THE MAMMALIAN FAUNA OF THE KLASIES RIVER MOUTH SITES, SOUTHERN CAPE PROVINCE, SOUTH AFRICA*

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Introduction

The Klasies River Mouth site complex is located on the southern coast of the Cape Province, roughly 130 km west of Port Elizabeth (Fig. 1). Excavations were organized by R. Singer and directed by J. J. Wymer from December 1966 to August 1967 and from February 1968 to July 1968. Wymer & Singer (1972) have published a brief summary of the results and are presently preparing a detailed monograph on the stratigraphy and artefacts. E. Voigt (1973*a*, *b*) has reported on the shellfish uncovered in the excavations, while K. W. Butzer, N. J. Shackleton, and G. Avery are preparing papers respectively on the sediments, oxygen-isotope composition of the shells, and bird bones. C. Poggenpoel has identified the small sample of excavated fish bones (derived almost exclusively from Later Stone Age levels) and his results will be presented in the monograph by Wymer and Singer. The purpose of the present paper is to present some of the basic data and analyses that lie behind summary accounts of the mammalian fauna that I have published previously (Klein 1974*a*, 1975*a*).

Cultural Stratigraphy and Geological Age of the Klasies Sites

In total, seven caves and shelters were excavated at Klasies River Mouth. Five of these—1, 1A, 1B, 1C, and 2, known together as the 'Main Site'—were contiguous, and there are at least some stratigraphic grounds for interrelating their fills. The remaining two—1D and 5—were separated from the Main Site by 200 m and 2 km respectively. All the caves provided artefacts; all but No. 2 provided identifiable faunal remains.

Taken in sum, the excavations revealed two major culture-stratigraphic units—Middle Stone Age in Caves 1, 1A, 1B, 1C, 2 and 5, and Later Stone Age in Caves 1, 1D, and 5. Geological evidence developed by Butzer (in prep.), supported by oxygen-isotope analysis of Klasies shells (Shackleton, in prep.) and 'amino-

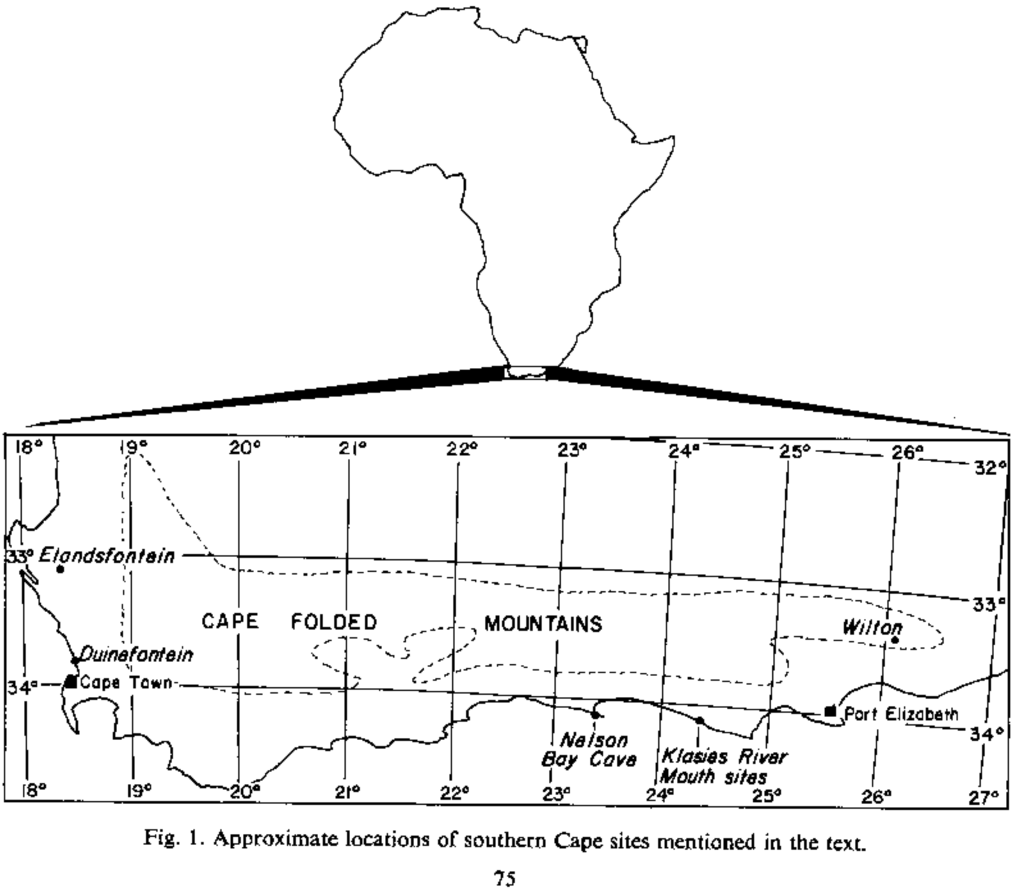

Fig. 1. Approximate locations of southern Cape sites mentioned in the text.

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acid racemization dates[1] on relevant Klasies bones (Bada & Deems 1975), places the beginning of the Klasies Middle Stone Age sequence at or near the beginning of the Last Interglacial, roughly 125 000 years ago. A series of twenty-seven ^{14}C dates indicate that the latest Middle Stone Age materials at Klasies are more than 30 000 years old (Wymer & Singer in prep.; also Klein 1974*a*: 254). Six concordant ^{14}C determinations place the entire Klasies Later Stone Age sequence within the last 5 000 years. The reasons for the obvious occupational hiatus, lasting at least 25 000 years, are not understood, but similar gaps of 15 000–30 000 years or more follow the Middle Stone Age in other southern Cape sites (Klein 1974*a*, 1975*b*; Tankard & Schweitzer 1974).

Wymer & Singer (in prep.) have recognized five cultural subdivisions or stages within the Klasies Middle Stone Age, referred to (from older to younger) as Middle Stone Age (MSA) I, MSA II, Howieson's Poort, MSA III, and MSA IV. Since the Howieson's Poort, MSA III, and MSA IV faunal samples are all fairly small, I have sometimes lumped them for the purposes of analysis below (see Tables 5 and 6). Wymer and Singer have subdivided the Later Stone Age (LSA) of Cave 1 into two stages—I (older) and II (younger). It is difficult to relate the LSA sample from Cave 5 to the Cave 1 sequence because of its small size, but Wymer and Singer believe it probably belongs to Stage II, which is supported by the ^{14}C determinations. The LSA from Cave 1D is clearly younger than that of either Caves 1 or 5, since, unlike them, it contains pottery throughout. I have arbitrarily labelled it LSA III (see Table 4). Since all the LSA faunal samples are small, I have lumped them in the analysis below.

Sorting and Counting of the Faunal Material

The faunal remains from the various Klasies sites were preliminarily sorted in the field, and all bones which were not regarded as taxonomically identifiable were discarded. In June–September 1972 and again in January–March 1974, I examined the potentially identifiable bones, now housed in the South African Museum (Cape Town). Since both my prior experience and the comparative materials to which I had access precluded a detailed study of the non-mammal bones, I made only a rough record of the relative abundance of bird, reptile, and fish remains in different levels. I subsequently turned over the bird and fish remains to appropriate specialists (G. Avery and C. Poggenpoel respectively). The reptile remains, belonging to sea turtles, land tortoises and snakes, have not been subjected to specialist study, but the sample is so tiny that detailed analysis would probably not provide significant information in any case.

The immediate aim of the mammal bone analysis was to obtain estimates of the minimum numbers of individuals by which each species was represented in each level of each site (Tables 1–4). To this end, I attempted to determine both the anatomical and taxonomic derivations of every bone. I generally separated the cranial and appendicular elements of each taxon into lefts and rights and used the higher sum (left or right) to calculate the minimum number of individuals represented by an element. For some appendicular elements, especially phalanges, depending upon the species, separation into lefts and rights (or even into fore and rear specimens) was either not feasible or did not provide an immediate estimate of the minimum number of individuals represented by an element. In such instances I divided the total for the element by an appropriate number (for example, by four in the case of each bovid phalange) to obtain a minimum numbers estimate. Similarly, with the exception of atlases, axes and sacra which I counted separately, I obtained estimates of the minimum numbers of individuals represented by vertebrae by dividing the total number sorted into a major category (cervicals 3–7, thoracics, and lumbars) by a figure appropriate to the category and taxon.

Beyond division into lefts and rights, I made use of age criteria in calculating the minimum numbers of individuals represented by various long bones and by teeth. For the long bones of any species, I assumed that homologous fused and unfused epiphyses must come from different individuals, even if one was left and the other right. For the teeth of each species, most of which occurred as loose, isolated examples, I used eruption and wear criteria to determine the likelihood that different kinds of teeth (P_4's, M_1's, M_2's, etc.) came from different individuals. In the case of the bovids, which are by far the best represented animals at Klasies, matching of isolated teeth by eruption and wear led not just to minimum individual estimates, but also to estimates of the numbers of individuals in successive dental age classes (see Table 8). These dental-age distributions are potentially interesting data in themselves. Of course, the fact that wear is continuous and that judgement of the amount of wear on a tooth is subjective to some extent means that both the age distributions and the minimum numbers that emerge from matching are not precise, but I believe they constitute very reasonable estimates, particularly relative to one another.

Although I was able to assign most Klasies cranial elements and most non-bovid post-cranial parts to species or at least to genus without much difficulty, I had less success with bovid post-cranial parts. The problem is that homologous post-cranial bones of all bovid species are remarkably similar morphologically, and it can be very difficult, if not impossible, to distinguish post-cranial bones of one species from those of another of comparable size, especially when, as at Klasies, the bones tend to be fragmentary. The minimum counts for the various bovid species as they appear in Tables 1–4 were thus calculated strictly on the basis of cranial remains, especially teeth. The bovid post-cranial bones were divided among five arbitrary size classes, the first four of which are roughly equivalent to ones used by Brain (1969*a*; see also Brain 1974 and Deacon 1972) in his study of the fauna from the Wilton Large Rock Shelter. The last class (Very Large) includes animals of a size not encountered by Brain. The size categories are: (1) *Small*, including blue duiker, grysbok, and oribi; (2) *Small Medium*, including vaalribbok, mountain reedbuck, springbok, and bushbuck; (3) *Large Medium*, including southern reedbuck, blue antelope, bastard hartebeest, hartebeest, wildebeest, and kudu; (4) *Large*, including eland and Cape buffalo, and (5) *Very Large*, including only giant buffalo. The division of bovid body parts among

TABLE 1. The minimum numbers of individuals by which each mammalian species is represented in the various horizons of Klasies River Mouth Cave 1

	LSA II	LSA I	MSA IV	MSA II					MSA I	
	1–6	7–12	13	14	15	16	17a	17b	37	38/39
Homo sapiens, Man				1/2	1	1	1/2		?1	?1
Papio ursinus, Chacma baboon	2		1	3	1	1			1	
Canis mesomelas, Black-backed jackal		1					1			
Mellivora capensis, Honey badger				1		1				
Aonyx capensis, Clawless Otter	2			2	1	2	1	1	1	
Genetta sp., Genet	?1									
Herpestes ichneumon, Egyptian mongoose				1	1	1				
H. pulverulentus, Cape grey mongoose				2		1	1	1		
Atilax paludinosus, Water mongoose				1						1
Hyaena brunnea, Brown hyena				1	1	1				
Felis libyca, Wildcat						1				
Felis cf. *caracal*, Caracal				1	1		1			
Panthera pardus, Leopard	1			4	1	1	1	2	1	
Arctocephalus pusillus, Cape fur seal	7	8	3	20	5	17	4	4	7	4
Mirounga leonina, Elephant seal				1						
Loxodonta africana, Elephant						1	1	1		
Procavia capensis, Rock hyrax		2	3	15	5	15	3	6	2	2
Diceros bicornis, Black rhinoceros				2		1	1		1	
Equus cf. *quagga*, Quagga				1			1		1	1
Potamochoerus porcus, Bushpig	?1			1	1				2	2
Phacochoerus aethiopicus, Warthog					1					2
Hippopotamus amphibius, Hippopotamus	1	2		4	1	2	1	2	5	1
Cephalophus monticola, Blue duiker	2	3								
Raphicerus melanotis, Cape grysbok	1	7		21	14	5	6	3	4	
Ourebia ourebi, Oribi						1	1			
Pelea capreolus, Vaalribbok	2	2	2	1		3	1			
Redunca cf. *arundinum*, Southern reedbuck			1	1	1		1		2	2
R. fulvorufula, Mountain reedbuck	1	1				1	2		3	1
Hippotragus leucophaeus, Blue antelope			4	8	4	6	7	7	11	5
Alcelaphus buselaphus, Hartebeest	5	3	2						1	2
Damaliscus sp., Bastard hartebeest				1		1				
Connochaetes sp., Wildebeest				1	1	2	2	2		5
Antidorcas sp., Springbok				1		2	1			
Tragelaphus scriptus, Bushbuck			1	6	8	2	3	1	1	2
T. strepsiceros, Kudu				2		5	1	2	3	
Taurotragus oryx, Eland		1	3	27	10	23	12	8	10	11
Syncerus caffer, Cape buffalo	7	7	4	5	3	9	4	8	7	4
Pelorovis antiquus, Giant buffalo			2	13	1	9	4	5	11	7
Hystrix africae-australis, Porcupine	3	1	1	10	4	3	1		2	1
Georychus capensis, Mole rat				2	3	1	1			
Lepus capensis, Cape hare				1						
Delphinidae, Dolphins		2	1	2	2	1	1	1	2	1
Other Cetacea, Whales				1					1	?1

different size classes has definite analytic utility, as is evidenced in the section below on the interpretation of Klasies body part frequencies.

Dating implications of the Klasies Fauna

A combination of ^{14}C determinations and geological/oxygen-isotope observations clearly bracket the Klasies Middle Stone Age fauna between the beginning of the Last (= Eem) Interglacial (*c.* 125 000 B.P.) and greater than 30 000 years ago. There is thus no need to use the fauna for dating purposes. However, the fact that the fauna has been securely dated by other means itself has important implications. With only one extinct genus (*Pelorovis*) and no more than a handful of extinct or probably extinct species (including especially the species of *Connochaetes, Damaliscus,* and *Antidorcas*), the Klasies assemblage certainly belongs to the 'Florisbad–Vlakkraal Faunal Span' as defined by Cooke (1967; see also Wells 1969). The Klasies data indicate clearly that the lower boundary of this faunal span lies no later than the beginning of the Upper Pleistocene. The implications of this in turn are that the considerably more archaic faunas of the preceding 'Vaal–Cornelia Faunal Span', such as the large assemblage from Elandsfontein (Hopefield) with its associated human remains, probably date from well

TABLE 2. The minimum numbers of individuals by which each mammalian species is represented in the various horizons of Klasies River Mouth Cave 1A

	MSA III					Howieson's Poort			MSA II									
	1–3	4	5	6	7–9	10–11	13–16	17–21	22	23–24	25	26	27	28–29	30	31	32–33	34
Homo sapiens, Man				1		?1					?1							
Papio ursinus, Chacma baboon					2		2	1										
Herpestes pulverulentus, Cape grey mongoose								2										
Atilax paludinosus, Water mongoose				1														
Panthera pardus, Leopard				1														
Felis libyca, Wildcat						1		1	1									
Felis cf. *caracal*, Caracal					1		1											
Arctocephalus pusillus, Cape fur seal			1	3	3	2	5	6	1	3	2		2	4	2	2	5	2
Loxodonta africana, Elephant								1										
Procavia capensis, Rock hyrax	4	1	2	3	3	4	4	4		1	1	1	1	1			2	1
Equus cf. *quagga*, Quagga					2	3	3	6										
Hippopotamus amphibius, Hippopotamus				1			1	2										
Raphicerus melanotis, Cape grysbok	2			1	1	1	6	2					1	1	1	1	1	1
Pelea capreolus, Vaalribbok				1			2										1	1
Redunca cf. *arundinum*, Southern reedbuck					1	1	1	3		1	1		1					
Hippotragus leucophaeus, Blue antelope	2			1		1	5	3	1	2		1	1	2		1	2	1
Damaliscus sp., Bastard hartebeest				1		3												
Connochaetes sp., Wildebeest					1	3		1										
Tragelaphus scriptus, Bushbuck								1										
T. strepsiceros, Kudu								1			2			1				
Taurotragus oryx, Eland	1		3	1	3	3	1	7		2		1	2	6	1		3	3
Syncerus caffer, Cape buffalo	2		1	4	1	6	2	4		3		1	1					
Pelorovis antiquus, Giant buffalo				1	1	5		2	1	1			2					1
Hystrix africae-australis, Porcupine							1	1					1				1	
Delphinidae, Dolphins						?1												

within the Middle Pleistocene (Klein 1973; see also Hendey 1974).

Paleoenvironmental implications of the Klasies Fauna

The Middle Stone Age sequence at Klasies begins in and on beach deposits at 6–8 m above present sea-level. The occurrence of remains of marine mammals, marine birds, fish and shellfish throughout suggests the sea was never very far away. It is possible that an apparent reduction in the amount of seal (Table 5) and marine birds (Avery, in prep.) in the youngest Middle Stone Age levels (Howieson's Poort/MSA Stages III & IV) reflects the onset of coastline retreat from the site (? in the earlier part of the Last Glacial), but on present data this reduction cannot be statistically verified.

In addition to possible indications of sea-level fluctuations, the Klasies data may provide some insight into past vegetation. At present, Klasies River Mouth is located only a few kilometres west of the eastern limit of the Knysna Forest in an area where patches of grassland and fynbos are interspersed with stands of bush and trees. Not surprisingly, the terrestrial fauna from the Later Stone Age horizons, all of which are younger than 5 000 years, suggests a similar forest–grassland–fynbos mosaic. The percentages of grassland creatures (equids and alcelaphines) and of creatures preferring more closed habitats (especially antelopes of the genera *Tragelaphus*, *Raphicerus*, and *Cephalophus*) are roughly comparable between the LSA fauna and that from the oldest MSA culture stage, MSA 1 (see Table 6). In MSA Stage II there is an apparent decrease in open country forms which may indicate an increase in the amount of closed vegetation. Although the reality of this faunal change cannot be statistically verified on the data presented in Table 6, the more detailed data of Table 1 argue strongly in favour of it. From Table 1, it is apparent there is a marked (and statistically significant) increase in *Raphicerus* and *Tragelaphus* and a corresponding decrease in open-country forms in the levels immediately overlying 38/39 in Cave 1. This change occurs within MSA Stage I (which is the reason it is not so apparent in the data of Table 6) and is very similar to the change in terrestrial fauna that I have documented in deposits dating to between 14 000 and 8000 B.P. at Nelson Bay Cave, roughly 130 km to the west (Klein 1972; see Fig. 2 here). At Nelson Bay, the increase in forms preferring bush or forest and the decrease in ones preferring more open country clearly

TABLE 3. The minimum numbers of individuals by which each mammalian species is represented in the various horizons of Klasies River Mouth Caves 1B and 1C

	KRM 1B–MSA 1													KRM 1C–MSA 1	
	1–3	4	5	6	7	8	9	10	11	12	13	14	15	36	37
Homo sapiens, Man								1							
Papio ursinus, Chacma baboon	1														
Canis mesomelas, Black-backed jackal	1														
Atilax paludinosus, Water mongoose								1							
Arctocephalus pusillus, Cape fur seal	3	2	1	2	3	2	1	3	2		1		1	2	4
Procavia capensis, Rock hyrax	3		3	3	1			1	2		1				
Potamochoerus porcus, Bushpig											1				
Hippopotamus amphibius, Hippopotamus				?1							1				
Raphicerus melanotis, Cape grysbok	4		1		2									1	1
Pelea capreolus, Vaalribbok			1												
Hippotragus leucophaeus, Blue antelope				2				1							
Alcephalus buselaphus, Hartebeest						1	1								1
Connochaetes sp., Wildebeest						1		1							
Tragelaphus scriptus, Bushbuck				1											
Taurotragus oryx, Eland	4	1		1		2	1							1	1
Syncerus caffer, Cape buffalo	1														1
Pelorovis antiquus, Giant buffalo				1											
Hystrix africae-australis, Porcupine				1											
Lepus capensis, Hare										1					
Delphinidae, Dolphins														1	

TABLE 4. The minimum numbers of individuals by which each mammalian species is represented in the various horizons of Klasies River Mouth Caves 1D and 5

	KRM 1D–LSA III					KRM 5–LSA II(?)			5–Mixed		5–MSA I(?)		
	1	2	3	4	5	Pit A	1	2	3	4	5	6	7
Homo sapiens, Man			1		1								
Papio ursinus, Chacma baboon								2					
Genetta genetta, Small-spotted genet							1						
Felis cf. *caracal*, Caracal									1				
Arctocephalus pusillus, Cape fur seal			2	1	1	2	2	5	3	?1			
Mirounga leonina, Elephant seal			1										
Potamochoerus porcus, Bushpig								2					
Hippopotamus amphibius, Hippopotamus								1					
Cephalophus monticola, Blue duiker								2					
Raphicerus melanotis, Cape grysbok								1			1		2
Ourebia ourebi, Oribi													1
Pelea capreolus, Vaalribbok								2					
Connochaetes sp., Wildebeest									1				
Tragelaphus scriptus, Bushbuck								2			2		
Taurotragus oryx, Eland													1
Syncerus caffer, Cape buffalo						1		2					
Pelorovis antiquus, Giant buffalo									1				
Hystrix africae-australis, Porcupine								1					
Delphinidae, Dolphins						1		1					

TABLE 5. The minimum numbers of seals and of equids and bovids represented in the various culture-stratigraphic units of the Klasies River Mouth Caves. Based on data in Tables 1–4

	LSA I–III	Howieson's Poort & MSA III & IV	MSA II	MSA I
Seals	23 (31%)^{a}	23 (16%)^{b}	73 (18%)^{c}	38 (22%)^{d}
Equids and Bovids	51 (69%)^{e}	125 (84%)^{f}	316 (82%)^{g}	131 (78%)^{h}
	74	148	389	169

Selected chi-square values

$\genfrac{}{}{0pt}{}{ad}{eh} = 1{,}59,\ p = 0{,}3\text{–}0{,}2,\quad \genfrac{}{}{0pt}{}{bd}{fh} = 2{,}02,\ p = 0{,}2\text{–}0{,}1,\quad \genfrac{}{}{0pt}{}{cd}{gh} = 0{,}802,\ p = 0{,}5\text{–}0{,}3,\quad \genfrac{}{}{0pt}{}{bc}{fg} = 0{,}556,\ p = 0{,}5\text{–}0{,}3$

coincide with the transition from the Last Glacial to the Holocene. It is possible that the analogous faunal change at Klasies River Mouth reflects the transition from the very end of the Glacial-before-Last to the Last Interglacial. The relatively more closed vegetational communities typical of interglacials would then characterize much of MSA I and all of MSA II (that is, most of the sequence exposed at Klasies). In the youngest MSA levels (Howieson's Poort/MSA III & IV), however, the representation of alcelaphines and equids increases substantially (Table 6), suggesting a shift back to more open vegetation, perhaps coinciding with the onset of the Last Glacial.

In an effort to determine if there was additional patterning in the Klasies species frequencies that was not obvious in an inspection of Tables 1–4, Figure 2, or in contingency table comparisons like those of Tables 5 and 6, I decided to undertake a multivariate statistical analysis of frequency variation in the bovids, the most common species represented in the various Klasies sites. My principal goal was to determine whether there were groups of species which were varying together in a meaningful way from level to level within the sites and, if so, whether these groups made sense in terms of the interpretations I had developed on the basis of less formal, more intuitive evaluation of Klasies bovid frequency changes.

Because the various multivariate statistical procedures that could be used to isolate covarying groups of bovid species work most reliably on matrices in which the ratio of observations (in this instance provenience units or stratigraphic levels) to variables (in this instance species) is as high as possible, I augmented the Klasies data with relevant ones from the late Pleistocene and early Holocene levels of Nelson Bay Cave. The rationale for this was the proximity of the two sites and the rough comparability of their surroundings. Historically and probably also in previous interglacials, bush and forest were more important in the vegetational mosaic near Nelson Bay than in the one near Klasies, leading perhaps to a higher relative frequency of small, non-gregarious browsers (especially grysbok and bushbuck) near Nelson Bay, but the environs of the two sites have probably always been sufficiently similar to be characterized by essentially the same frequency interrelationships among shared species.

The matrix of Klasies and Nelson Bay bovid species frequencies submitted to multivariate analysis was basically the same one used to compile Figure 2, except that it included raw frequencies rather than percentages and stratigraphic levels rather than cultural stages for Klasies 1 and Nelson Bay (the separate levels of which contained large enough numbers of individuals for the analysis). Later Holocene Nelson Bay levels with positively identified or possible sheep remains were excluded because of the obvious possibility that the introduction of sheep affected the frequency interrelationships of the wild species that are the principal object of interest here. Two species – grey duiker and 'giant hartebeest' – were dropped from the analysis because they exhibited so little frequency variation in

TABLE 6. The minimum numbers of equids and alcelaphines and of *Tragelaphus*, *Raphicerus* and *Cephalophus* in the various culture-stratigraphic units of the Klasies River Mouth Caves. Based on data in Tables 1–4

	LSA I–III	Howieson's Poort & MSA III & IV	MSA II	MSA I
Equids and alcelaphines	8 (33%)^{a}	18 (53%)^{b}	14 (14%)^{c}	8 (28%)^{d}
Tragelaphus, *Raphicerus* and *Cephalophus*	16 (67%)^{e}	16 (47%)^{f}	86 (86%)^{g}	21 (72%)^{h}
	24	34	100	29

Selected chi-square values

$\genfrac{}{}{0pt}{}{ab}{ef} = 1{,}47,\ p = 0{,}3\text{–}0{,}2,\quad \genfrac{}{}{0pt}{}{bc}{fg} = 19{,}07,\ p < 0{,}001,\quad \genfrac{}{}{0pt}{}{cd}{gh} = 2{,}05,\ p = 0{,}2\text{–}0{,}1,\quad \genfrac{}{}{0pt}{}{bd}{fh} = 3{,}17,\ p = 0{,}1\text{–}0{,}05,$

$\genfrac{}{}{0pt}{}{ad}{eh} = 0{,}023,\ p = 0{,}9\text{–}0{,}8.$

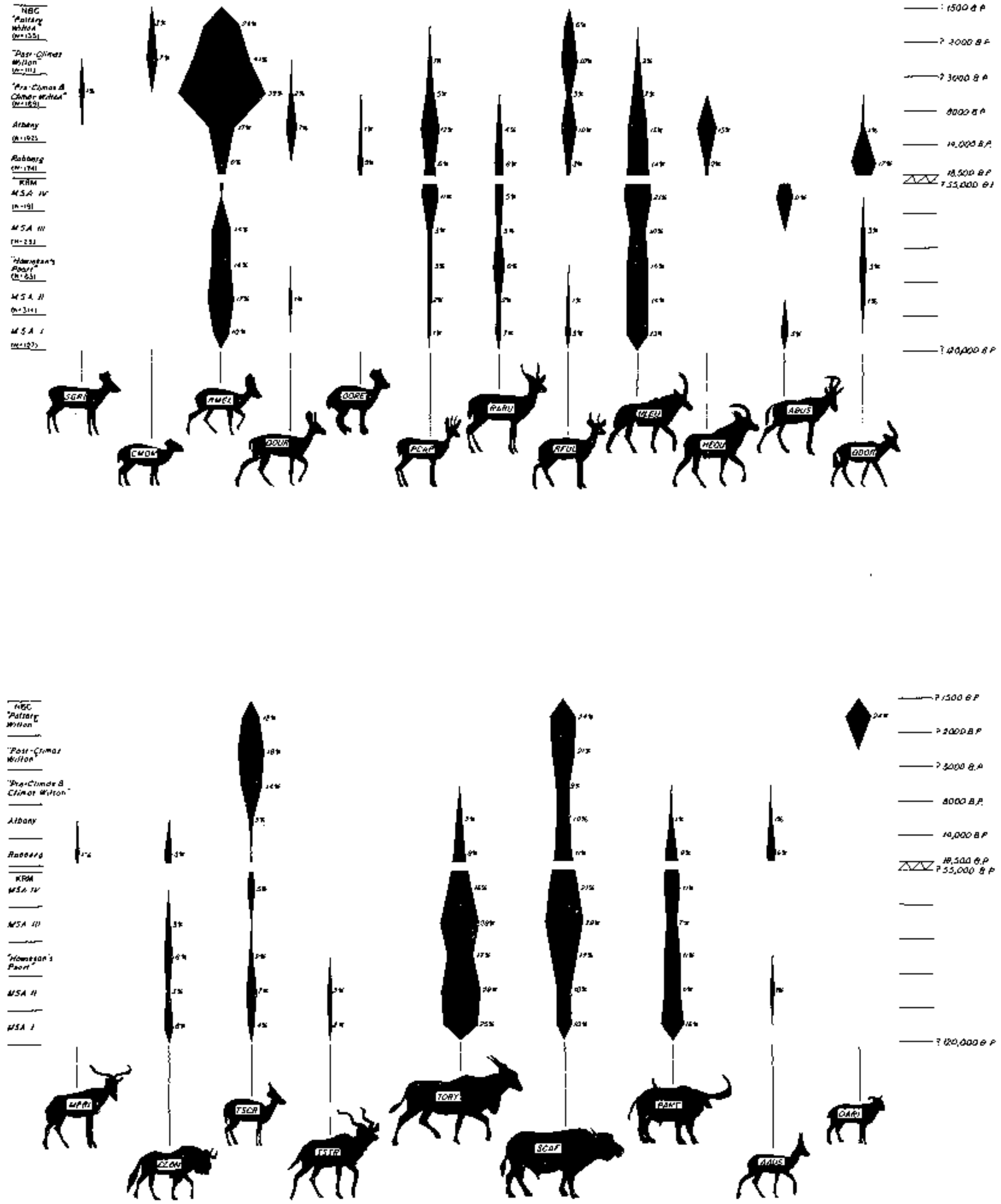

Fig. 2. The relative frequencies of different bovid taxa in the various culture stratigraphic units of Klasies River Mouth and Nelson Bay Cave. Note that the samples from the different units vary considerably in size so that not all the fluctuations in the figure are statistically significant. Note also the major time break between the top of the Klasies (MSA) sequence and the bottom of the Nelson Bay one (LSA). [SGRI = *Sylvicapra grimmia*, CMON = *Cephalophus monticola*, RMEL = *Raphicerus melanotis*, OOUR = *Ourebia ourebi*, OORE = *Oreotragus oreotragus*, PCAP = *Pelea capreolus*, RARU = *Redunca* cf. *arundinum*, RFUL = *Redunca fulvorufula*, HLEU = *Hippotragus leucophaeus*, HEQU = *Hippotragus equinus*, ABUS = *Alcephalus buselaphus*, DDOR = *Damaliscus* sp., MPRI = *Megalotragus priscus*, CCON = *Connochaetes* (*Connochaetes*) sp., TSCR = *Tragelaphus scriptus*, TSTR = *Tragelaphus strepsiceros*, TORY = *Taurotragus oryx*, SCAF = *Syncerus caffer*, PANT = *Pelorovis antiquus*, AAUS = *Antidorcas australis*, OARI = *Ovis aries*.]

TABLE 7. Bovid species with loadings $\geq 0{,}71$ on one or other Varimax rotated principal component in the six component solution of the Klasies River Mouth and Nelson Bay Cave species frequency matrix. There were no species with high negative loadings on any component

COMPONENTS					
1	2	3	4	5	6
Oribi Vaalribbok Mountain reedbuck Roan antelope	Klipspringer Bastard hartebeest Springbok	Southern reedbuck Blue antelope Cape buffalo	Eland Kudu Giant buffalo	Grysbok Bushbuck	Hartebeest

the levels that were included. The multivariate procedure used to search for covarying groups of species was principal components analysis, performed on the University of Chicago's IBM 370/168 Computer using the method 'PA1' and appropriate options of the subprogramme 'FACTOR' from the *Statistical Package for the Social Sciences* (Nie *et al.* 1975). The results of a principal components analysis are a series of 'components' to which each of the original variables (in this case species) is correlated to a greater or lesser degree. The strength of correlation is expressed by a loading or weight varying between $-1{,}00$ and $+1{,}00$. Variables that load highly on a particular component are presumed to vary together in a systematic way.

Table 7 presents the six component solution of the Klasies and Nelson Bay bovid data 'simplified' so that only species with loadings $\geq 0{,}71$ on a (Varimax rotated) component are listed. This means that every species in Table 7 has more than 50% ($\geq 0{,}71 \times 0{,}71$) of its frequency variation explained by the component on which it is listed, which makes it reasonably likely that it is meaningfully associated with other species on the component. The number of components for interpretation (and rotation) was determined by the number with eigenvalues close to or greater than 1. (The eigenvalue of the sixth initial component was actually slightly less than 1 (0,91), but was closer to the eigenvalue of the fifth component (1,13) than to that of the seventh (0,53), leading me to choose the six component solution.) Together, the six initial components explained 86,9% of the variance in the original bovid species matrix.

Examination of the raw frequencies that were used to generate the principal components indicates that some of the associations of species in Table 7 were determined mainly by Nelson Bay data and pertain to interpretation of the Klasies material only in pointing to potentially interesting differences between Klasies and Nelson Bay. Thus, for example, the association of oribi, vaalribbok, mountain reedbuck, and roan (on Component 1) has been determined mainly by the covariation of these species in the 14000 to 8000 B.P. (Albany Industry) levels of Nelson Bay. The roan is completely absent in the Klasies fauna, perhaps because it failed to penetrate south of the Cape Folded Mountains until *c.* 14000 B.P., after which it may have been common for only a few millenniums. The oribi, vaalribbok, and mountain reedbuck are generally less abundant in levels in which they occur at Klasies than in levels in which they occur at Nelson Bay. This may be due to subtle vegetational differences or to cultural differences between the Klasies and Nelson Bay hunters. In the case of the vaalribbok and mountain reedbuck, it might also reflect the rockier, more rugged relief of the immediate vicinity of Nelson Bay.

The association between klipspringer on the one hand and bastard hartebeest and springbok on the other (on Component 2) is due mainly to the co-occurrence of these creatures in the 18000 to 14000 B.P. (Robberg Industry) levels of Nelson Bay. In a sense the association is spurious since the klipspringer probably occupied the rocky cliffs in which the cave itself is located, while bastard hartebeest and springbok lived on the surrounding grassy plain. The association came about because all three species were probably similarly (adversely) affected by the relatively dramatic vegetational changes that occurred near Nelson Bay, beginning *c.* 14000 B.P. None of them occur in Nelson Bay deposits younger than 12 000–10 000 years. Klipspringer does not occur at all at Klasies, perhaps because the near-by topography was less suitable than at Nelson Bay or perhaps because the Klasies sequence nowhere intersects 'full glacial' vegetational conditions like those reflected in the 18000–14000 B.P. deposits of Nelson Bay.

The remaining associations (on Components 3 through 6) are determined at least as much or more by Klasies as by Nelson Bay data. Covariation of reedbuck, blue antelope, and Cape buffalo (on Component 3) probably reflects a common preference for habitats with good cover or shade near water and perhaps also dietary concentration on less palatable grasses. Grysbok and bushbuck (on Component 5) are very closely associated today in relatively closed vegetational settings in the south-central Cape. *A priori*, it might seem strange that hartebeest would occur by itself (on Component 6) rather than with other open-country grazers, especially bastard hartebeest and springbok (on Component 2). However, data from several southern Cape sites, including Klasies and Nelson Bay, suggest that hartebeest was locally more common in interglacials, while bastard hartebeest, springbok, and wildebeest were more common in glacials. The failure of hartebeest to covary with bastard hartebeest and springbok may therefore reflect differences in temperature tolerance. Wildebeest is the only species in the analysis which failed to have a loading of $\geq 0{,}71$ on any component, but it is probably significant that its highest loading (0,59) occurs on Component 2 with bastard hartebeest and springbok. I suspect the addition of more data (additional stratigraphic levels) to the analysis would have brought out the association of wildebeest and these other species more clearly.

Perhaps the most interesting association in Table 7 is the one among eland, kudu, and giant buffalo (on Component 4). Covariation between eland and kudu was perhaps predictable, but *a priori* the enormous hornspan and moderately high-crowned teeth of the giant buffalo would suggest more likely association with open-country grazers such as wildebeest, bastard hartebeest, and springbok. It is possible the grouping of giant buffalo with kudu and eland is an artefact of the mathematics on this particular set of data, and clearly such an unexpected result should be checked with data from other sites. For the moment, in so far as the bivariate (product–moment) correlation coefficients between species generated as an intermediate step in the principal components analysis support at least the association between giant buffalo and eland, perhaps the possibility should be considered that, like the eland, as recently studied by Hillman (1974), the giant buffalo preferred relatively open country with substantial islands and galleries of tree and shrub growth to which it gravitated for shade, if not for food.

Subsistence Implications of the Klasies Fauna

The information on Middle Stone Age subsistence that Klasies River Mouth has provided deserves special attention because it includes the oldest known evidence for the systematic exploitation of marine resources. The inferred antiquity of coastal resource exploitation at Klasies is on the order of 125 000 years, and it may in fact date from a time not long after people first began to make extensive use of aquatic foods. In both Europe and Africa, Acheulian sites presumed to have been near the sea at time of occupation have so far failed to provide evidence of more than incidental coastal exploitation (Isaac 1971). The evidence from Klasies is especially interesting because it may shed some light on the evolution of marine resource utilization. Thus, shells, seal bones and penguin bones are abundant, while fish bones and those of flying birds are relatively rare. In the Klasies LSA levels and also in other Holocene and terminal Pleistocene sites on the southern Cape coast with amounts of seal and shell comparable to that in the Klasies MSA levels, fish remains are abundant to superabundant, and penguin, though present, is far subordinate in frequency to cormorant, gannet, etc. (Avery, in prep.). The implication may be that active fishing and fowling (for airborne birds) was beyond the technological capabilities of the early Upper Pleistocene inhabitants of Klasies River Mouth. An estimate of just when active fishing and fowling came about may not be obtainable since the relevant sites, dating by inference to the middle or later Upper Pleistocene, are probably under water.

The terrestrial creatures they hunted provide further insight into the subsistence activities of the Klasies MSA people. Like later inhabitants of the region they focused their terrestrial hunting primarily on the artiodactyls, by far the most abundant available game. It is very difficult to gauge their overall success in hunting artiodactyls, first because 'minimum numbers' like those in Tables 1–4 probably seriously underestimate the actual numbers of animals killed—many more may be represented in the unidentifiable bone and still others may never have reached the site—and second, because the size of the human group involved and the total amount of time it spent at the site remain unknown and perhaps unknowable. Still, some possible limitations on the hunting capabilities of the Klasies people may be implied by the fact that, in contrast to later peoples, they concentrated their attention on the most docile of the available large bovids (eland) and largely ignored the (? too dangerous) suids, one or both species of which was probably abundant in the vicinity. It is further interesting that the eland remains belong overwhelmingly to adults, while the other very large bovids—the buffaloes—are represented to a very large extent by young to very young individuals (Table 8). The age distribution of the giant buffalo is particularly striking since there are remarkably few individuals between new-born (Class

Table 8. The frequencies of bovids in different dental states in the Middle Stone Age levels of Klasies River Mouth Caves 1, 1A, 1B and 1C. I = dP4 erupting to erupted, but essentially unworn; II = M1 erupting to erupted, but essentially unworn; III = M2 erupting to erupted, but essentially unworn; IV = M3 erupting to erupted, but essentially unworn; V = P4 erupting to erupted, but essentially unworn; VI = P4 in early to mid-wear; VII = P4 in late wear

	DENTAL STATES						
	I	II	III	IV	V	VI	VII
Raphicerus melanotis, Cape grysbok	4	7	18	24	12	14	1
Ourebia ourebi, Oribi	—	—	—	—	1	—	—
Pelea capreolus, Vaalribbok	—	1	2	4	2	3	—
Redunca cf. *arundinum*, Southern reedbuck	—	4	3	1	2	7	—
Redunca fulvorufula, Mountain reedbuck	1	1	2	1	—	2	—
Hippotragus leucophaeus, Blue antelope	8	9	12	10	7	21	11
Alcephalus buselaphus, Hartebeest	1	1	1	2	—	3	—
Damaliscus sp., Bastard hartebeest	—	—	—	3	1	1	—
Connochaetes sp., Wildebeest	2	2	4	4	—	7	1
Antidorcas sp., Springbok	—	—	1	1	—	2	—
Tragelaphus scriptus, Bushbuck	—	—	2	11	8	8	—
Tragelaphus strepsiceros, Kudu	4	4	—	2	—	3	—
Taurotragus oryx, Eland	10	10	13	20	23	62	14
Syncerus caffer, Cape buffalo	21	13	4	6	5	16	5
Pelorovis antiquus, Giant buffalo	28	2	2	4	4	21	6

TABLE 9. The minimum numbers of small bovids (grysbok and oribi) represented by various skeletal elements in the different Middle Stone Age levels of Klasies River Mouth Cave 1

	13	14	15	16	17a	17b	37	38/39	*Total*
Frontlet	–	2	3	3	1	2	1	–	12
Occipital	–	–	–	–	1	–	–	–	1
Maxilla	–	13	6	1	3	3	1	–	27
Mandible	–	19	12	5	7	–	3	–	46
Atlas	–	6	1	1	2	–	–	–	10
Axis	–	2	3	2	2	1	–	2	12
Cervical vertebrae 3–7	1	2	1	1	1	–	1	1	8
Thoracic vertebrae	–	2	1	2	1	1	1	1	9
Lumbar vertebrae	1	2	1	1	1	1	1	1	9
Sacral vertebrae	–	1	–	1	–	1	–	–	3
Caudal vertebrae	–	–	–	–	–	–	–	–	–
Scapula	–	19	13	11	5	6	–	–	54
Proximal humerus	–	1	2	–	–	–	1	–	4
Distal humerus	1	5	5	7	4	1	1	–	24
Proximal radius	–	2	–	1	–	2	1	1	7
Distal radius	1	1	–	2	–	1	1	–	6
Proximal ulna	–	2	3	2	3	–	–	–	10
Carpals	–	–	–	–	–	–	–	–	–
Proximal metacarpal	–	1	–	1	1	1	–	–	4
Distal metacarpal	–	1	–	1	–	1	–	–	3
Innominate	–	9	6	5	3	4	2	1	30
Proximal femur	–	4	4	2	3	–	–	1	14
Distal femur	–	3	3	5	1	–	1	–	13
Patella	–	–	–	–	1	–	–	–	1
Proximal tibia	–	1	2	4	3	–	1	1	12
Distal tibia	2	2	2	3	2	1	1	–	13
Astragalus	1	1	2	3	1	1	–	–	9
Calcaneum	1	6	5	3	3	1	1	–	20
Naviculo-cuboid	1	1	–	1	1	1	–	–	5
Other tarsals	–	–	–	–	–	–	–	–	–
Proximal metatarsal	–	2	–	3	–	–	–	1	6
Distal metatarsal	–	1	2	1	2	1	1	–	8
Phalanges	1	1	1	1	–	1	–	–	5

I) and physically mature (Classes V–VII). The giant buffalo must have been an especially formidable prey, and I have suggested elsewhere (Klein 1974*b*, 1975*a*) that the Klasies MSA people perhaps met the challenge by concentrating on females in advanced pregnancy or even in the process of giving birth.

A hunting strategy concentrating on pregnant giant buffalo cows would have been particularly rational if the giant buffalo had a restricted breeding season. In an attempt to determine this and at the same time establish whether people were only at the site for roughly the same, limited time each year, I measured the crown heights of giant buffalo and other larger bovid molars. If both conditions – seasonally restricted breeding and seasonally limited site occupation – were met, then the distribution of crown heights for any given tooth should be characterized by several more or less equidistant modes. This is because seasonally limited hunting of a seasonally breeding species would result in the capture of individuals belonging to discrete age cohorts separated by a period equivalent to the length of the non-breeding season, a series of months during which the teeth were wearing, but not being returned to the site. Kurtén (1953) was probably the first to use a multimodal distribution of crown heights to infer seasonal breeding in a fossil species (three species of Pliocene bovids from China). Among others, Voorhies (1969) and Reher (1974) successfully applied the idea to Pliocene pronghorn antelope from Nebraska and terminal Pleistocene bison from Wyoming respectively. In contrast, none of the crown height distributions I established for Klasies giant buffalo or other larger bovids displayed clearcut multimodality, perhaps because the samples of measurable specimens were too small or because they were drawn from populations spread over too long a time interval.

The implications of Klasies body part data

Analysis of the frequencies of the body parts by which a species is represented may provide insights into how it was butchered or utilized by prehistoric people. Even more basically, some understanding of the causes of body part frequency variation is essential to the interpretation of species frequencies since they are based on body part frequencies.

Tables 9–24 present the minimum numbers of individuals represented by different body parts for various taxa in the Middle Stone Age levels of Klasies Cave 1, the only one of the Klasies sites to provide body part

TABLE 10. The minimum numbers of small medium bovids (vaalribbok, springbok, mountain reedbuck and bushbuck) represented by various skeletal elements in the different Middle Stone Age layers of Klasies River Mouth Cave 1

	13	14	15	16	17a	17b	37	38/39	*Total*
Frontlet	—	1	—	—	1	—	3	1	6
Occipital	—	—	1	1	1	—	1	1	5
Maxilla	1	4	2	4	3	1	1	—	16
Mandible	2	7	8	6	5	1	3	3	35
Atlas	—	1	—	1	—	—	1	2	5
Axis	—	3	1	3	1	1	1	1	11
Cervical vertebrae 3–7	1	2	1	1	1	1	1	1	9
Thoracic vertebrae	—	1	—	1	1	1	1	1	6
Lumbar vertebrae	—	2	1	2	1	1	1	1	9
Sacral vertebrae	1	—	—	—	—	1	—	1	3
Caudal vertebrae	—	1	—	—	—	—	—	—	1
Scapula	—	15	4	9	6	6	2	4	46
Proximal humerus	1	2	—	1	—	1	1	—	6
Distal humerus	1	7	1	4	1	—	2	2	18
Proximal radius	—	4	1	2	—	1	—	—	8
Distal radius	—	3	1	—	—	—	1	1	6
Proximal ulna	—	1	—	1	2	—	2	—	6
Carpals	—	1	—	—	—	—	—	1	2
Proximal metacarpal	—	—	1	3	—	—	—	—	4
Distal metacarpal	—	—	—	1	3	—	2	—	6
Innominate	—	4	2	2	1	2	1	9	21
Proximal femur	—	3	1	3	1	—	1	—	9
Distal femur	—	3	—	2	1	2	2	2	12
Patella	1	1	2	—	1	—	—	—	5
Proximal tibia	—	3	1	1	1	—	1	—	7
Distal tibia	1	3	3	1	1	1	2	2	14
Astragalus	—	4	2	1	1	1	2	1	12
Calcaneum	1	2	3	4	3	1	1	1	16
Naviculo-cuboid	—	1	—	1	—	—	—	—	2
Other tarsals	—	—	—	—	—	—	—	—	—
Proximal metatarsal	—	2	—	2	1	1	1	1	8
Distal metatarsal	—	2	1	—	—	2	—	3	8
Phalanges	1	1	1	1	1	1	1	1	8

samples large enough for meaningful analysis. (Hominid remains have been omitted since they will be treated in detail later by Singer.) I have not attempted to analyse the Klasies 1 body part data completely here, partly for reasons of space, but also because a truly detailed analysis would require information I do not have, especially on the factors accounting for relative bone durability and on the particular pre- and post-depositional destructive agencies to which various bones were subjected. What I have tried to do is to isolate some of the more important determinants of body part frequencies in the bovids, which are by far the commonest animals at Klasies.

(1) *The effects of differences in bone density and time of epiphyseal fusion*

In a study of an assemblage of goat bones collected around Hottentot villages along the Kuiseb River in the Namib Desert, South West Africa, Brain (1967, 1969*b*) argued that the relative infrequency of certain bones versus others was largely a reflection of differential bone density and of differences in time of epiphyseal fusion (the two are in fact closely related, since denser epiphyses are generally ones which fuse earlier and epiphyseal density tends to be greater after fusion). Thus, distal humeri which are denser than proximal humeri and which undergo epiphyseal fusion earlier in bovids were much better represented than proximal humeri (proximal humeri were in fact totally absent from Brain's sample). For the same reasons of greater density and earlier time of epiphyseal fusion, proximal radii were more common than distal radii, proximal femora than distal femora, and distal tibiae than proximal tibiae in Brain's sample.

Given differences in density and in times of epiphyseal fusion, the proportions of opposite ends of bovid humeri, radii, femora, and tibiae would be expected to vary among sites partly because of sampling error, partly because the different ends might reach sites in very different proportions to begin with, partly because the age composition of fossil herds might vary from site to site, and partly because the destructive factors to which the bones were subjected would vary among sites. In the case of Brain's goat bones, he acted as the accumulator and picked up all he could find. Roughly half the animals were juveniles in which epiphyseal fusion was certainly not complete. The destructive factors were butchering by people,

TABLE 11. The minimum numbers of large medium bovids (southern reedbuck, blue antelope, kudu, hartebeest, bastard hartebeest and wildebeest) represented by various skeletal elements in the different Middle Stone Age layers of Klasies River Mouth Cave 1

	13	14	15	16	17a	17b	37	38/39	*Total*
Frontlet	2	3	—	5	2	4	2	2	20
Occipital	—	3	—	2	3	1	1	—	10
Maxilla	3	7	3	9	5	6	10	9	52
Mandible	5	11	5	9	9	9	13	10	71
Atlas	—	8	1	3	2	—	1	—	15
Axis	—	1	—	1	2	1	1	1	7
Cervical vertebrae 3–7	—	4	—	1	1	2	1	2	11
Thoracic vertebrae	—	3	1	1	1	1	1	1	9
Lumbar vertebrae	—	3	—	1	1	1	1	1	8
Sacral vertebrae	—	3	—	—	1	—	1	—	5
Caudal vertebrae	—	1	1	—	—	1	1	—	4
Scapula	—	11	3	7	4	5	7	4	41
Proximal humerus	—	—	—	1	1	1	—	1	4
Distal humerus	1	6	2	1	2	—	2	4	18
Proximal radius	1	2	—	—	1	—	2	3	9
Distal radius	—	2	1	—	1	1	2	3	10
Proximal ulna	—	4	2	1	1	—	2	1	11
Carpals	—	1	1	1	—	2	2	4	11
Proximal metacarpal	1	5	2	2	2	2	2	5	21
Distal metacarpal	—	2	—	2	1	1	1	3	10
Innominate	1	3	1	2	1	3	3	8	22
Proximal femur	—	2	—	1	1	1	1	1	7
Distal femur	—	2	—	1	3	1	1	1	9
Patella	—	1	—	1	—	2	1	1	6
Proximal tibia	—	2	—	—	1	2	1	2	8
Distal tibia	—	9	2	2	1	2	5	6	27
Astragalus	—	7	2	3	2	3	5	10	32
Calcaneum	1	5	2	3	1	1	3	6	22
Naviculo-cuboid	—	1	—	2	2	1	3	3	12
Other tarsals	2	—	—	1	—	—	—	1	4
Proximal metatarsal	—	3	2	1	2	1	1	7	17
Distal metatarsal	—	1	2	—	1	1	1	2	8
Phalanges	1	2	1	1	1	1	2	2	11

chewing and digesting by people and dogs, and exposure to the elements on the surface around villages. In the case of Klasies, the collectors were Middle Stone Age hunter–gatherers who did not necessarily concentrate all the bones that were available to them (see below), and the destructive factors included not only butchering, chewing, and digesting, but also post-depositional leaching, trampling, and burning to a degree or in a form not applicable to Brain's sample. Also, the Klasies bovids include a different proportion of individuals whose epiphyseal fusion was probably complete. Still, even a rapid examination of Table 25 shows that, as in the case of the Kuiseb goats, those ends of bovid long bones at Klasies which are denser and fuse earlier tend to be more common than their less dense opposite ends that fuse later.

For Brain's goats and probably also for the bovids represented in Table 25, the differences in density and in time of epiphyseal fusion are greatest for the opposite ends of the humerus and tibia, and least for the opposite ends of the radius and femur. It is not surprising therefore that the greatest frequency discrepancies at Klasies are between the opposite ends of the humerus and of the tibia. The last row of Table 25 divides different-sized Klasies bovids between ones in which little or no epiphyseal fusion had probably taken place (dental age categories I and II) and ones in which some or all epiphyses were probably fused (dental age categories III through VII). Comparison of the bottommost row of Table 25 with higher rows will show that as the percentage of Class I and II individuals increases there is a tendency for frequency discrepancies between opposite epiphyses of the same bone to increase as well. (The highest percentages of Classes I and II are for the Large and Very Large Bovids which also exhibit the greatest frequency discrepancies between ends of the same bone.) This is the expected result if relative density is playing an important role in determining frequency discrepancies among body parts.

(2) *The effects of species size*

Based on summary data from Tables 9–13, Figure 3 clearly suggests that the pattern of body part representation at Klasies differs according to the size of the bovid being considered. In order to evaluate the data in the figure more fully, I applied two tests to determine the likelihood that the differences between bovids of any two size categories were statistically significant. The first test, 'chi-square', took into account only the frequencies of different body parts as they are presented in the figure. The second test, 'Kolomogorov–Smirnov', took into account both the frequencies and the particular way in which the body parts have been arranged in the figure, from scapula down to carpals and smaller tarsals. From the figure, it is obvious that this arrangement reflects the order of relative representation of body parts in small bovids, from the most common body part to the least common. The Kolmogorov-Smirnov test thus in part determines the likelihood that the relative order of body part representation characteristic of the small bovids also characterizes the other size groups.

The results of the chi-square and Kolmogorov–Smirnov tests are presented in the caption of Figure 3. In combination with an intuitive appreciation of the figure, the statistical results suggest that small and small medium bovids are characterized by roughly the same patterns of relative body part representation. Large and very large bovids are also very similar to one another in relative body part representation, but strikingly different from small and small medium bovids. The pattern of body part representation in the remaining size category—large medium bovids—can be shown to be significantly different from all the others when only frequencies are considered (chi-square), but is not significantly different from the pattern in the small medium bovids when both frequencies and the order of presentation in Figure 3 are taken into account (Kolmogorov–Smirnov). Overall, in combination with a subjective evaluation of Figure 3, the statistical results suggest to me that the pattern of body part representation in the large medium bovids is roughly intermediate between that of the smaller and that of the larger bovids.

As a first step in interpreting the differences in relative body part representation among the different-sized bovids, I collapsed the data in Tables 9–13 and Figure 3 into Table 26. This table presents the relative frequencies of major regions of the skeleton for each bovid size category. Supported by chi-square results I have not presented here, the numbers in Table 26 suggest that the ratio of cranial to postcranial parts increases, while the ratio of limb-bones to foot-bones decreases with size of bovid. The statistical significance of the relationship between increasing size and an increase in the ratio of cranial to postcranial parts appears particularly clearcut. There are no obvious size-related trends or significant differences among the various size categories in the relative representation of maxillae versus mandibles, axial versus appendicular elements, or fore limbs versus rear limbs.

I believe that the differences in the cranial/postcranial and limb-bone/foot-bone ratios among bovid size categories at Klasies reflect mainly what Perkins and Daly (1968) have called the 'schlepp effect'. Basically, they postulated that hunters were likely to bring home smaller animals intact, but they would probably bring back only selected parts of larger animals. This is because larger animals would be butchered at the place of the kill and the less useful parts would be left there. In documenting the operation of the 'schlepp effect' at the early Holocene ('Neolithic') hunters' site of Suberde in Turkey, Perkins & Daly showed specifi-

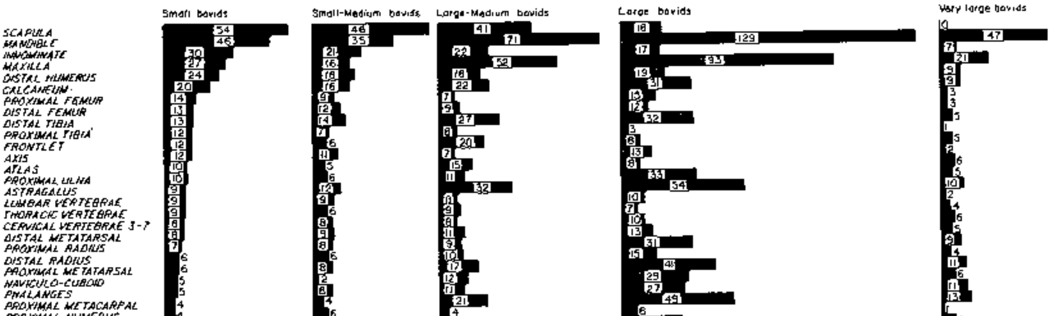

Fig. 3. The minimum numbers of different-sized bovids represented by different skeletal elements in the Middle Stone Age deposits of Klasies River Mouth Cave 1. The results of chi-square and Kolmogorov–Smirnov tests for the significance of differences in relative frequencies between the different size categories are presented below. Values indicating differences significant at the 0,05 level or below are underlined.

Chi-square results

Small Medium	23,31			
Large Medium	76,30	57,49		
Large	249,95	187,60	98,66	
Very Large	147,53	120,19	71,64	37,67
	Small	Small Medium	Large Medium	Large

Kolmogorov–Smirnov results

Small Medium	1,13			
Large Medium	2,33	0,86		
Large	4,49	2,82	2,63	
Very Large	3,42	2,40	2,03	0,41
	Small	Small Medium	Large Medium	Large

TABLE 12. The minimum numbers of large bovids (Cape buffalo and eland) represented by various skeletal elements in the different Middle Stone Age layers of Klasies River Mouth Cave 1

	13	14	15	16	17a	17b	37	38/39	*Total*
Frontlet	—	2	—	3	1	1	1	—	8
Occipital	—	5	—	3	1	3	3	2	17
Maxilla	5	25	8	26	4	7	10	8	93
Mandible	5	29	12	25	16	13	15	14	129
Atlas	1	4	—	1	—	—	—	2	8
Axis	—	5	—	3	3	—	2	—	13
Cervical vertebrae 3–7	—	5	2	2	1	1	1	1	13
Thoracic vertebrae	—	2	1	1	1	1	1	—	7
Lumbar vertebrae	—	4	—	2	1	1	1	1	10
Sacral vertebrae	—	2	—	1	1	1	—	—	5
Caudal vertebrae	—	1	1	1	1	—	1	1	6
Scapula	—	8	—	2	2	2	2	2	18
Proximal humerus	—	4	—	—	—	—	1	1	6
Distal humerus	1	8	—	7	1	1	1	—	19
Proximal radius	—	16	1	3	1	2	6	2	31
Distal radius	1	8	2	1	—	1	1	1	15
Proximal ulna	—	11	3	6	1	2	10	—	33
Carpals	1	18	4	9	3	6	4	4	49
Proximal metacarpal	—	14	2	6	3	7	7	10	49
Distal metacarpal	—	9	—	6	2	2	4	3	26
Innominate	—	6	—	3	1	1	3	3	17
Proximal femur	1	7	—	5	1	—	1	—	15
Distal femur	—	4	—	2	2	—	3	1	12
Patella	—	7	1	6	2	1	2	4	23
Proximal tibia	—	2	—	—	—	1	—	—	3
Distal tibia	—	13	2	6	2	5	2	2	32
Astragalus	1	31	1	8	3	3	4	3	54
Calcaneum	—	13	2	3	1	6	1	5	31
Naviculo-cuboid	1	9	2	4	5	3	3	2	29
Other tarsals	—	3	2	4	4	1	3	3	20
Proximal metatarsal	—	17	—	5	1	6	6	6	41
Distal metatarsal	—	3	1	1	1	3	1	—	10
Phalanges	1	8	3	4	2	2	3	4	27

cally that larger bovids tended to be represented disproportionately well by their foot-bones versus leg-bones, just as at Klasies. They postulated that the Suberde people discarded many larger bovid limb-bones at the kill sites, but brought back the feet either as handles in the skins (used as carrying containers for the meat?) or because the feet were particularly valued, perhaps as sources of sinews for sewing. It is possible that one or the other explanation for a disproportionately high representation of larger bovid feet also pertains to Klasies.

Beyond feet, it appears that the Klasies people selectively brought back larger bovid skulls (as compared to postcranial elements). The reasons for this may only be imagined with the data on hand, but frequent damage on larger bovid dental crowns suggests that a desire to have the jaws for use as tools may have played a role.

The relatively consistent under-representation of maxillae versus mandibles in all the Klasies bovids is probably due to the greater durability of the mandible in all species. The tendency for nearly equal representation of rear limbs and fore limbs probably reflects the comparative durability of various fore-limb and rear-limb elements in each size of bovid and the failure of the 'schlepp effect' to favour one extremity over the other. The reasons for the apparently consistent under-representation of axial vs. appendicular elements are discussed in the next section.

(3) *The effects of site type: 'occupation sites' versus 'kill/butchery sites'*

If the 'schlepp effect' indeed operates with respect to larger bovids, then it is reasonable to expect that there would be significant differences in relative body part frequencies between a 'base camp' or 'occupation site' like Klasies 1 and a 'kill or butchery site' occupied by people with similar cultural affinities. I know of only one probable Middle Stone Age kill site in sub-Saharan Africa from which data on large bovid skeletal part frequencies are available. This is Duinefontein 2, located near Melkbosstrand in the south-western Cape (Klein 1976). Although the Duinefontein 2 sample is small (reflecting the small scale of the excavations so far), supported by chi-square results I have not presented here, Table 27 at least suggests that it is complementary to the Klasies 1 sample in the relative representation of large bovid cranial and post-cranial elements, that is, the possibility exists that the crania which are 'over-represented' at Klasies 1 were

TABLE 13. The minimum numbers of very large bovids (giant buffalo) represented by various skeletal elements in the different Middle Stone Age layers of Klasies River Mouth Cave 1

	13	14	15	16	17a	17b	37	38/39	*Total*
Frontlet	—	1	—	1	1	—	1	1	5
Occipital	—	—	—	1	—	—	—	—	1
Maxilla	1	4	—	3	1	—	8	4	21
Mandible	2	13	1	9	4	5	8	5	47
Atlas	—	4	—	—	2	—	—	—	6
Axis	—	—	1	—	—	—	1	—	2
Cervical vertebrae 3–7	—	2	—	—	1	1	1	—	5
Thoracic vertebrae	—	1	—	1	—	1	1	—	4
Lumbar vertebrae	—	—	—	1	—	—	1	—	2
Sacral vertebrae	—	1	—	1	—	—	—	—	2
Caudal vertebrae	—	—	—	—	—	—	—	—	—
Scapula	—	—	—	—	—	—	—	—	—
Proximal humerus	—	1	—	—	—	—	—	—	1
Distal humerus	1	5	—	2	—	1	—	—	9
Proximal radius	—	4	—	1	2	—	2	—	9
Distal radius	—	2	—	1	—	—	1	—	4
Proximal ulna	—	3	—	1	1	—	—	—	5
Carpals	1	4	1	3	1	1	2	2	15
Proximal metacarpal	—	4	—	1	2	1	3	2	13
Distal metacarpal	—	2	—	1	—	1	1	—	5
Innominate	—	3	—	1	—	1	1	1	7
Proximal femur	—	1	—	1	—	1	—	—	3
Distal femur	—	—	—	—	—	1	2	—	3
Patella	—	4	—	—	—	—	1	—	5
Proximal tibia	—	—	—	—	—	1	—	—	1
Distal tibia	—	2	—	1	—	1	—	1	5
Astragalus	—	5	—	—	1	—	2	2	10
Calcaneum	—	3	1	1	1	—	1	2	9
Naviculo-cuboid	—	3	—	—	—	—	—	3	6
Other tarsals	—	5	2	2	2	—	1	2	14
Proximal metatarsal	—	4	—	2	—	1	3	1	11
Distal metatarsal	—	3	—	1	—	1	1	—	6
Phalanges	1	2	1	1	1	1	2	2	11

TABLE 14. The minimum numbers of hippopotamus represented by various skeletal elements in the different Middle Stone Age layers of Klasies River Mouth Cave 1. Elements not listed do not occur in any layer

	13	14	15	16	17a	17b	37	38/39
Maxilla	—	3	—	1	1	2	3	1
Mandible	—	4	1	2	1	1	5	1
Radius	—	—	—	1	—	—	—	—
Carpus	—	1	—	—	—	—	—	—
Metacarpus	—	1	—	1	—	—	—	—
Innominate	—	—	1	—	—	—	1	—
Patella	—	—	—	1	—	—	—	—
Astragalus	—	—	—	—	1	—	—	—
Calcaneum	—	—	1	—	—	—	—	—
Other tarsals	—	1	—	—	—	—	—	—
Metatarsus	—	1	—	—	—	—	—	—
Phalanges	—	1	1	1	1	—	1	—

Table 15. The minimum numbers of suids (bushpig and warthog) represented by various skeletal elements in the different Middle Stone Age layers of Klasies River Mouth Cave 1. Layers not listed are ones in which no suid remains occurred. Skeletal elements not listed are ones that do not occur in any layer

	14	15	37	38/39
Maxilla	—	—	—	3
Mandible	—	2	2	2
Metacarpus	—	—	—	1
Femur	1	?1	1	—
Astragalus	—	—	—	1
Calcaneum	—	—	?1	1

Table 16. The minimum numbers of quagga and rhino represented by various skeletal elements in the different Middle Stone Age layers of Klasies River Mouth Cave 1. Layers not listed are ones in which no equid or rhino remains occurred. Skeletal elements not listed are ones that do not occur in any layer

	Quagga					*Rhino*			
	14	16	17a	37	38/39	14	16	17	37
Maxilla	—	—	—	—	—	2	—	1	1
Mandible	1	—	1	—	—	—	1	1	—
Calcaneum	1	—	—	—	—	1	—	—	—
Smaller tarsals	—	—	1	—	—	1	—	—	—
Phalanges	—	—	—	1	1	1	1	—	—

Table 17. The minimum numbers of rock hyraxes represented by different skeletal elements in the various Middle Stone Age layers of Klasies River Mouth Cave 1. Elements not listed are ones that do not occur in any layer

	13	14	15	16	17a	17b	37	38/39
Maxilla	2	14	3	15	2	1	1	2
Mandible	3	15	5	8	2	2	2	2
Atlas	—	1	1	2	—	—	—	—
Cervical vertebrae 3–7	—	1	—	—	—	—	—	—
Thoracic vertebrae	—	1	—	—	—	—	—	—
Sacral vertebrae	—	—	1	1	—	—	—	—
Scapula	—	1	—	2	1	1	—	—
Humerus	2	12	1	7	—	2	1	1
Radius	—	—	—	1	—	—	—	—
Ulna	—	2	2	—	—	—	—	—
Innominate	—	5	—	4	1	1	1	—
Femur	1	12	4	11	3	6	2	1
Tibia	—	6	2	6	2	—	1	—

TABLE 18. The minimum numbers of leopards represented by various skeletal elements in the different Middle Stone Age layers of Klasies River Mouth Cave 1

	13	14	15	16	17a	17b	37	38/39
Maxilla	—	2	—	—	—	2	—	—
Mandible	—	4	1	—	—	—	—	—
Atlas	—	1	—	—	—	—	—	—
Axis	—	3	—	—	—	—	—	—
Cervical vertebrae 3–7	—	2	—	—	—	—	—	—
Thoracic vertebrae	—	1	—	—	—	—	—	—
Lumbar vertebrae	—	1	—	—	—	—	—	—
Caudal vertebrae	—	1	—	—	—	—	—	—
Ribs	—	1	—	—	—	—	—	—
Scapula	—	2	—	—	—	—	—	—
Humerus	1	3	—	—	—	—	—	—
Radius	—	3	1	—	—	—	1	—
Ulna	—	3	—	—	—	—	—	—
Carpus	—	1	—	—	—	—	—	—
Metacarpus	—	2	—	1	—	1	—	—
Innominate	—	3	—	—	—	—	—	—
Femur	—	3	—	—	—	—	—	—
Tibia	—	2	—	—	—	—	—	—
Fibula	—	1	—	—	—	—	1	—
Astragalus	—	1	—	—	—	1	—	—
Calcaneum	—	2	—	—	—	1	—	—
Other tarsals	—	1	—	1	1	1	—	—
Metatarsus	—	1	—	—	—	1	—	—
Phalanges	—	1	—	1	—	1	—	—

TABLE 19. The minimum numbers of smaller felids (caracal and wildcat) and hyena represented by various skeletal elements in the different Middle Stone Age layers of Klasies River Mouth Cave 1. Layers not listed are ones in which no smaller felid or hyena remains occurred. Skeletal elements not listed are ones that do not occur in any layer

	Caracal			*Wildcat*	*Hyena*		
	14	15	17a	16	14	16	37
Maxilla	—	—	—	—	1	1	—
Mandible	—	—	—	—	1	—	—
Scapula	—	—	—	1	—	—	—
Humerus	—	1	—	—	1	—	—
Ulna	1	—	—	—	1	1	—
Innominate	1	—	—	—	—	—	—
Metatarsus	—	—	1	—	—	—	—

TABLE 20. The minimum numbers of mongooses represented by different skeletal elements in the various Middle Stone Age layers of Klasies River Mouth Cave 1. Layers not listed are ones in which no mongoose remains occurred. Skeletal elements not listed are ones that do not occur in any layer.

	Egyptian mongoose			*Cape grey mongoose*				*Water mongoose*	
	14	15	16	14	16	17a	17b	14	19
Maxilla	—	—	—	—	1	—	—	—	—
Mandible	—	1	1	—	—	1	1	1	1
Humerus	—	1	1	1	—	—	—	—	—
Innominate	1	—	—	—	—	—	—	—	—
Femur	—	—	—	1	—	—	—	—	—
Tibia	1	—	1	2	—	—	—	—	—

TABLE 21. The minimum numbers of otters and honey badgers represented by different skeletal elements in the various Middle Stone Age layers of Klasies River Mouth Cave 1. Layers not listed are ones in which no otter or honey badger remains occurred. Skeletal elements not listed are ones that do not occur in any layer

	Otter						*Honey badger*	
	14	15	16	17a	17b	37	14	16
Braincase fragments	1	—	—	—	—	1	—	—
Mandible	—	1	2	1	1	1	1	—
Atlas	—	—	—	—	—	1	1	—
Axis	—	—	1	—	—	—	—	—
Scapula	—	—	—	1	—	—	—	1
Humerus	1	—	—	—	—	—	1	1
Ulna	—	—	1	—	—	—	—	1
Femur	—	—	—	—	1	—	1	1
Tibia	—	—	1	—	—	—	—	—
Astragalus	—	—	1	—	—	—	—	—
Calcaneum	—	—	—	—	—	—	—	1
Metatarsus	—	—	1	—	—	—	—	—

TABLE 22. The minimum numbers of seals represented by various skeletal elements in the different Middle Stone Age layers of Klasies River Mouth Cave 1

	13	14	15	16	17a	17b	37	38/39	*Total*
Occipital	—	2	1	—	1	1	—	1	6
Maxilla	—	5	1	2	1	1	2	2	14
Mandible	—	10	1	10	2	2	4	2	31
Atlas	—	4	—	1	—	1	3	2	11
Axis	—	4	—	1	1	1	2	—	9
Cervical vertebrae 3–7	—	—	—	2	—	—	2	1	5
Thoracic vertebrae	—	1	—	1	1	1	1	1	6
Lumbar vertebrae	—	2	—	2	—	1	2	1	8
Sacral vertebrae	—	1	1	—	—	—	—	—	2
Caudal vertebrae	—	—	—	1	1	—	—	—	2
Scapula	—	18	3	8	—	—	6	2	37
Proximal humerus	2	17	4	15	4	4	7	3	56
Distal humerus	3	20	2	17	4	4	7	3	60
Proximal radius	1	12	2	6	4	2	6	2	35
Distal radius	—	10	2	4	4	1	5	3	29
Proximal ulna	—	6	1	3	1	2	4	1	18
Distal ulna	—	5	2	4	3	2	5	—	21
Carpals	—	2	1	1	2	—	4	1	11
Metacarpals	1	4	3	3	2	3	3	3	22
Innominate	—	7	1	7	—	2	5	4	26
Proximal femur	—	7	5	8	1	3	3	2	29
Distal femur	—	11	5	8	2	4	3	4	37
Patella	—	—	1	1	—	—	—	—	2
Proximal tibia	2	6	—	4	—	1	2	1	16
Distal tibia	1	4	1	2	—	1	—	—	9
Proximal fibula	—	—	—	1	—	1	—	—	2
Distal fibula	1	2	1	2	1	—	1	—	8
Astragalus	—	5	2	3	—	—	1	1	12
Calcaneum	—	4	1	3	2	—	2	—	12
Other tarsals	—	1	—	1	1	—	1	1	5
Metatarsals	—	3	2	2	1	1	2	2	13
Phalanges	1	1	1	1	1	1	1	1	8

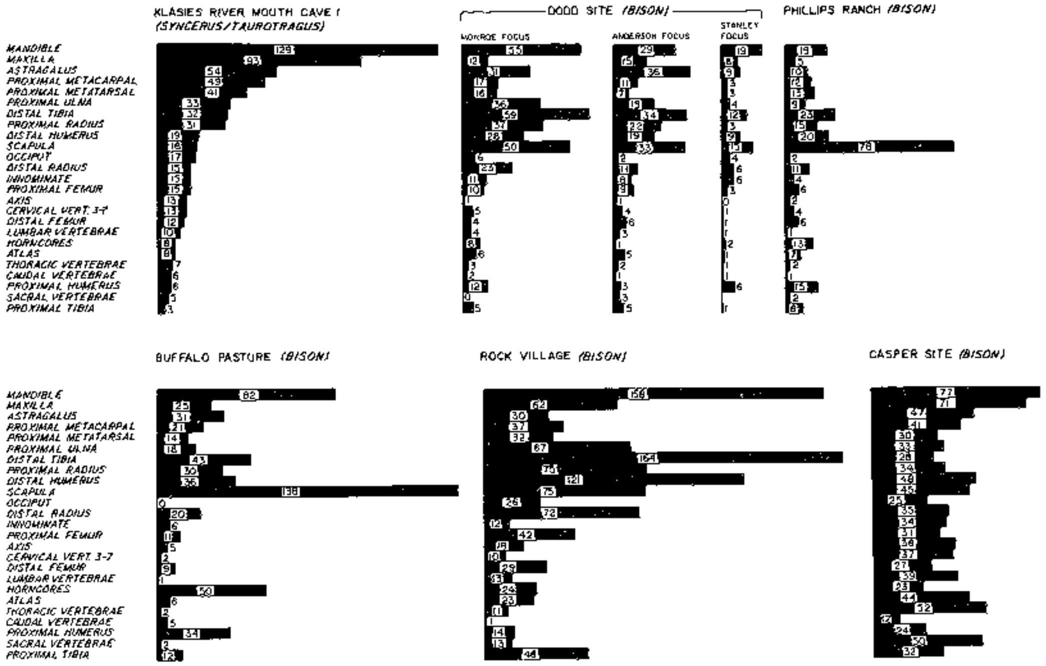

Fig. 4. The minimum numbers of large bovids represented by different skeletal elements in the Middle Stone Age deposits of Klasies River Mouth Cave 1 and various North American Indian sites. (Data for the Dodd site, Phillips Ranch, Buffalo Pasture and Rock Village from White 1953, 1954*a*, 1954*b*; data for the Casper Site from Frison 1974.)

selectively removed from sites like Duinefontein 2. More clearly, Table 27 shows that the large bovids at Duinefontein 2 are relatively better represented than those at Klasies 1 by bones of the axial (versus appendicular) skeleton. This suggests that axial bones (especially vertebrae) of large bovids were among those elements more likely to be left at a kill site.

In order to examine this proposition more closely, I have undertaken a comparison between the body part frequencies of the Klasies large bovids and those of bison in several North American Indian sites. This comparison is made graphically in Figure 4 and in terms of major regions of the skeleton in Table 27. The Indian sites are of two types: a group of four—Dodd (with three levels), Phillips Ranch, Buffalo Pasture, and Rock Village—which are late pre- or early post-European contact villages in the Dakotas, and one—the Casper Site—which is a 10 000-year-old ('Paleoindian') kill site in Wyoming. The choice of sites for comparison was determined by the ease with which published body part data could be compared directly with those from Klasies and by the relatively large sizes of the samples. For the village sites, the published body part counts—the minimum numbers of individuals represented by each body part (White 1953, 1954*a*, 1954*b*)—were calculated in exactly the same way as those for Klasies. For the kill site, I had to calculate some of the 'minimum numbers' counts myself from more general published body part data (Frison 1974), and except for mandibles, maxillae, and vertebrae, the figures for the kill site in Figure 4 and Table 27 are only approximations. The list of body parts on which there was frequency information from the village sites determined the list that was included in Figure 4.

Examination of both Figure 4 and Table 27 shows that there is considerable variation among the North American sites in the relative frequencies of various body parts. However, the village sites differ from the kill site and resemble Klasies in exhibiting numerous and especially dramatic frequency discrepancies among various body parts. The village sites are also like Klasies in that bones in the lower half of the list in Figure 4 tend to be substantially less common than those in the upper half. In contrast, at the kill site, body parts represented in the lower half of the list exhibit frequencies more comparable to those in the upper half. A rapid examination of Figure 4 shows that most of the body parts in the lower half of the list are vertebrae of different kinds—the gross visual contrast in the histograms derives mainly from the fact that vertebrae are relatively much more common at the kill site than at the village sites or at Klasies. The relatively higher frequency of vertebrae at the kill sites is brought out again in Table 27 where it can be seen that the axial/appendicular ratio for the kill site is significantly higher than for any of the other sites (except Duinefontein 2). Although direct comparisons of published data from yet further sites with the data in Figure 4 and Table 27 are often difficult because of the form

TABLE 23. The minimum numbers of baboons, jackals, hares and elephants represented by different body parts in the various Middle Stone Age layers of Klasies River Mouth Cave 1. Layers not listed are ones in which no baboon, jackal, hare or elephant remains occurred. Skeletal elements not listed are ones that do not occur in any layer

	Baboon					*Jackal*	*Hare*	*Elephant*		
	13	14	15	16	37	17	14	16	17a	17b
Maxilla	—	1	1	1	—	1	—	1	—	—
Mandible	—	1	—	—	—	—	—	—	1	1
Scapula	—	1	—	—	—	—	1	—	—	—
Humerus	—	3	—	—	—	—	—	—	—	—
Radius	—	2	—	—	—	—	—	—	—	—
Ulna	1	2	—	—	—	—	—	—	—	—
Metacarpus	—	1	—	—	—	—	—	—	—	—
Innominate	—	2	—	—	—	—	—	—	—	—
Femur	—	2	—	—	—	—	1	—	—	—
Tibia	—	2	—	—	—	—	—	—	—	—
Calcaneum	—	1	—	—	1	—	—	—	—	—
Metatarsus	—	1	—	1	—	—	—	—	—	—

in which various authors present faunal information, my reading on other sites has convinced me that the tendency for axial bones, especially vertebrae, to be left at the place a large animal was killed is very widespread. It in fact reflects general structural principles of the skeleton and of the distribution of meat and marrow on and in it, so that the very same tendency to leave axial bones behind not only characterizes human hunters, but other large predators as well (see, for example, Shipman & Phillips 1976).

Table 27 shows that the Klasies 1 axial/appendicular and fore-limb/rear-limb ratios do not appear to differ from those of the various Indian village sites any more than they sometimes differ from one another. The observed variation in these ratios probably reflects differences among occupation sites in post-depositional destructive factors such as leaching, trampling and burning, differences in the distance from a site at which kills were ordinarily made, and differences in hunting, butchering and food-preparation techniques as well as the selection of different specific body parts for tool use or manufacture. The exceptionally low axial/appendicular ratios that characterize the Phillips Ranch and Buffalo Pasture sites, for example, are direct reflections of the large number of bison scapulae that were modified to make agricultural hoes at those sites. At the Rock Village site, located considerably to the north in an area where farming was less practical aboriginally, modified scapulae (and scapulae in general) were substantially less common, which may be seen as at least partly responsible for the higher axial/appendicular ratio at Rock Village.

Klasies 1 does appear to fall significantly outside the range of variation of the Indian Village sites in the

TABLE 24. The minimum numbers of porcupines and mole rats represented by various skeletal elements in the different Middle Stone Age layers of Klasies River Mouth Cave 1. Layers not listed are ones in which no porcupine or mole rat remains occurred. Skeletal elements not listed are ones that do not occur in any layer

	Porcupine								*Mole rat*			
	13	14	15	16	17a	17b	37	38/39	14	15	16	17
Maxilla	—	3	4	1	—	—	2	—	1	—	1	—
Mandible	—	10	1	1	1	—	1	—	2	3	1	1
Axis	—	1	—	1	1	—	—	—	—	—	—	—
Cervical vertebrae 3–7	—	1	1	—	—	—	—	—	—	—	—	—
Caudal vertebrae	—	1	—	—	—	—	—	—	—	—	—	—
Scapula	—	1	—	—	—	—	—	—	—	—	—	—
Humerus	—	4	1	3	—	—	—	1	—	—	—	—
Radius	—	4	—	2	—	—	—	—	—	—	—	—
Ulna	—	5	—	2	—	—	—	—	—	—	—	—
Innominate	—	4	—	2	—	—	—	—	—	—	—	—
Femur	—	8	2	2	—	—	—	—	—	—	—	—
Patella	—	1	1	1	—	—	—	—	—	—	—	—
Tibia	1	5	1	1	—	—	—	—	—	—	—	—
Astragalus	—	—	—	—	1	—	—	—	—	—	—	—
Calcaneum	—	2	1	2	1	—	—	—	—	—	—	—
Metatarsus	—	1	1	—	—	—	—	—	—	—	—	—

TABLE 25. The minimum numbers of different-sized bovids represented by proximal and distal ends of various limb-bones in the Middle Stone Age deposits of Klasies River Mouth Cave 1 (data from Tables 9–13). The last row contains the numbers of individuals in dental stages I and II (younger) and III–VII (older) as defined in the caption of Table 8

	Small Bovids	*Small Medium Bovids*	*Large Medium Bovids*	*Large Bovids*	*Very Large Bovids*	*Totals*
HUMERUS						
Proximal.	4	6	4	6	1	21
Distal	24	18	19	19	9	88
RADIUS						
Proximal.	7	8	9	31	9	64
Distal	6	6	10	15	4	41
FEMUR						
Proximal.	14	9	7	15	3	48
Distal	13	12	9	12	3	49
TIBIA						
Proximal.	12	7	8	3	1	31
Distal	13	14	27	32	5	91
AGE CLASSES						
I and II	7 (13%)	3 (7%)	28 (30%)	36 (43%)	27 (52%)	
III through VII	47	39	64	48	25	

TABLE 26. The minimum numbers of individual bovids of different sizes represented by major regions of the skeleton in the Middle Stone Age deposits of Klasies River Mouth Cave 1 (data extracted from Tables 9–13). The figures in parentheses represent pertinent ratios.

The minimum number of individuals represented by the:	*Small Bovids*	*Small Medium Bovids*	*Large Medium Bovids*	*Large Bovids*	*Very Large Bovids*
Maxilla	27	16	52	93	21
	(0,58)	(0,45)	(0,73)	(0,72)	(0,44)
Mandible	46	35	71	129	47
Most abundant cranial element . . .	46	35	71	129	47
	(0,85)	(0,76)	(1,73)	(2,38)	(3,13)
Most abundant post-cranial element . .	54	46	41	54	15
Most abundant axial element (*a*) . . .	30	21	22	17	7
	(0,55)	(0,45)	(0,53)	(0,31)	(0,46)
Most abundant appendicular element (*b*)	54	46	41	54	15
Most abundant limb-bone (*c*)	24	18	27	32	9
	(1,20)	(1,12)	(0,84)	(0,59)	(0,60)
Most abundant foot-bone (*d*)	20	16	32	54	15
Most abundant fore limb-bone (*e*) . .	24	18	18	49	15
	(1,20)	(1,12)	(0,56)	(0,90)	(1,07)
Most abundant rear limb-bone (*f*) . .	20	16	32	54	14

NOTES:

(*a*) Axial bones: vertebrae and innominates.
(*b*) Appendicular bones: scapula, limb-bones, carpals/tarsals, metapodials, and phalanges.
(*c*) Limb-bones: humerus, radius, ulna, femur, and tibia.
(*d*) Foot-bones: carpals/tarsals, metapodials, and phalanges.
(*e*) Fore limb excluding scapula, but including carpals and metacarpals.
(*f*) Rear limb excluding innominate, but including tarsals and metatarsals.

TABLE 27. The minimum numbers of Cape buffalo and eland represented by major regions of the skeleton at Klasies River Mouth Cave 1 and Duinefontein 2, Cape Province, versus the minimum numbers of bison represented by the same regions at various North American Indian sites. (Klasies 1 and Duinefontein 2, original data; Rock Village, Phillips Ranch, Buffalo Pasture and Dodd site, data from White 1953, 1954*a*, 1954*b*; Casper site, data from Frison 1974.) The figures in parentheses represent pertinent ratios

The minimum number of individuals represented by:	*'Kill/butchery sites'*		*'Occupation sites'*						
	Casper Site	Duine-fontein 2	Klasies 1	Rock Village	Phillips Ranch	Buffalo Pasture	Dodd Site Foci		
							Monroe	Anderson	Stanley
Maxilla . . .	71	2	93	62	5	25	12	15	8
	(0,92)	(1,00)	(0,72)	(0,39)	(0,26)	(0,30)	(0,22)	(0,52)	(0,42)
Mandible . . .	77	2	129	158	19	82	55	29	19
Most abundant cranial element .	77	2	129	158	19	82	55	29	19
	(1,48)	(0,33)	(2,39)	(0,96)	(0,24)	(0,59)	(0,93)	(0,81)	(1,27)
Most abundant postcranial element	48	6	54	164	78	138	59	36	15
Most abundant axial element . .	52	6	15	23	7	6	11	8	6
	(1,08)	(3,00)	(0,28)	(0,14)	(0,09)	(0,04)	(0,19)	(0,22)	(0,40)
Most abundant appendicular element . . .	48	2	54	164	78	138	59	36	15
Most abundant limb-bone . . .	48	2	32	164	23	43	59	34	12
	(1,02)	(1,00)	(0,59)	(4,43)	(1,77)	(1,39)	(1,90)	(0,94)	(1,33)
Most abundant foot-bone . . .	47	2	54	37	13	31	31	36	9
Most abundant fore-limb bone .	48	1	49	121	20	36	37	19	9
	(1,02)	(0,50)	(0,91)	(0,74)	(0,87)	(0,84)	(0,63)	(0,53)	(0,75)
Most abundant hind-limb bone .	47	2	54	164	23	43	59	36	12

cranial/postcranial ratio, the limb-bone/foot-bone ratio, and perhaps also in the mandible/maxilla ratio. It is possible the higher proportion of mandibles at Klasies is largely a result of the greater durability of the mandible in the face of more intense post-depositional destructive factors. To an extent, differential bone durability and post-depositional destruction may also have raised the Klasies cranial/postcranial ratio and lowered the limb-bone/foot-bone one versus the Indian sites. But I think the main cause of the differences between Klasies and the Indian sites in these last two ratios was the greater propensity of the Klasies people to bring home large bovid skulls and feet versus other skeletal elements.

In conclusion, it is clear that comparison of the Klasies larger bovid body part frequencies with those of the Indian sites supports the notion that the 'schlepp effect' operated on the Klasies larger bovids, especially in bringing about a low axial/appendicular ratio. One potential objection that may still be raised, however, is that the axial/appendicular ratio is similarly low for the Klasies smaller bovids (Table 26) on which the 'schlepp effect' is not supposed to have operated, at least to the same extent.

In order to determine if the reasons for the low axial/appendicular ratios were in fact likely to have been the same for various bovids, I undertook an analysis of the frequency variation of axial and appendicular elements from level to level within the Klasies site. Since such an analysis would obviously be more meaningful if the frequencies were relatively high and exhibited a reasonable amount of variation, I merged Tables 9 and 10 (with frequencies of small and small medium bovid body parts) into one table, and Tables 12 and 13 (with frequencies of large and very large bovid body parts) into another. Justification for the mergers was that the relative body part frequencies of small bovids were shown above not to differ significantly from those of small medium bovids, and the same was true for the relative frequencies of large and very large bovid body parts.

Each of the merged tables was then submitted to principal components analysis using the same computer program and providing the same general kinds of results discussed above in the section on the paleoenvironmental implications of the Klasies fauna. The Klasies body part matrices are statistically less than ideal for a principal components analysis which argues for caution in attempting detailed interpretations of the results. Additionally, to be convincing and non-circular, detailed interpretations would require more independent information than I have on the durability characteristics of different bones in relation to the various pre- and post-depositional destructive agencies to which they were subjected. I have therefore not presented the detailed results here and have limited myself mainly to interpretations based on clearcut contrasts between the two principal components solutions (one for the smaller bovids and the other for the larger ones). On a gross level, the two solutions indicate that the pattern of covariation between smaller bovid vertebrae and other body parts is quite different from the pattern of covariation between larger bovid vertebrae and other body parts. Visual inspection of the bivariate (product-moment) correlation coefficients between vertebrae and other body parts generated as an intermediate step in the principal components analysis leads to the same conclusion. It follows that the reasons for the low axial/appendicular ratios in the smaller bovids are almost certainly different from those for the similarly low ratios in the larger bovids. More particularly, while the low ratio in the larger bovids is probably due mainly to the 'schlepp effect', in the smaller bovids it is probably due mainly to the greater impact of pre- and post-depositional destructive agencies on smaller bovid bones. Compared to larger bovid vertebrae, smaller bovid ones were probably more likely to end up over or in the fire or in someone's mouth, and they would have been less resistant to destruction from these factors than various smaller bovid appendicular elements.

The principal components solutions for the smaller and larger bovid body parts show other gross differences besides those relevant to vertebrae. One interesting contrast is that to account for a reasonable (and the same) amount of variance in the original body part matrices requires more components for the smaller bovids than for the larger ones. This suggests a simpler underlying structure—fewer important determinants—behind the body part frequency variation in the larger bovids. The much larger number of high positive correlations that exist among larger bovid body parts points to the same conclusion. Basically, I think the more complex structure that apparently underlies the smaller bovid data reflects the greater importance of durability features in determining smaller bovid body part frequencies. These features include not just density, but also probably size, shape, strength of attachment to other bones, and the likelihood that fragmentation will leave pieces that are still recognizable. The reason that durability features were probably more important for smaller bovid body parts than for larger bovid ones is that smaller size itself meant that smaller bovid parts were more susceptible to destruction than larger bovid ones, particularly in butchering and food preparation. I plan to explore this point further in the analysis of comparable body part data I have from other southern African archaeological faunas.

Summary and Conclusions

The essentially modern taxonomic aspect of the Klasies MSA fauna, with no more than a handful of extinct forms, in combination with its well-established early Upper Pleistocene age, suggests strongly that faunas such as the one from Elandsfontein (Hopefield), containing a whole series of archaic and extinct forms, are of Middle Pleistocene age. The presence of remains of marine creatures throughout the Klasies MSA sequence indicates that the coast was never very far away, though a relative reduction in marine remains in the most recent MSA levels may reflect the initiation of coastline retreat (? at the beginning of the Last Glacial). Fluctuations in the frequencies of different kinds of antelopes and of equids in the MSA sequence suggest changes in vegetation from more open (? at the very end of the Glacial-before-Last or beginning of the Last Interglacial) to more closed (? in the full Last Interglacial) back to more open (? in the earlier Last Glacial). The Klasies MSA levels have provided the earliest known evidence for the systematic exploitation of marine resources, while at the same time suggesting that MSA peoples exploited both marine and terrestrial resources differently and perhaps less effectively than LSA peoples in the same habitat. Finally, at least for the MSA levels of Klasies 1, it seems probable that larger bovid body part frequencies were determined by the preferential return of selected body parts (especially feet and skulls) to the site, followed by relatively unintense pressure from destructive agencies, while smaller bovid body part frequencies were determined by the return of more or less whole carcasses followed by significantly more intense pre- and post-depositional destructive pressures.

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References

Bada, J. L. & Deems, L. 1975. Accuracy of dates beyond the ^{14}C dating limit using the aspartic acid racemization technique. *Nature (Lond.)* **255**: 218–219.

Brain, C. K. 1967. Hottentot food remains and their meaning in the interpretation of fossil bone assemblages. *Scient. Pap. Namib Desert Res. Stn.* **32**: 1–11.

Brain, C. K. 1969*a*. Faunal remains from the Wilton Large Rock Shelter. *In* Deacon, J., Re-excavation and Description of the Wilton Type-site, Albany District, Eastern Cape. Unpublished M.A. Thesis: University of Cape Town.

Brain, C. K. 1969*b*. The contribution of Namib Desert Hottentots to an understanding of Australopithecine bone accumulations. *Scient. Pap. Namib Desert Res. Stn.* **39**: 13–22.

Brain, C. K. 1974. Some suggested procedures in the analysis of bone accumulations from southern African Quaternary sites. *Ann. Transv. Mus.* **29**: 1–5.

Cooke, H. B. S. 1967. The Pleistocene sequence in South Africa and problems of correlation. *In* Bishop, W. W. & Clark, J. D., *eds. Background to Evolution in Africa*: 175–183. Chicago: University of Chicago Press.

Deacon, J. 1972. Wilton, an assessment after fifty years. *S. Afr. archaeol. Bull.* **27**: 10–48.

Frison, G. C. *ed.* 1974. *The Casper Site.* New York: Academic Press.

Hendey, Q. B. 1974. Faunal dating of the Late Cenozoic of southern Africa, with special reference to the Carnivora. *Quaternary Res.* (*N.Y.*) **4**: 149–161.

Hillman, C. 1974. Ecology and behavior of the wild eland. *African Wildlife Leadership Foundation News* **9** (3): 6–9.

Isaac, G. Ll. 1971 The diet of early man: aspects of archaeological evidence from Lower and Middle Pleistocene sites in Africa. *Wld. Archaeol.* **2**:278–298.

Klein, R. G. 1972. The late Quaternary mammalian fauna of Nelson Bay Cave (Cape Province, South Africa): its implications for megafaunal extinctions and environmental and cultural change. *Quaternary Res.* (*N.Y.*) **2**: 135–142.

Klein, R. G. 1973. Geological antiquity of Rhodesian Man. *Nature, Lond.* **244**: 311–312.

Klein, R. G. 1974*a*. Environment and subsistence of prehistoric man in the southern Cape Province, South Africa. *Wld. Archaeol.* **5**: 249–284.

Klein, R. G. 1974*b*. A provisional statement on terminal Pleistocene mammalian extinctions in the Cape Biotic Zone (southern Cape Province, South Africa). *S. Afr. archaeol. Soc., Goodwin Ser.* **2**: 39–45.

Klein, R. G. 1975*a*. Middle Stone Age man–animal relationships in southern Africa: evidence from Klasies River Mouth and Die Kelders. *Science* **190**: 265–267.

Klein, R. G. 1975*b*. Ecology of stone age man at the southern tip of Africa. *Archaeology* **28**: 238–247.

Klein, R. G. 1976. A preliminary report on the 'Middle Stone Age' open-air site of Duinefontein 2, (Melkbosstrand, South-Western Cape Province, South Africa). *S. Afr. archaeol. Bull.* **31**: 12–20.

Kurtén, B. 1953. On the variation and population dynamics of fossil and recent mammal populations. *Acta zool. fenn.* **76**: 1–122.

Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K. & Bent, D. H. 1975. *Statistical Package for the Social Sciences.* New York: McGraw-Hill.

Perkins, D. & Daly, P. 1968. A hunters' village in Neolithic Turkey. *Scient. Am.* **219** (11): 97–106.

Reher, C. A. 1974. Population study of the Casper Site bison. *In* Frison, G. C., *ed. The Casper Site*: 113–124. New York: Academic Press.

Shipman, P. & Phillips, J. E. 1976. On scavenging by hominids and other carnivores. *Cur. Anthrop.* **17**: 170–172.

Tankard, A. J. & Schweitzer, F. 1974. The geology of Die Kelders Cave and environs: a plaeoenvironmental study. *S. Afr. J. Sci.* **70**: 365–369.

Voigt, E. 1973*a*. Klasies River Mouth: an exercise in shell analysis. *Transv. Mus. Bull.* **14**: 14–15.

Voigt, E. 1973*b*. Stone Age mulluscan utilization at Klasies River Mouth Caves. *S. Afr. J. Sci.* **69**: 306–309.

Voorhies, M. R. 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. *University of Wyoming Contributions to Geology Special Paper* No. 1.

Wells, L. H. 1969. Faunal subdivision of the Quaternary in southern Africa. *S. Afr. archaeol. Bull.* **24**: 93–95.

White, T. E. 1953. Observations on the butchering technique of some aboriginal peoples. No. 2. *Am. Antiq.* **19**: 160–164.

White, T. E. 1954*a*. Observations on the butchering technique of some aboriginal peoples. No. 4. *Am. Antiq.* **19**: 257–259.

White, T. E. 1954*b*. Observations on the butchering technique of some aboriginal peoples. No. 5. *Am. Antiq.* **19**: 259–262.

Wymer, J. J. & Singer, R. 1972. Middle Stone Age settlements on the Tzitzikama coast, eastern Cape Province, South Africa. *In* Ucko, P. J., Tringham, R. & Dimbleby, G. W., *eds. Man, Settlement and Urbanism*: 207–210. London: Duckworth.

LINKED CITATIONS

- Page 1 of 2 -

The Mammalian Fauna of the Klasies River Mouth Sites, Southern Cape Province, South Africa

Richard G. Klein

The South African Archaeological Bulletin, Vol. 31, No. 123/124. (Dec., 1976), pp. 75-98.

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References

The Diet of Early Man: Aspects of Archaeological Evidence from Lower and Middle Pleistocene Sites in Africa

Glynn Isaac

World Archaeology, Vol. 2, No. 3, Subsistence. (Feb., 1971), pp. 278-299.

Stable URL:

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Richard G. Klein

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Observations on the Butchering Technique of Some Aboriginal Peoples No. 2
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Observations on the Butchering Technique of Some Aboriginal Peoples Nos. 3, 4, 5, and 6
Theodore E. White
American Antiquity, Vol. 19, No. 3. (Jan., 1954), pp. 254-264.
Stable URL:
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Observations on the Butchering Technique of Some Aboriginal Peoples Nos. 3, 4, 5, and 6
Theodore E. White
American Antiquity, Vol. 19, No. 3. (Jan., 1954), pp. 254-264.
Stable URL:
http://links.jstor.org/sici?sici=0002-7316%28195401%2919%3A3%3C254%3AOOTBTO%3E2.0.CO%3B2-H