swartklip 1 on False Bay (Hendey & Hendey 1968; Klein 1975a), and Sea Harvest at Saldanha Bay (Hendey 1974; Klein unpub.). The Klasies River Mouth, Swartklip and Sea Harvest samples are particularly large and informative.

The bones in the Klasies River Mouth caves were accumulated primarily, if not exclusively, by Middle Stone Age people. Variation in sand grain size through the Klasies profile suggests sea level fluctuations nearby that can be correlated with substages of isotope stage 5 (Butzer in Singer & Wymer 1982). The correlations are supported by oxygen-isotope readings on Klasies marine shells that indicate that offshore waters were cooler during inferred periods of lower sea level (Shackleton in Singer & Wymer 1982). Fig. 1 shows that deposits formed at Klasies during isotope substages 5d and 5b are relatively richer in alcelaphine antelopes (wildebeest, hartebeest, and/or bontebok) and equids than are deposits correlated with the higher sea level of intervening substage 5c. In contrast, the deposits correlated with 5c are relatively richer in grysbok and bushbuck.

The pattern of faunal change from deposits correlated with 5d into ones correlated with 5c is in fact broadly reminiscent of the pattern of change in deposits formed during the climatically comparable transition from the last glacial to the present interglacial at nearby Nelson Bay Cave. (In terms of isotope stages, the transition at Nelson Bay would be from Stage 2 to Stage 1, about 12 000 years ago.) The fact that the two sites share a pattern of faunal change that coincides closely with a shared pattern of climatic change inferred from other evidence argues especially strongly that climatic change (not cultural change) was the ultimate cause of faunal change at both sites.

Besides broad similarities, the Klasies and Nelson Bay faunas that

Raphicerus melanotis Antidorcas australis Redunca arundinum Taurotragus oryx Hippopotamus amphibius Equus capensis

Pelorovis antiquus Pelea capreolus Connochaetes gnou Hippotragus leucophaeus Tragelaphus strepsiceros Ceratotherium simum Equus quagga

3/1 532/17 1/1 365/18 781/31 546/34 227/12 193/10 149/8 6/1 57/5 26/2 5/1

Panthera leo Felis libyca Herpestes ichneumon Aonyx capensis Ictonyx striatus Vulpes chama Bathyergus suillus

Panthera pardus Felis serval Hyaena brunnea Atilax paludinosus Mellivora capensis Lycaon pictus Canis mesomelas

1/1 61/4 66/3 21/1 19/3 6/1 4/1 10/3 11/2 1/1 7/2 38/2 377/20 19/4

SWARTKLIP I.

R.G.K. & K.C-U. 5/4/82

Fig. 4 The relative abundance of large mammal species in the fossil brown hyaena lair at Swartklip 1. "-/-" is the number of bones/minimum number of individuals (MNI) from which they must come. The hatched bars are proportional in breadth to the MNI's.

accumulated under broadly comparable ('interglacial') conditions exhibit some important differences. Especially striking is the great abundance of eland and giant buffalo (Pelorovis antiquus) at Klasies and the rarity of suids there. On analogy with Nelson Bay, at least the bushpig should be relatively common in those deposits where grysbok and bushbuck are well-represented.

It is possible that the abundance of eland and the rarity of suids at Klasies reflects the Klasies hunters' preference for relatively docile species (like eland) and the hunters' inability to obtain relatively dangerous ones (like bushpig). The (Middle Stone Age) artefacts made by the Klasies people are very different from the (Later Stone Age) ones made by the Nelson Bay people, and there is reason to suppose that only the Nelson Bay people possessed weapons like the bow and arrow that allowed hunters to attack dangerous prey from a distance.

Alternatively, it is possible that the local environment during substage 5c times differed from the present interglacial environment in ways that were especially favourable to eland and unfavourable to bushpig. Perhaps the same conditions were especially favourable to the giant buffalo, or perhaps the giant buffalo's grazing habits actually helped to create a special and distinctive environment that has no historic counterpart. The giant buffalo became extinct at the beginning of the present interglacial roughly 10 000 years ago, which itself constitutes an argument against strict comparability between the last interglacial and present interglacial environments near Nelson Bay and Klasies.

Finally, it is possible that eland were so abundant at Klasies because the cliffs nearby were ideal for driving eland to their death. Among the ungulates found at Klasies, eland were probably the ones most amenable to driving. Additionally, unlike the other ungulates at the site which are represented mainly by very young and by old individuals, the eland is well represented by prime-age adults (Klein 1979). The implication is that other ungulates were stalked individually and only the weakest, most vulnerable ones were usually obtained. In contrast, the high proportion of prime-age adult eland suggests hunting with a method that netted entire groups. The most likely method is driving. Unfortunately, the available evidence does not permit a clear choice among the alternative explanations for eland abundance at Klasies. It is similarly abundant in the much smaller Middle Stone Age sample from Die Kelders Cave 1 near Gansbaai, believed to date from the early part of the 'last glacial' (equivalent to isotope stage 4) (Klein 1975b,1976; Tankard & Schweitzer 1976). However, once again it is unclear if the reason is primarily environmental or cultural.

Geomorphic/sedimentologic data and methods similar to those employed in drawing palaeoenvironmental inferences from the Klasies River Mouth deposits indicate that the Swartklip fauna accumulated in the interval equivalent to isotope substage 5d, while the Sea Harvest fauna belongs to the broadly comparable, but more recent substage 5b (Butzer pers. comm.). In both cases,
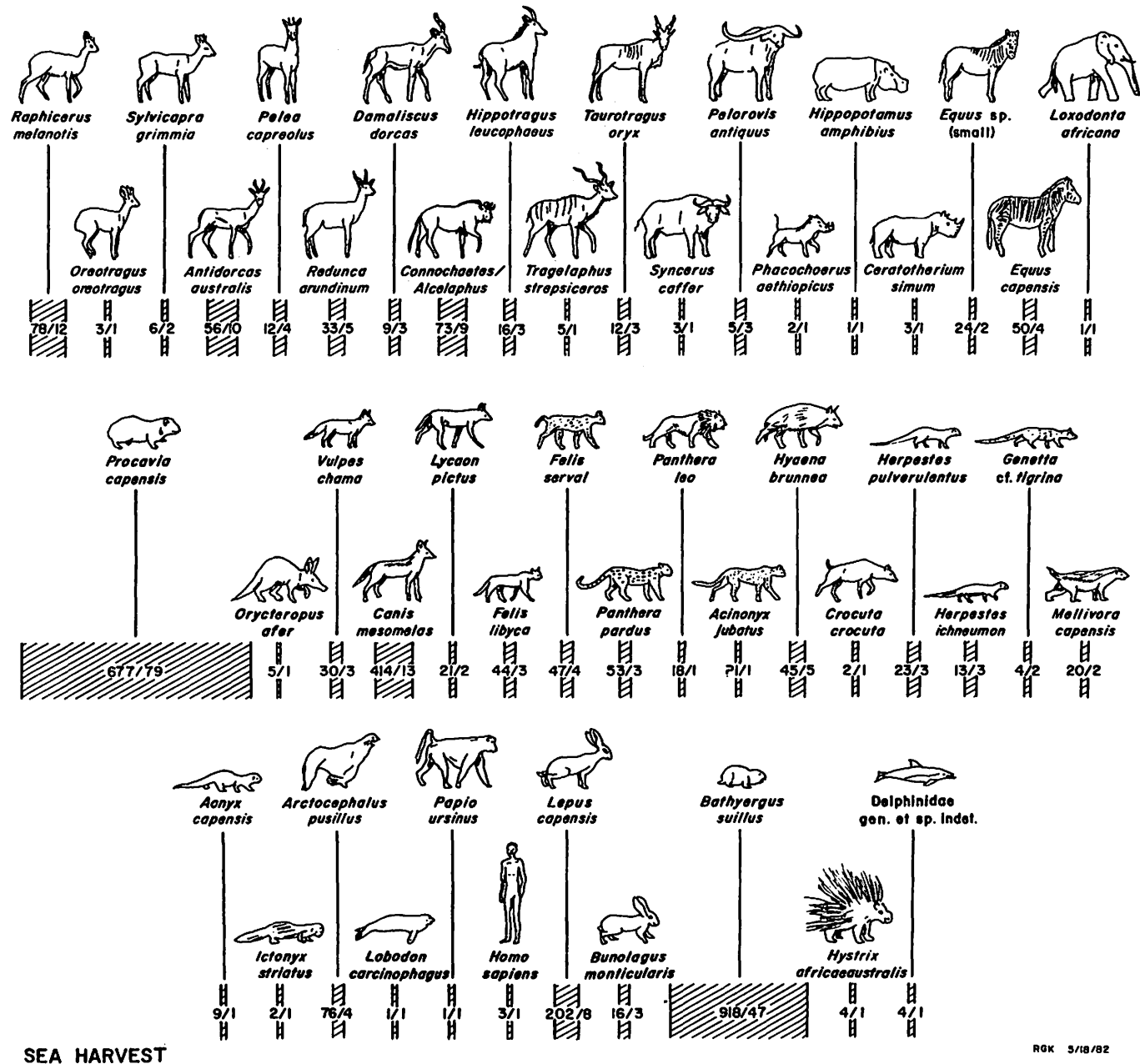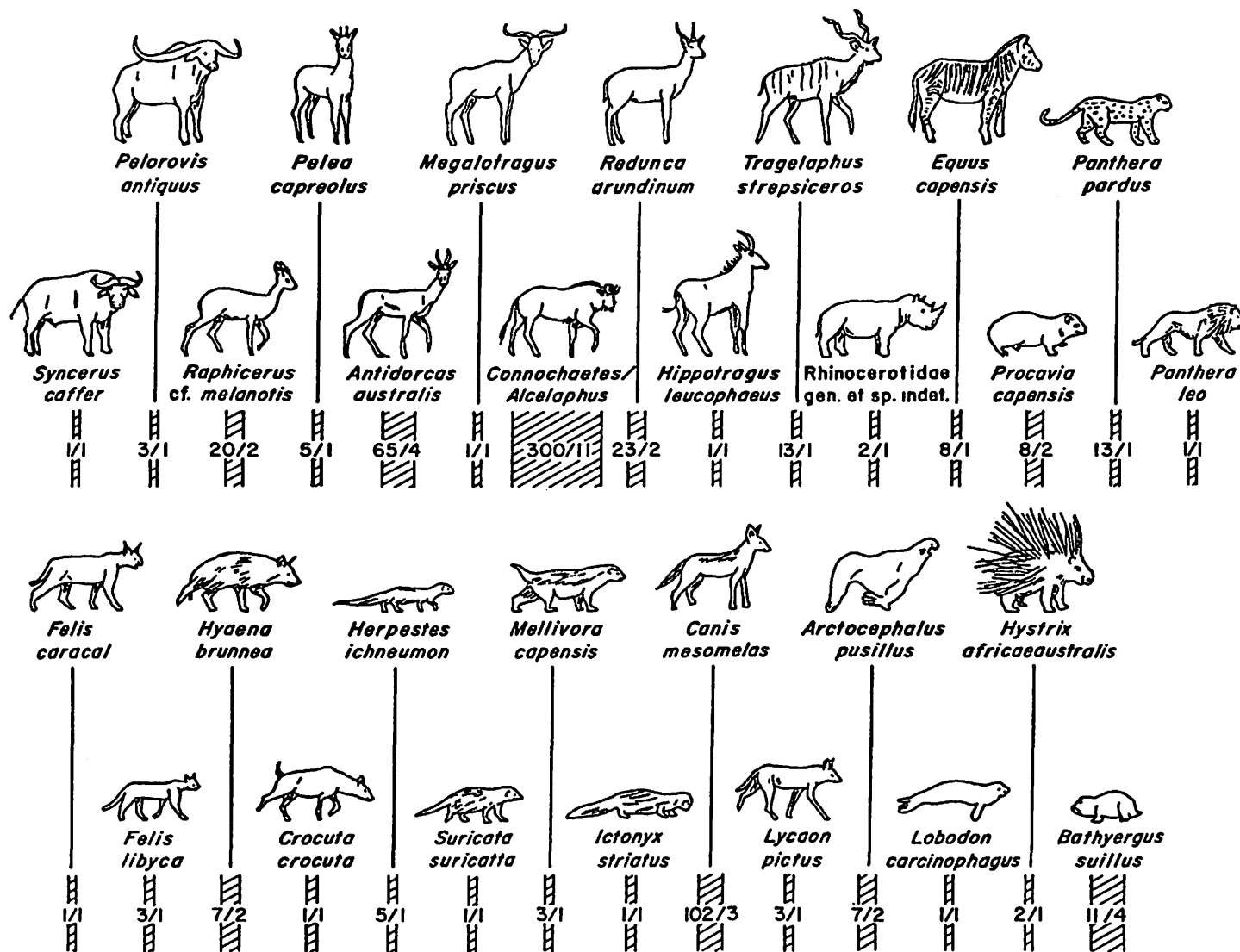
SEA HARVEST

Fig. 5 The relative abundance of large mammal species in the Sea Harvest faunal locality, Saldanha Bay. For bovids, "-/-" is the number of teeth and jaws/minimum number of individuals (MNI) from which they must come. For other species "-/-" is the total number of bones/MNI. The hatched bars are proportional in breadth to the MNI's.

HOEDJIES PUNT

Pelorovis antiquus	Pelea capreolus	Megalotragus priscus	Redunca arundinum	Tragelaphus strepsiceros	Equus capensis	Panthera pardus	

Syncerus caffer	Raphicerus cf. melanotis	Antidorcas australis	Connochaetes/ Alcelaphus	Hippotragus leucophaeus	Rhinocerotidae gen. et sp. indet.	Procavia capensis	Panthera leo
1/1	3/1	20/2	5/1	65/4	1/1	300/11	23/2	1/1	13/1	2/1	8/1	8/2	13/1	1/1

Felis caracal	Hyaena brunnea	Herpestes ichneumon	Mellivora capensis	Canis mesomelas	Arctocephalus pusillus	Hystrix africaeaustralis

	Felis libyca	Crocuta crocuta	Suricata suricatta	Ictonyx striatus	Lycaon pictus	Lobodon carcinophagus	Bathyergus suillus
1/1	3/1	7/2	1/1	5/1	1/1	3/1	1/1	102/3	3/1	7/2	1/1	2/1	11/4

RGK 5/13/82

Fig. 6 The relative abundance of large mammal species in the Hoedjies Punt faunal occurrence, Saldanha Bay. "-/-" is the number of bones/the minimum number of individuals (MNI)· from which they must come. The hatched bars are proportional in breadth to the MNI's.

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the climatic conditions were essentially 'glacial', in spite of the 'last interglacial' (sensu lato) age assignment. In both fossil faunas, the most abundant ungulates are grazers that were rare or absent historically (Figs 4 and 5). This suggests once again that 'glacial' climatic conditions in the fynbos region favoured an expanded role for grasses in the regional vegetational mosaic.

Unlike the sites that have been discussed so far, neither Swartklip nor Sea Harvest is an archaeological occurrence. Instead, they represent places to which bones were brought by carnivores (probably the brown hyaena). In consequence of this, compared to archaeological faunas they are relatively rich in bones of carnivores, especially bones of black-backed jackals, probably killed by the hyaenas in contests for carrion. Sea Harvest is also very rich in bones of small mammals (hyrax, mole rats and hares), perhaps accumulated at the site by a small carnivore or owl. However, the fact that grazers dominate heavily among the ungulates at both Swartklip and Sea Harvest is a further strong argument that grazer abundance in archaeological sites dating from similar 'glacial' episodes reflects the genuine abundance of grazers nearby. The alternative -- that they are abundant in the archaeological sites because of a strong (and inexplicable) ancient human preference for rare species -- seems highly unlikely.

Several other late Quaternary carnivore sites in the fynbos zone have provided faunas basically similar to those from Swartklip and Sea Harvest in the high proportion of historically rare or absent grazers (e.g. Figs 6 and 7). So far, at most of these sites, there is no independent basis for determining what the environment was like at the time the bones accumulated, but it seems likely it was 'glacial' in the same sense that it was at Swartklip and Sea Harvest. The reason that 'glacial' faunas appear to be so much more common than 'interglacial' ones is probably that 'glacial' climatic conditions were far more common than 'interglacial' ones during the late Quaternary. At the same time, it is important to point out that with the exception of Boomplaas, there are no sites in the fynbos zone (and few in southern Africa as a whole) that have provided faunas clearly dating from the main part of the 'last glacial' (equivalent to isotope stage 3, between 64 000 and 32 000 years ago). The most probable reason is that hyperarid climate prevailed, reducing human and animal populations to levels with very low archaeological/palaeontological visibility.

EARLY AND MIDDLE QUATERNARY FAUNAS

Hendey (1978) has argued convincingly that the mammal fauna from the 'lower levels' of Baard's Quarry, Langebaanweg is of latest Pliocene or earliest Pleistocene (= early Quaternary) age. So far, no other early Quaternary faunas have been recovered in the fynbos region. Although the
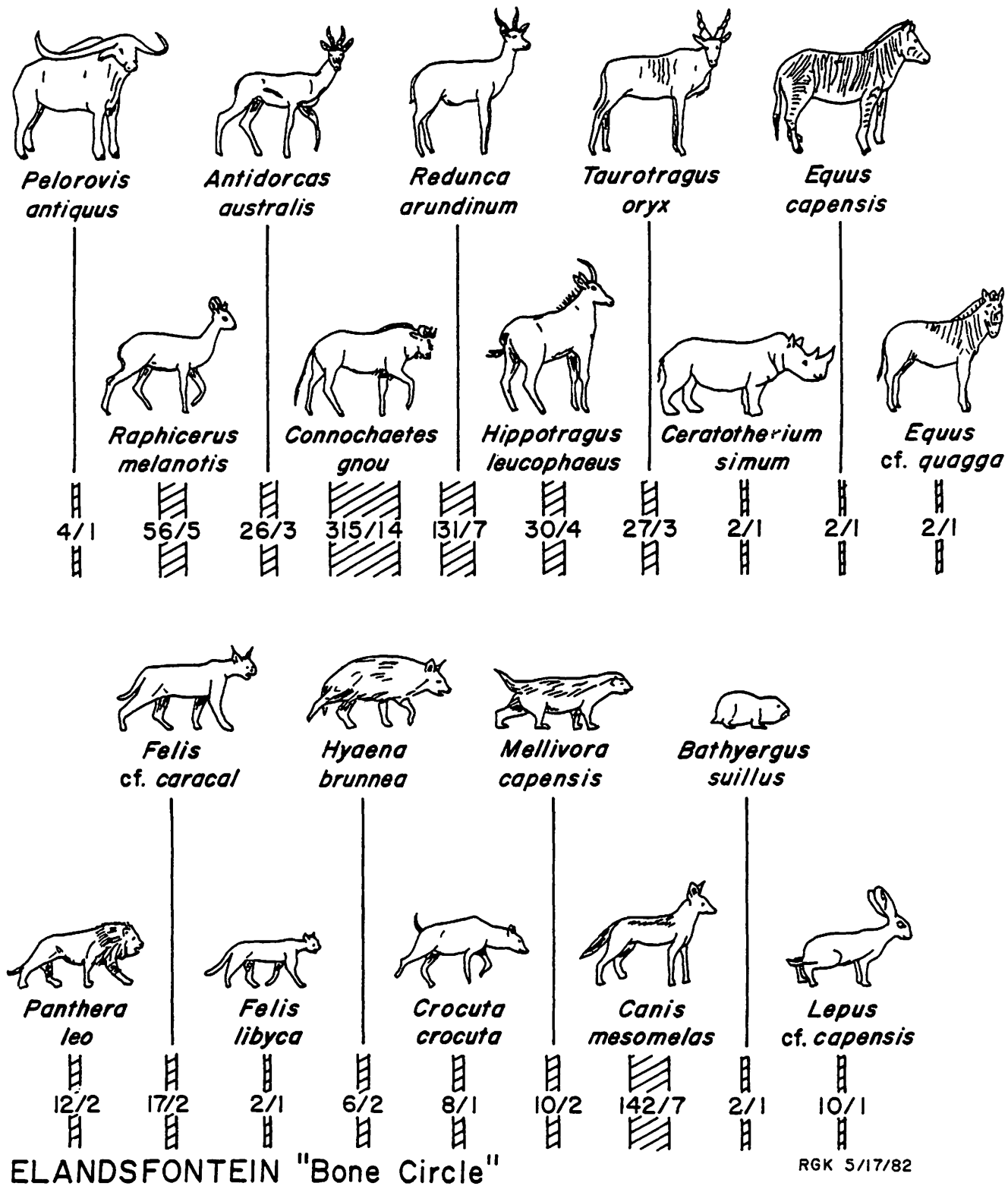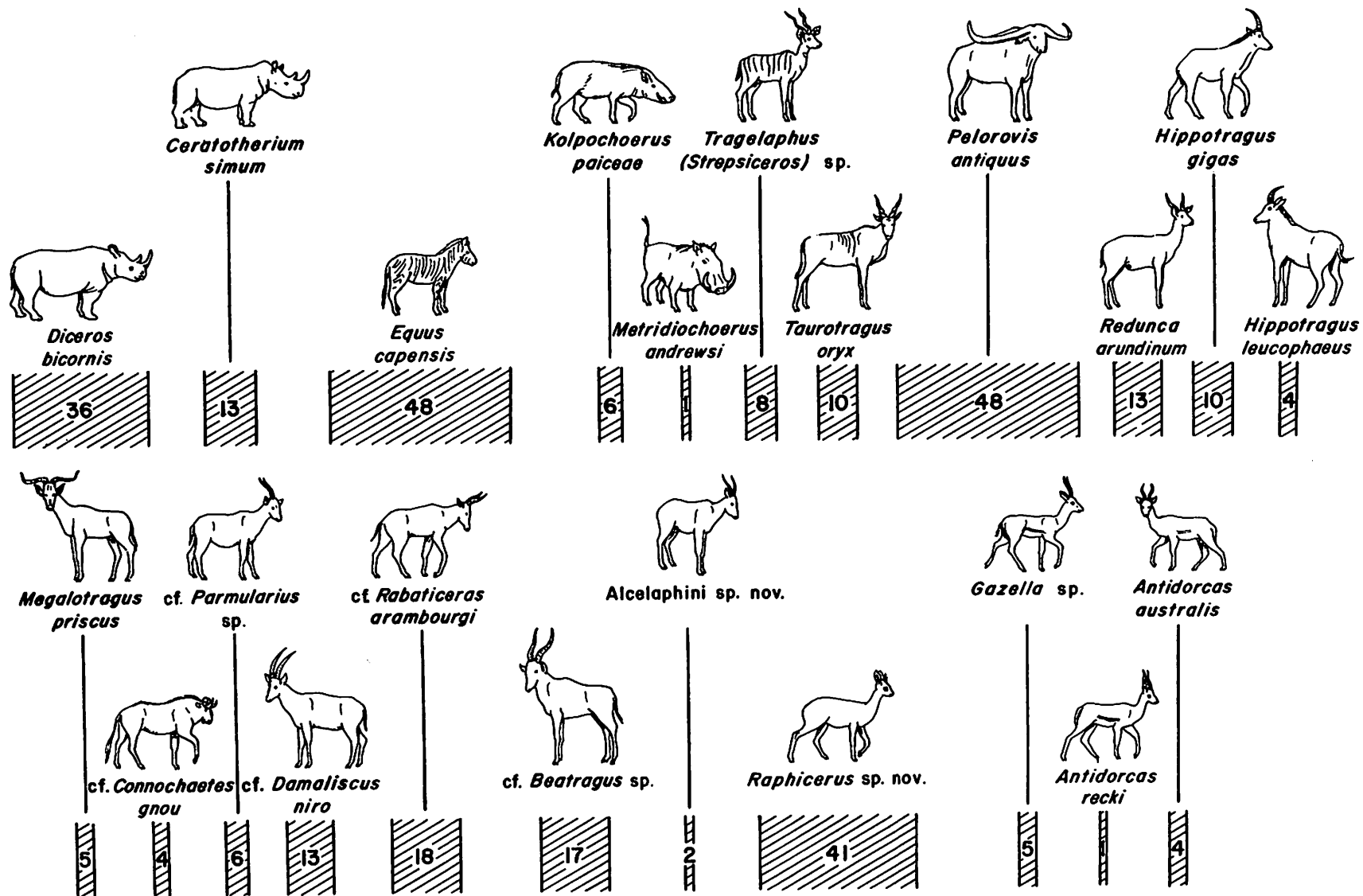
Pelorovis antiquus	Antidorcas australis	Redunca arundinum	Taurotragus oryx	Equus capensis

	Raphicerus melanotis	Connochaetes gnou	Hippotragus leucophaeus	Ceratotherium simum	Equus cf. quagga
4/1	56/5	26/3	315/14	131/7	30/4	27/3	2/1	2/1	2/1

Felis cf. caracal	Hyaena brunnea	Mellivora capensis	Bathyergus suillus

Panthera leo		Felis libyca	Crocuta crocuta	Canis mesomelas	Lepus cf. capensis
12/2	17/2	2/1	6/2	8/1	10/2	142/7	2/1	10/1

ELANDSFONTEIN "Bone Circle"

RGK 5/17/82

Fig. 7   The relative abundance of large mammal species in the Elandsfontein "Bone Circle".   "-/-" is the number of bones/minimum number of individuals (MNI) from which they must come.   The hatched bars are proportional to the MNI's.

Fig. 8 The relative abundance of equid, suid and bovid species in the middle Quaternary fauna of Elandsfontein. Inside each hatched bar is the minimum number of individuals (MNI) by which each species is represented. The breadth of each bar is proportional to the MNI.

Baard's Quarry fauna is clearly much younger than the main ('E' Quarry = early Pliocene) fauna from Langebaanweg, there is nothing about it to suggest environmental conditions different from those that pertained at Langebaanweg earlier on, as discussed by Hendey (this volume).

Middle Quaternary mammals are considerably better known. There is a small sample recently recovered from Skurwerug at Saldanha Bay (Hendey, pers. comm.), small, probably late Middle Pleistocene, samples from Bloembos near Darling (Cooke 1955) and from Duinefontein 2 near Melkbosstrand (Klein 1976), and a very large sample from Elandsfontein near Hopefield (Hendey 1974). The Bloembos sample is notable because it has provided the sole Quaternary record of the giraffe (Giraffa camelopardalis) in the fynbos zone. This is direct evidence for the presence of trees in a local environment that was largely treeless historically. However, it is the large and diverse Elandsfontein sample which is potentially most informative from a palaeoenvironmental point of view.

Similar to many of the late Quaternary faunas discussed in the last section, the Elandsfontein middle Quaternary fauna is relatively rich in alcelaphine antelopes (at least six different species, including Connochaetes gnou, Parmularius sp., Damaliscus niro, Rabaticeras arambourgi and ?Beatragus sp.), equids and other grazers (Fig. 8). This implies that grasses played a more important role in the ancient environment than they did historically. However, the Elandsfontein fauna also contains a giraffid (Sivatherium olduvaiense) and a civet cat (Viverra civetta), indicating the grassland contained trees. With regard to rhinoceroses, both the black (which was present historically) and the white (Ceratotherium simum) (which was not) are represented, but the black is clearly more numerous, indicating that suitable browse was common in the vicinity. Suids are not common overall, but between the two that are present, Kolpochoerus paiceae, a probable browser, outnumbers Metridiochoerus andrewsi, a probable grazer. In sum, in contrast to the late Quaternary 'glacial' faunas which tend to suggest open grassland with relatively little bush or thicket, the Elandsfontein fauna suggests a vegetation in which grass and bush were more equally represented.

It is important to emphasize that Elandsfontein is a very different kind of site than any of the late Quaternary ones discussed previously. The middle Quaternary bones lie on one or more palaeosurfaces where they are currently being exposed by deflation. Associations of bones in anatomical order are common and many (?most) of the animals represented probably lie at or near the places where they died. Carnivore-gnawed bones and hyaena coprolites are probably more numerous than artefacts, and death was probably more often from 'natural' causes than from human action. Porcupine gnawing is also quite common, and many of the bones may have come from now-deflated porcupine lairs. The overwhelming majority of bones in the present sample were collected from the surface, without record of their associations or of their provenience within the site. This means that it is impossible to

estimate how many may have come from semi-articulated skeletons, how many were associated with artefacts or coprolites, and so forth. Even with these problems in mind, however, the overall composition of the fauna still suggests an environment that was qualitatively different in important respects from any known late Quaternary one.

MEAN INDIVIDUAL SIZE AND CLIMATE

Mean individual size has been shown to vary with climate in a number of mammalian species, particularly carnivores and micromammals (small rodents and insectivores). Kurten (1959, 1965) has presented some examples and discussed the reasons for size variation, including Bergmann's Rule and so-called population density factors. Bergmann's Rule states that if all other things are equal, individuals of a species will be larger in colder climates. This is because as an animal grows, its volume, which produces heat, increases more rapidly than its skin area, which dissipates it.

Bergmann's Rule has been shown particularly to characterize carnivores, though there are many species that do not obey it. The reason is apparently that 'other things' are not always equal. Probably most important is the fact that individuals must be able to find sufficient food to maintain a larger body. It is in this context that 'population density factors' become important. In particular, increased body size will probably be selected against, if it reduces the number of individuals the environment can support below the critical level necessary for successful reproduction. Through its effect on food supply, a change in climate, even greater cold, might thus actually induce a reduction in mean individual body size.

Avery (1982) has shown that mean size in several southern African micromammal species is probably related to variation in temperature or precipitation, but otherwise very little research of this kind has been done in southern Africa. In a study designed to explore the possibility of a linkage between climate and size in somewhat larger mammals, I am currently compiling measurements on bones of black-backed jackal, Cape fox, brown hyaena, caracal, grey mongoose, rock hyrax, Cape mole rat and Cape grysbok. These are species which are abundant in sites of various ages within the fynbos region.

The study is incomplete, in that many more recent comparative specimens must be measured to confirm the patterns that appear to be emerging. The measurements compiled so far suggest that individual carnivore size generally varies with temperature in a way that would be predicted from Bergmann's Rule, that is, in the various carnivore species, mean individual size increases as mean annual temperature decreases. The pattern in the three herbivorous species is more complex, but appears to be broadly related to precipitation. In particular, at least within the fynbos zone, as

precipitation increases, average hyrax size appears to decrease, while average mole rat and grysbok size appear to increase.

As an example of what is involved, Fig. 9 presents measurements on black-backed jackal first molar (M1) lengths. Average tooth size reflects average body size in most mammalian species, while jackal dentitions are common both in museum comparative collections and in fossil samples where the jackal itself is well represented. A further advantage to measuring the M1 is that it is readily identifiable to species, so there is no danger of confusing what is really a change in jackal species with a change in mean individual size within a single species.

Fig. 9 shows that Cape and Namibian jackals tend to be substantially larger than ones from Equatorial East Africa, as would be expected if Bergmann's Rule were operative. The figure also shows that modern Cape jackals tend to be significantly smaller than the ones represented at Swartklip 1. This is also in keeping with the operation of Bergmann's Rule, since geomorphic evidence indicates that the Swartklip fauna accumulated under very cool conditions. The Sea Harvest jackals were apparently intermediate in average size between modern Cape ones and the very large specimens from Swartklip. This is consistent with the fact that, unlike the Swartklip fauna, the Sea Harvest one contains some marine elements, suggesting accumulation at a time of somewhat higher sea level and less cool ambient temperatures.

The only jackals similar in size to the Swartklip ones are those from the 'Bone Circle' at Elandsfontein. This is an late Quaternary fossil hyaena lair in which the species representation is essentially identical to that at Swartklip (Inskeep & Hendey 1966; Klein unpub.) (compare Figs 5 and 7). The implication is that the 'Bone Circle' formed under climatic conditions very similar to those at Swartklip. Interestingly, the jackals associated with the middle Quaternary fauna at Elandsfontein (labelled 'other' in Fig. 9) are significantly smaller than the 'Bone Circle' ones. They are in fact similar in average size to modern Cape jackals. Together with the fact that the Elandsfontein middle Quaternary grysbok is very large, this may mean that the middle Quaternary fauna accumulated under relatively warm and wet conditions without parallel in the late Quaternary. As discussed in the last section, the taxonomic composition of the middle Quaternary fauna may be used to support the same conclusion. The relatively warm, wet conditions involved may be the ones that promoted the growth of yellowwood forests on the Cape Flats, as reported by Schalke (1973). Alternatively, it is possible these forests are much older than the middle Quaternary. Until recently, they were assigned to the late Quaternary on the basis of radiocarbon dates that are assumed to be finite, but which may well be infinite.
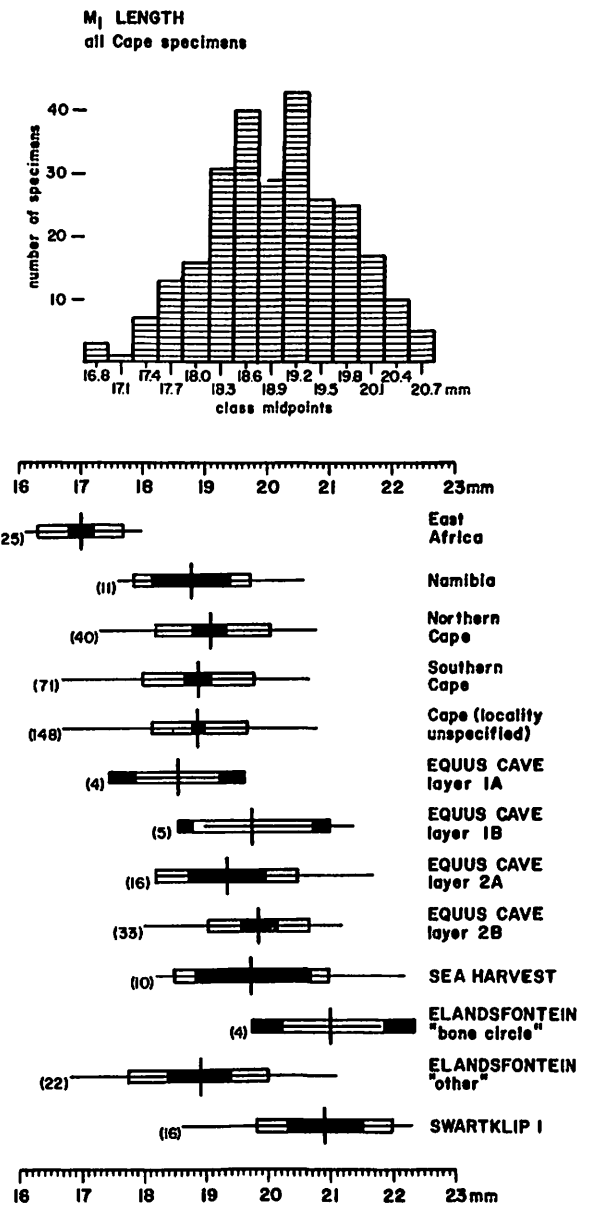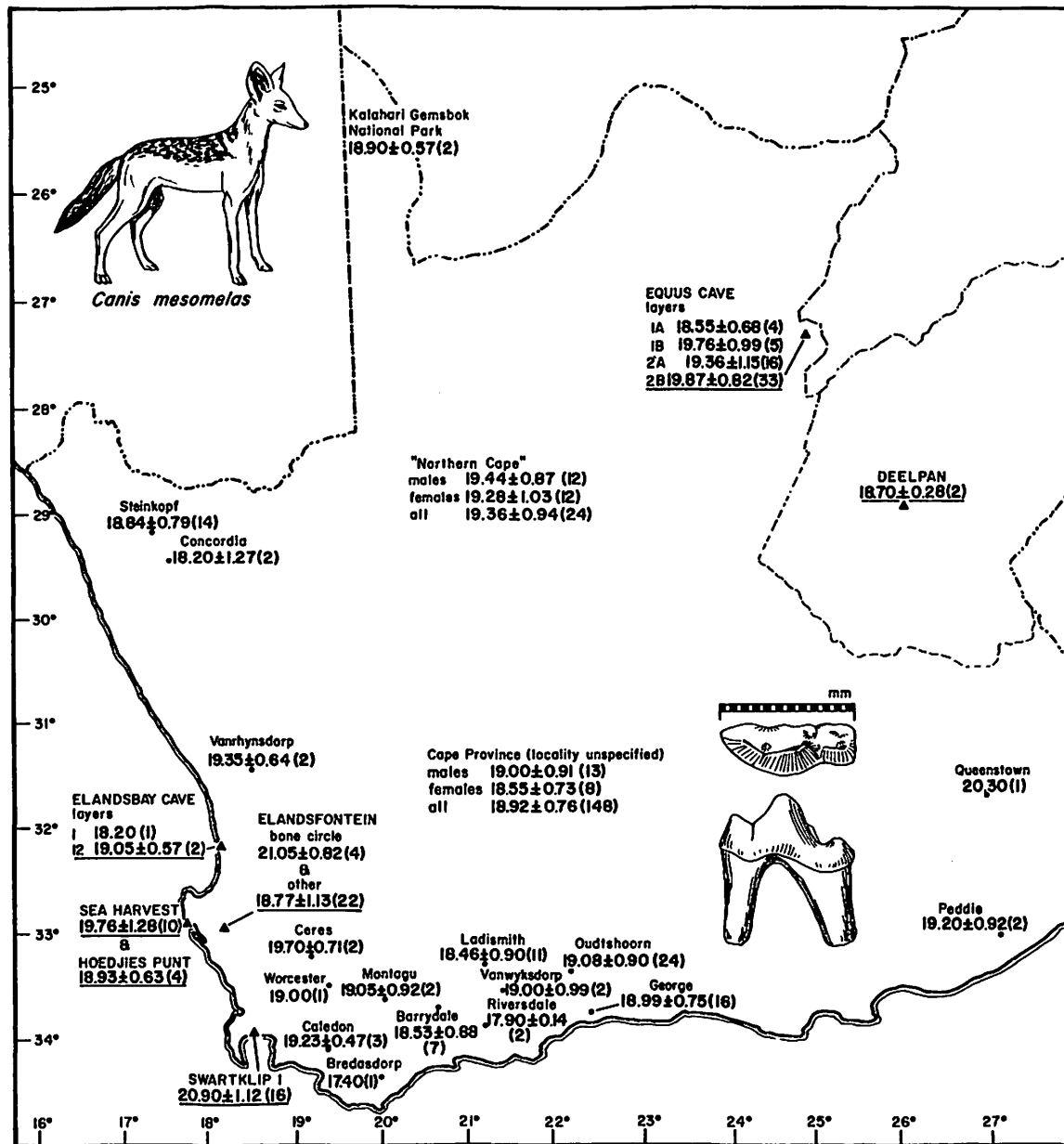
M₁ LENGTH
all Cape specimens — rendered: M_1 LENGTH, all Cape specimens

Map labels:

Canis mesomelas

Kalahari Gemsbok
National Park
18.90±0.57(2)

25°, 26°, 27°, 28°, 29°, 30°, 31°, 32°, 33°, 34°

Steinkopf
18.84±0.79(14)

Concordia
18.20±1.27(2)

"Northern Cape"
males   19.44±0.87 (12)
females 19.28±1.03 (12)
all   19.36±0.94 (24)

EQUUS CAVE
layers
IA 18.55±0.68 (4)
IB 19.76±0.99 (5)
2A 19.36±1.15 (16)
2B 19.87±0.82 (33)

DEELPAN
18.70±0.28(2)

Vanrhynsdorp
19.35±0.64 (2)

Cape Province (locality unspecified)
males   19.00±0.91 (13)
females 18.55±0.73 (8)
all   18.92±0.76 (148)

Queenstown
20,30(1)

ELANDSBAY CAVE
layers
I   18.20 (1)
2 19.05±0.57 (2)

ELANDSFONTEIN
bone circle
21.05±0.82(4)
&
other
18.77±1.13(22)

SEA HARVEST
19.76±1.28(10)
&
HOEDJIES PUNT
18.93±0.63(4)

Ceres
19.70±0.71(2)

Ladismith
18.46±0.90(11)

Oudtshoorn
19.08±0.90 (24)

Peddie
19.20±0.92(2)

Worcester
19.00(1)

Montagu
19.05±0.92(2)

Vanwyksdorp
19.00±0.99(2)

Riversdale
17.90±0.14
(2)

George
18.99±0.75(16)

Caledon
19.23±0.47(3)

Barrydale
18.53±0.88
(7)

Bredasdorp
17.40(1)

SWARTKLIP I
20.90±1.12 (16)

mm

16°, 17°, 18°, 19°, 20°, 21°, 22°, 23°, 24°, 25°, 26°, 27°

Right side histogram:

M_1 LENGTH
all Cape specimens

number of specimens
40 —
30 —
20 —
10 —

16.8 17.4 18.0 18.6 19.2 19.8 20.4
  17.1 17.7 18.3 18.9 19.5 20.1 20.7 mm
class midpoints

Box plot:

16 17 18 19 20 21 22 23mm

(25) East Africa
(11) Namibia
(40) Northern Cape
(71) Southern Cape
(148) Cape (locality unspecified)
(4)   EQUUS CAVE layer IA
(5)   EQUUS CAVE layer IB
(16) EQUUS CAVE layer 2A
(33) EQUUS CAVE layer 2B
(10) SEA HARVEST
(4)   ELANDSFONTEIN "bone circle"
(22) ELANDSFONTEIN "other"
(16) SWARTKLIP I

16 17 18 19 20 21 22 23mm

Fig. 9

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Fig. 9. (Left). A map showing the provenience of recent and fossil samples of Cape Province black-backed jackals whose lower first molars (Ml's) have been measured in an analysis of size change through time and space. Recent collection localities are in lower case and the approximate location of each is marked by a circle at the spot of a relevant administrative centre. The number before the "+" in each instance is the mean Ml length; the number immediately after the "+" is the standard deviation and the number in parentheses is the number of specimens measured. Numbers characterizing the fossil samples are underlined. Analysis of the numbers indicates that there is little, if any, significant variation among the recent Cape samples. This is the basis for lumping them for comparison with the fossil samples. (Right Upper): The frequency distribution of Ml lengths in the total sample of modern black-backed jackals from the Cape Province. The slight bimodality probably reflects slight sexual dimorphism in Ml length, which is more clearly indicated by the means calculated for the males and females separately. (Right Lower): The mean (vertical line), observed range (horizontal line), standard deviation (white bar), and 95% confidence limits for the mean (black bar) for Ml lengths in the black-backed jackal samples. The means for samples whose 95% confidence limits (black bars) do not overlap may be considered statistically different at the 0,05 level or below.

CONCLUSION

Fossil large mammals from the fynbos zone indicate conditions broadly like modern ones during the last 5-3000 years, preceded by distinctly different conditions during most of the late Quaternary. Conditions were especially different during the late Quaternary 'glacial' episodes, when large grazing ungulates greatly outnumbered the browsers and mixed feeders that dominated the fynbos fauna historically. The implication is that grasses played a much more prominent role in the regional vegetation during 'glacials' than they did historically.

The early and middle Quaternary large mammal fauna of the fynbos region is relatively poorly known, but limited evidence again suggests conditions different from historic ones and also a pattern of environmental change that differed from the late Quaternary pattern.

Judging by the large mammals, Quaternary environmental change was probably more dramatic in the fynbos zone than in any other part of Africa excepting the Sahara and the Maghreb (Klein 1980 and in press). Parallels with the Maghreb are particularly interesting, given its recent climatic and vegetational similarity to the fynbos zone. In the Maghreb, as in the fynbos

region, late Quaternary 'glacial' faunas appear to have been dominated by stereotypic African grazing species, including wildebeest, zebra, warthog and white rhinoceros that were rare or absent in 'interglacial' times.

The large mammals suggest that conditions similar to recent ones in the fynbos region were relatively rare during the Quaternary. During much of the Quaternary the fynbos zone or biome would probably have been difficult to distinguish from adjacent zones on faunistic grounds. The precise implications for fynbos plant communities are unclear, but will probably emerge from the kind of palaeobotanical research reported elsewhere in this volume.

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