

The mammalian fauna associated with an archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape Province, South Africa

Richard G. Klein ^{a,*}, Graham Avery ^{b,c}, Kathryn Cruz-Urbe ^d, Teresa E. Steele ^{e,f}

^a Program in Human Biology, Stanford University, Building 80, Inner Quad, Stanford, CA 94305, USA

^b Department of Cenozoic Studies, Natural History Division, Iziko South African Museum, P. O. Box 61, Cape Town 8000, South Africa

^c Department of Archaeology, University of Cape Town, Private Bag, Rondebosch 7700, South Africa

^d Department of Anthropology, Northern Arizona University, Box 15200, Flagstaff, AZ 86001, USA

^e Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig 04103, Germany

^f Department of Anthropology, University of California, One Shields Avenue, Davis, CA 95616, USA

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Abstract

The Elandsfontein site, Western Cape Province, South Africa, is well known for an archaic hominin skullcap associated with later Acheulean artifacts. The site has also provided nearly 13,000 mammalian bones that can be identified to skeletal part and taxon. The assemblage derives from 49 species, 15 of which have no historic descendants. Comparisons to radiometrically dated faunas in eastern Africa indicate an age between 1 million and 600 thousand years ago. Unique features of the fauna, including the late occurrence of a dirk-toothed cat and a sivathere, may reflect its geographic origin in a region that was notable historically for its distinctive climate and high degree of biotic endemism. Together, taxonomic composition, geomorphic setting, and pollen extracted from coprolites indicate the proximity of a large marsh or pond, maintained by a higher water table. The small average size of the black-backed jackals implies relatively mild temperatures. The sum of the evidence places bone accumulation during one of the mid-Pleistocene interglacials that were longer and cooler than later ones, including the Holocene.

The geomorphic context of the fauna presents no evidence for catastrophe, and most deaths probably resulted from attritional factors that disproportionately killed the young and old. However, only the dental-age profile of long-horned buffalo supports this directly. Field collection methods biased skeletal-part representation, but originally, it probably resembled the pattern in the younger, marsh-edge Acheulean occurrence at Duinefontein 2, 45 km to the south. Excavation there exposed multiple vertebral spreads, which probably mark carcasses from which hominins or large carnivores removed the meatier elements. Bone damage at both sites suggests that, despite abundant artifacts, hominins were much less important than carnivores in the bone accumulation. Together with limited observations from other sites, Elandsfontein and Duinefontein provisionally suggest that Acheulean-age hominins obtained few large mammals, whether by hunting or scavenging.

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Introduction

The Elandsfontein farm and Acheulean site (33°05'S, 18°15'E) are located approximately 18 km east of the Atlantic shore and 95 km north-northwest of Cape Town in the Western Cape Province of South Africa (Fig. 1). The site is sometimes called Hopefield or Saldanha after towns located 11 km

* Corresponding author.

E-mail addresses: rklein@stanford.edu (R.G. Klein), gavery@iziko.org.za (G. Avery), Kathryn.Cruz-Urbe@nau.edu (K. Cruz-Urbe), steele@eva.mpg.de (T.E. Steele).

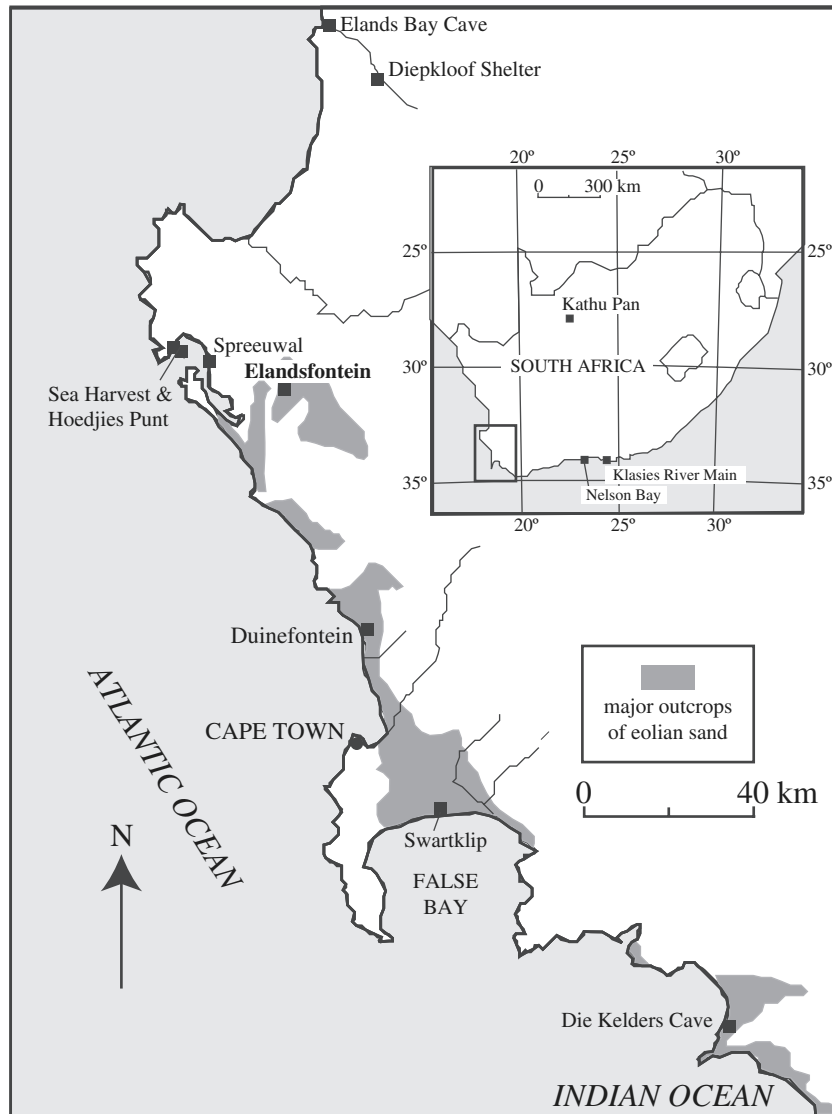


Fig. 1. The locations of the South African sites mentioned in the text [modified after Butzer (2004: Fig. 1)].

northwest and 26 km northeast, respectively. It is best known for a hominin skull cap that has been variously referred to *Homo rhodesiensis*, “archaic” *H. sapiens*, or *H. heidelbergensis* (Drennan, 1953; Singer, 1954; Rightmire, 1998, 2001). The skull lay on a deflation surface or “bay” within an extensive dune field. Other similar bays have provided a fragment of human mandibular ramus, more than 160 later Acheulean bifaces, thousands of associated flake tools and flaking debris, and nearly 13,000 iron-mineralized mammalian fossils. The objects are tightly associated with a calcareous duricrust that we call Elandsfontein Main, or EFTM, to distinguish it from overlying horizons that have also provided bones and occasional Middle Stone Age (MSA) artifacts.

We recently finished sorting the EFTM mammalian bones, and we aim here to summarize their implications for the geologic antiquity, paleoenvironment, and paleoecology of the site. More than 90% were collected unsystematically from deflation surfaces in the 1950s and early 1960s, and to reconstruct their original occurrence, we depend heavily on the

somewhat younger Acheulean site at Duinefontein (DFT) 2, about 45 km south of EFTM. As discussed below, the artifacts and bones at DFT2 occur in a similar geomorphic context, but they were still sealed in place, and they were recovered by excavation, mainly between 1996 and 2002 (Klein et al., 1999; Cruz-Urbe et al., 2003).

From our observations of the EFTM bones and basic similarities between EFTM and DFT2, we conclude that, despite the abundance of Acheulean artifacts, hominins played little role in shaping the EFTM bone assemblage. Instead, like DFT2, EFTM appears to have been a place where artifacts and bones accumulated mostly independent of one another, near a water hole that attracted both people and other large mammals. Published reports on other Acheulean or Acheulean-age sites in similar geomorphic context also fail to implicate hominins importantly in the bone accumulation, and as a hypothesis for further testing, we suggest that Acheuleans and their contemporaries had little impact on the contemporaneous large-mammal communities.

Geomorphic setting

The EFTM artifacts and bones accumulated on quartz- and shell-rich sands transported by wind from the Atlantic shore. Similar sand bodies occur at various points along the Western Cape coast (Fig. 1), and carbonate in the comminuted shell helped to buffer bones from dissolution. At Elandsfontein, recent deflation has thoroughly mobilized the sand mantle, exposing, covering, and then re-exposing long-buried bones and artifacts. In 1965–66, seventeen trial excavations to recover Acheulean artifacts and bones before deflation were largely fruitless. The single exception was “Cutting 10,” which exposed 456 bones and 208 artifacts, including 50 bifaces, below a low mound of intact sands within a large deflation bay (Klein, 1978b; Singer and Wymer, 1968). The biface concentration was remarkable and anomalous for the site as a whole, but the bone sample was too small to illuminate the nature of the overall bone-artifact association. Thus, for this purpose, we rely on the much larger sample from DFT2, about 45 km to the south. The DFT2 artifacts and bones occur within a sand body that closely resembles the one at EFTM, but deflation has been much less severe, and the bones and artifacts remain in place over large areas, sealed in a 15–20-cm-thick band that appears to mark a former land surface.

The circumstances that created the sand bodies at Elandsfontein, Duinefontein, and other west-coast localities are perhaps most clearly revealed in the Geelbek Dunefield, about 5 km west of Elandsfontein. Pedogenic horizons formed on and within the Geelbek sands mark stable periods between recurrent episodes of sand transport inland, beginning in the mid-Pleistocene and extending into the Holocene (Felix-Henningsen et al., 2003; Kandel et al., 2003). Mass movement inland is generally thought to have occurred during periods of lower sea level, when the exposed continental shelf provided a fresh sand supply. However, the most recent transport episode has been linked to a mid-Holocene high sea-level stand, when sands eroded from older, previously stabilized dunes became available for transport (Compton and Franceschini, 2005). Locally, any natural or cultural event that removed or reduced the vegetation cover could mobilize sand, particularly during summer, when strong southerly winds are common, the sands are driest, and veldt fires reduce the vegetation cover. The event that exposed bones and artifacts at Elandsfontein occurred in or before 1906, when local residents first reported fossils in deflation bays between dunes. The size of the wind-eroded area has fluctuated through time, and it is rapidly shrinking today, due mainly to the encroachment of introduced Australian wattles (*Acacia* spp.). Figure 2 shows the exposed area as it appeared from the air in 1976, when it extended up to 3 km from north to south and 1.6 km from east to west.

No deep sections exist at Elandsfontein, and the geologic context of artifacts and bones must be inferred mainly from surface geomorphology. Figure 3 summarizes the local stratigraphy reconstructed by Butzer (1973) from his own observations and those of Mabbutt (1956, 1957). The oldest conspicuous feature is a calcrete ridge, up to 10 m high and 60 m wide, that extends for about 1 km along the north-south



Fig. 2. The Elandsfontein site from the air in 1976.

axis of the site. Its origins and age are debatable, but it probably represents the indurated core of a Pliocene or early Pleistocene dune. It unquestionably antedates the artifact-and-bone occurrences at the site, since these lie in sands that abut against it. The sands are interrupted by two duricrusts—the nodular, calcareous one that we call EFTM and a higher-lying compact, ferruginous one. Two discontinuous ferricrete ridges—1.5–5.0 m high, 2.0 m wide, and more than 1.0 km long—snake across the site within the sands overlying the upper (ferruginous) duricrust. They have been variously interpreted as the spines of ancient dunes (Mabbutt, 1956), the podsollic B-horizons of fossil soils on a dipping slope (Deacon, 1964; Partridge, 1982), or channel or subchannel expressions of former streams (Butzer, 1973).

The lower, EFTM calcareous crust has provided all of the Acheulean bifaces and the abundant iron-mineralized bones on which we focus here. The surface of the upper ferruginous crust has delivered occasional bones, perhaps deflated from the overlying sands, and extremely rare but well-made leaf-shaped (Still Bay) points and other likely MSA artifacts. The sands above the ferruginous crust have produced artifact-poor, coprolite-rich bone accumulations that appear to represent fossil hyena dens (Avery, 1989). The most completely described is the “Bone Circle,” a roughly circular concentration about 4.5 m across (Inskip and Hendey, 1966). It contained numerous tooth-marked bones and carnivore (especially jackal) fossils that pinpoint hyenas as the bone accumulators (Klein, 1983). The bones in the various fossil dens are well preserved, but generally lack the characteristic iron mineralization of bones from the EFTM crust.

Ferruginous and calcareous sediments intergrade at Elandsfontein, and iron often coats calcareous nodules in the EFTM crust. The crust originated when dissolved carbonates precipitated from rainwater in the subsoil, and the ferruginization followed at a time when the water table was much higher and shallow ponds or marshes filled surface depressions (Roberts, 1996). Anoxic, acidic water from the ponds dissolved iron that had been brought up from bedrock below (Roberts, 1996) or introduced as an aerosol (Butzer, 2004) and then released it at points of contact with calcareous

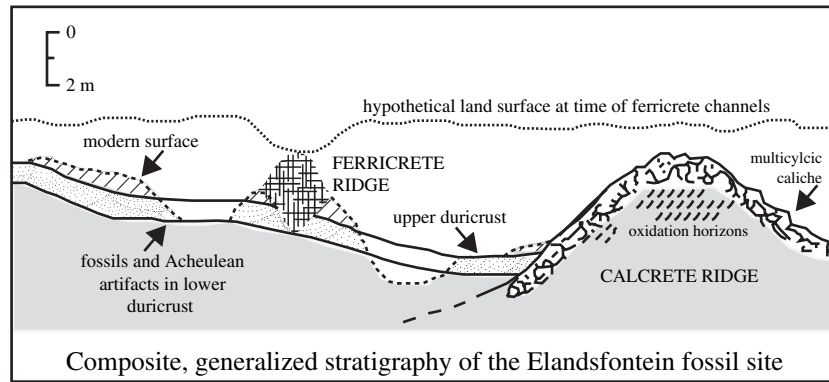


Fig. 3. Composite, generalized stratigraphy of Elandsfontein [modified after Butzer (1973: 235)].

(alkaline) near-surface sediments (or bones). Higher interglacial sea level, greater rainfall, or both could explain the higher water table. The mammalian fauna, described below, together with pollen identified in fourteen associated hyena coprolites by E.M. van Zinderen Bakker and J.A. Coetzee (Singer and Wymer, 1968), confirms that water stood nearby when EFTM formed, and the attraction of water to people and animals could explain why artifacts and bones are so common. Similar ponds or marshes that formed when the water table intersected the surface probably explain the thorough ferruginization of the sands at DFT2 and the EFTM-like occurrence of artifacts and bones. Screening and bulk sampling at DFT2 yielded thousands of bones from eight amphibian species, which corroborate the geochemical indications for fresh surface water (Sampson, 2003).

Deacon (1975) and Partridge (1982) have argued that the EFTM crust marks a former water table to which objects were lowered by persistent deflation over a span of perhaps tens or even hundreds of thousands of years. If this is accepted, individual bones and artifacts could vary widely in age. The fauna, as described below, might suggest this too, partly because it is among the most diverse assemblages ever recovered at an African Pleistocene site, and partly because it includes species that elsewhere appear to have succeeded one another over a period of a half-million to a million years.

However, the surfaces of freshly exposed EFTM bones never exhibit traces of prior sand abrasion, and an erosional lag is inconsistent with “Cutting 10,” where bones and artifacts were sealed on the calcareous duricrust beneath intact sands. Persistent deflation is also an improbable explanation for the broadly similar artifact-and-bone spreads at DFT2, where the bones often occur in anatomical or near-anatomical order and the paleosurface on which they lie undulates and dips weakly from east to west. Butzer (1973) found no geomorphological evidence for deflation or dune formation in the interval between the development of the EFTM crust and historic times, and he concluded that the crust is the subsoil manifestation of a gently rolling, nondunal land surface. Depressions in this surface could have held the ponds whose acidic waters dissolved iron and ferruginized the sediments and the bones.

In sum, geomorphic observations provide no reason to suppose that the EFTM fauna is a composite of two or more faunas that are widely separated in time. The EFTM crust could comprise different crusts exposed in different parts of the site, particularly on opposite sides of the main calcrete ridge, but the basic homogeneity and limited metric variability of species samples gathered from widely separated interdunal bays (Klein, 1982, 1986; Klein and Cruz-Urbe, 1991; see below) suggest that time differences are limited. The extraordinary homogeneity of the biface sample (Singer and Crawford, 1958; Malan, 1962; Singer and Wymer, 1968) also suggests accumulation over a relatively short interval.

Taxonomic composition

Table 1 lists the larger mammalian taxa in the EFTM fauna, in five progressively younger regional faunas, and in the historic fauna. Following prior practice (e.g., Klein and Cruz-Urbe, 2000), we define a larger mammal as one in which average adult weight equals or exceeds 0.75 kg. It is on larger mammals that hunter-gatherers are most likely to concentrate, and smaller mammals—mainly small rodents and insectivores—abound only in sites or layers where a paucity of artifacts suggests that they were collected by raptors (Avery, 1982). The distinction between larger and smaller mammals is essentially academic for EFTM, since the recovery procedure produced no smaller-mammal bones.

The EFTM list in Table 1 depends heavily on specialist studies of baboons (Singer, 1962; Dechow and Singer, 1984), carnivores (Ewer and Singer, 1956; Hendey, 1974), elephants (Maglio, 1973: 25–29), equids (Churcher, 1986; Eisenmann, 2000), rhinoceroses (Hooijer and Singer, 1960a), hippopotamuses (Hooijer and Singer, 1960b), suids (Singer and Keen, 1955; Keen and Singer, 1956; Cooke and Wilkinson, 1978: 473), giraffids (sivatheres) (Singer and Boné, 1960), and bovids (Klein and Cruz-Urbe, 1991). We are responsible for the taxonomic assignments in the other faunas. The nomenclature for extant forms follows Skinner and Smithers (1990). Hereafter, we use mainly vernacular names and we provide Linnaean equivalents only for species that are not included in Table 1.

Table 1

The large-mammal species represented in the historic fauna near Elandsfontein and in the fossil assemblages from Elandsfontein Main (EFTM), Duinefontein 2 (DFT2), Spreeuwal (SPW), Swartklip 1 (ZW1), Diepkloof Rock Shelter (DRS), and Elands Bay Cave (EBC)

Taxa	EFTM	DFT2	SPW	ZW1	DRS	EBC	Historic
Insectivora							
<i>Erinaceus frontalis</i>					1/1	152/20	
Lagomorpha							
<i>Lepus capensis</i> , Cape hare	74/5	146/8					X
<i>Lepus saxatilis</i> , scrub hare							X
<i>Lepus</i> spp., Cape and/or scrub hare			1/1		241/12	368/18	X
Rodentia							
<i>Bathyergus suillus</i> , dune mole rat	173/14	2382/108	1/1	18/4	165/13	2973/157	X
<i>Hystrix africaeaustralis</i> , porcupine	7/2	5/1			11/2	51/2	X
Pholidota							
<i>Phataginus</i> sp., pangolin	2/1						
Primates							
† <i>Theropithecus oswaldi</i> , gelada baboon	9/5						
<i>Papio ursinus</i> , chacma baboon					2/1	40/3	X
* <i>Homo heidelbergensis</i> , fossil hominin	2/1						
<i>H. sapiens</i> , modern humans					2/1		X
Pinnipedia							
<i>Arctocephalus pusillus</i> , Cape fur seal						6666/98	X
Carnivora							
<i>Canis mesomelas</i> , black-backed jackal	411/22	50/3		404/21	7/1	82/3	X
<i>Vulpes chama</i> , Cape fox	22/4			35/2		1/1	X
<i>Lycan pictus</i> , hunting dog	28/2			7/2			
<i>Ictonyx striatus</i> , striped polecat	3/1	18/4		1/1		43/6	X
<i>Mellivora capensis</i> , honey badger	62/6			8/2		7/1	X
<i>Aonyx capensis</i> , clawless otter				9/3			X
<i>Viverra civetta</i> , civet cat	2/1						
<i>Genetta genetta</i> aut <i>tigrina</i> , genet cat		4/1				1/1	X
<i>Herpestes ichneumon</i> , Egyptian mongoose	25/2	7/1		6/1		4/1	X
<i>Herpestes pulverulentus</i> , gray mongoose					6/2	73/7	X
<i>Atilax paludinosus</i> , water mongoose	1/1						?
<i>Suricata suricatta</i> , slender-tailed mongoose	29/5						
<i>Crocuta crocuta</i> , spotted hyena	4/1						
<i>Parahyaena brunnea</i> , brown hyena	43/9	2/1		21/3			X
Hyaenidae, spotted and/or brown hyena	118/12	52/1			8/1		X
<i>Proteles cristatus</i> , aardwolf							X
<i>Felis libyca</i> , wildcat	14/2	2/1		31/4	20/1	22/2	X
<i>Felis caracal</i> aut <i>serval</i> , caracal or serval	244/12	4/1		74/4	22/3	43/2	X
<i>Panthera leo</i> , lion	61/8	7/1		69/4			X
<i>Panthera pardus</i> , leopard	(?)14/3			1/1	2/1	27/1	X
† <i>Megantereon whitei</i> , dirk-toothed cat	15/2						
Tubulidentata							
<i>Orycteropus afer</i> , aardvark						35/2	X
Proboscidea							
* <i>Loxodonta atlantica</i> , Atlantic elephant	383/14						
<i>Loxodonta africana</i> , African elephant		9/1				7/1	X
Hyracoidea							
<i>Procavia capensis</i> , rock hyrax					99/10	650/30	X
Perissodactyla							
† <i>Equus capensis</i> , Cape zebra	2313/118		42/3	31/2	6/1	62/3	
<i>Equus quagga</i> , quagga	36/7	63/3	12/2	7/1		15/1	
<i>Equus zebra</i> , mountain zebra							X
<i>Equus</i> sp. indet., indeterminate zebra					18/3	91/3	
<i>Diceros bicornis</i> , black rhinoceros	79/13	1/1	14/3			7/1	X
<i>Ceratotherium simum</i> , white rhinoceros	7/2	6/2		63/7			
Rhinocerotidae, black and/or white rhino	918/48	49/4	71/3		8/1	32/2	X
Artiodactyla							
<i>Hippopotamus amphibius</i> , hippopotamus	171/6	5/1		6/2	5/1	27/2	X
<i>Potamochoerus porcus</i> , bushpig						1/1	
† <i>Kolpochoerus paiceae</i> , extinct bushpig	69/13						
† <i>Metridiochoerus andrewsi</i> , extinct warthog	4/4						
<i>Phacochoerus aethiopicus</i> , warthog							?
Suidae sp(p), suids	83/16					6/1	

Table 1 (continued)

Taxa	EFTM	DFT2	SPW	ZW1	DRS	EBC	Historic
† <i>Sivatherium maurusium</i> , sivathere	49/8						
<i>Taurotragus oryx</i> , eland	184/54	8/2	8/2	18/6	7/2	121/11	X
<i>Tragelaphus strepsiceros</i> , greater kudu	64/8	65/10		14/3			
<i>Oryx gazella</i> , gemsbok	16/7	1/1	6/1				
† <i>Hippotragus gigas</i> , “giant hippotragine”	71/18						
<i>Hippotragus leucophaeus</i> , blue antelope	43/6	14/3	5/2	58/11	1/1	6/1	
<i>Redunca arundinum</i> , southern reedbuck	164/52	17/4	2/1	132/38		3/1	
<i>Alcelaphus buselaphus</i> , Cape hartebeest							X
* <i>Rabaticeras arambourgi</i> , Arambourg’s hartebeest	187/45						
† <i>Damaliscus</i> aff. <i>lunatus</i> , tsessebe-like antelope	113/19						
<i>Damaliscus dorcas</i> , bontebok			7/2				X
†? <i>Damaliscus niro</i> , bontebok-like antelope	112/14						
†? <i>Damaliscus</i> sp. nov., bastard hartebeest	26/9						
†? <i>Parmularius</i> sp. nov., bastard hartebeest	39/5						
<i>Connochaetes gnou</i> , black wildebeest	130/46	146/20	19/4	100/15	3/2		
<i>Alcelaphini</i> sp. indet., wildebeest or hartebeest					5/2	29/4	X
† <i>Megalotragus priscus</i> , “giant hartebeest”	31/5		1/1				
<i>Sylvicapra grimmia</i> , grey duiker						112/11	X
<i>Pelea capreolus</i> , Vaalribbok				1/1			X
* <i>Gazella</i> sp., gazelle	26/11						
* <i>Antidorcas recki</i> , Reck’s springbok	8/4						
† <i>Antidorcas australis</i> , southern springbok	12/7			77/13			
<i>Antidorcas</i> sp.(p.), springboks	32/12					1/1	
<i>Oreotragus oreotragus</i> , klipspringer					8/1	6/1	X
<i>Raphicerus melanotis</i> , Cape grysbok	310/51	62/7		119/27		67/20	X
<i>Raphicerus campestris</i> , steenbok					1/1	70/18	X
<i>Raphicerus</i> sp(p), grysbok and/or steenbok			1/1		27/4	1071/83	X
† <i>Pelorovis antiquus</i> , long-horned buffalo	470/52	150/20	15/3	2/1	6/1		
<i>Syncerus caffer</i> , Cape buffalo						33/5	?
†Tribe indet., gen. et sp. nov., “spiral horn”	13/7						
Small bovids	479/51	420/8	6/1	556/27	438/9	5719/85	X
Small-medium bovids	134/22	20/2	6/1	432/14	86/3	150/5	X
Large-medium bovids	2564/207	1231/35	140/10	1943/60	114/2	38/4	X
Large bovids	1708/71	1647/21	130/7	220/11	60/2	483/15	X
Very large bovids	2543/70		16/3	4/1	6/1		

Notes: Table 2 provides background information on the sites. The numbers for taxa in the fossil faunas are the NISPs (number of identified specimens) over the MNIs (minimum number of individuals the NISP must represent). Asterisks designate extinct species that probably or certainly evolved into living forms. Daggers mark species that became extinct without issue. Sources: Duinefontein 2 (Cruz-Uribe et al., 2003); Spreeuwal (Klein and Avery, unpublished); Swartklip 1 (Hendey and Hendey, 1968; Klein, 1983); Diepkloof Rock Shelter (Parkington and Poggenpoel, 1987; Parkington et al., 2005; Tribolo et al., 2005b; Klein and Steele, unpublished); and Elands Bay Cave (Klein and Cruz-Uribe, 1987; Parkington, 1988).

The Western Cape has furnished numerous other Quaternary faunas we could have chosen for comparison, but those in Table 1 represent the range in both taxonomic composition and mode of accumulation. Table 2 details their geologic context, age, and artifactual associations, if any. Two of the faunas—from DFT2 and Spreeuwal—accumulated like EFTM in the open air near fresh water; one—from Swartklip 1—originates from a fossil hyena den; and the remaining two—from Diepkloof Rock Shelter and Elands Bay Cave—come from archaeological cave deposits [MSA and Later Stone Age (LSA), respectively]. For each taxon at each site, Table 1 presents the number of identified specimens (NISP) and the minimum number of individuals (MNI) from which the specimens must have come. Figures 4–6 illustrate the proportional representation of each taxon at EFTM, based on its MNI. One or more of the authors was involved in sorting each fauna, and the same recording methodology was employed throughout. Klein and Cruz-Uribe (1984) described the assumptions behind the MNI calculations. The archaeological sites contain multiple

layers, but the MNIs in the table were calculated as if each site contained only one layer, that is, as if the bones in the different layers all came from the same individuals. The MNIs are thus conservative, since the alternative approach—to sum the MNIs for different layers—would produce roughly the same relative taxonomic representation, but it would appear to be based on much larger numbers.

Within each faunal assemblage, ease of identification varied from species to species, depending on whether closely related species of similar size were present and on the degree of bone fragmentation. This is particularly great in the archaeological cave samples, due partly to human butchery and partly to post-depositional leaching and profile compaction. In general, cranial parts allowed the most secure species identifications, and postcranial bones were often more difficult to separate, particularly between species of hares, hyenas, rhinoceroses, zebras, pigs, and bovids of approximately equal size. For each problematic species, Table 1 presents numbers based only on securely identified elements (mainly dentitions, or for the

Table 2
The context, geologic age, and artifact associations at southern African sites used for comparison to EFTM

Site	Context	Geologic age and basis for assessment	Artifact associations
DFT1	Assemblage excavated from tunnels thought to represent a fossil hyena den.	Undated, but fauna similar to that of ZW1 implies relatively cool, grassy conditions during a late Pleistocene cold phase.	No artifacts; numerous hyena coprolites, tooth-damaged bones, and large-carnivore bones imply accumulation by hyenas.
DFT2	Excavated spread of artifacts and bones on a paleosurface within ferruginized eolian sands.	270 ka (optically stimulated luminescence).	Acheulean.
DRS	Fill of a large quartzite overhang, perched above the south bank of the Verlorenvlei, a seasonal river that enters the Atlantic Ocean at Elands Bay, 18 km to the west.	>40 ka (^{14}C assay of charcoal); probably mainly late Isotope Stage 5 and early Stage 3, between roughly 115 and 55 ka, based on fauna, artifacts, and thermoluminescence readings on heated quartzite and silcrete artifacts.	Multiple layers and lenses with MSA artifacts divided among six or more successive culture-stratigraphic units.
EBC	Excavated fill of a coastal cave.	Fossiliferous deposits dated between 13.6 and 7.9 ka immediately below ones dated between about 4.3 and 0.3 ka (^{14}C assay of charcoal.)	Multiple layers and lenses with LSA artifacts divided among three or more successive culture-stratigraphic units.
EFTBC	Circular concentration of bones in the sands above the ferruginous duricrust at Elandsfontein.	Undated, but fauna identical to that of ZW1 implies accumulation under similarly cool conditions.	No artifacts; numerous hyena coprolites, tooth-damaged bones, and large-carnivore bones imply accumulation by hyenas.
HDP1	Bone assemblage excavated from two or more adjacent fissure or cavity fills within calcareous eolianite.	Between 300 and 200 ka (infrared stimulated luminescence, thermoluminescence), but possibly much younger (stratigraphic context, associated fauna).	No artifacts; numerous hyena coprolites, tooth-damaged bones, and large-carnivore bones imply accumulation by hyenas.
NBC	Excavated fill of a coastal cave.	18–0.5 ka (^{14}C assay of charcoal, ostrich eggshell, and marine shell).	Multiple layers and lenses with LSA artifacts divided among four successive culture-stratigraphic units.
KRM	Excavated fill of a coastal cave complex (Caves 1, 1A, 1B, and 2) at the mouth of the Klasies River.	Between 127 and 57 ka (electron-spin-resonance on teeth; thermoluminescence on heated artifacts; geologic context; faunal associations).	Multiple layers and lenses with MSA artifacts divided among four or more successive culture-stratigraphic units.
RDC	Fill of a cave exposed in the wall of a limestone quarry.	Undated, but probably >40 ka, based on the artifacts and fauna.	MSA
SPW	2.5-m-thick sequence of fossiliferous marsh or lake deposits outcropping in the intertidal zone adjacent to Langebaan Lagoon. Bones occur primarily in gray or black humified bands. Items collected mainly following wave erosion of the deposits.	>56 ka (U-series reading on a capping calcrete); interval of lower sea level (?Global Isotope Stage 6, later 5, or 4) based on occurrence at sea level and the exclusively terrestrial composition of the fauna.	? MSA (3 flakes, others probably missed during collection in the swash zone).
ZW1	Fissure fill 1.5 m high and 6 m across, exposed at 16–18 m above sea level in an eolianite cliff fronting False Bay.	>40 ka (^{14}C assay of associated ostrich eggshell); interval of lower sea level based on the exclusively terrestrial composition of the fauna; possibly Isotope Stage 6 [between 186 and 130 ka (racemization of ostrich eggshell)] or later Isotope Stage 5 [(between 115 and 71 ka) (correlation of sea level changes recorded in the eolianite sequence with the global marine record)].	No artifacts; numerous hyena coprolites, tooth-damaged bones, and large-carnivore bones imply accumulation by hyenas.

Sources: Diepkloof Rock Shelter (DRS) (Parkington and Poggenpoel, 1987; Parkington et al., 2005; Tribolo et al., 2005a, b); Duinefontein 1 (DFT1) (Klein, 1983); Duinefontein 2 (DFT2) (Klein et al., 1999; Feathers, 2002; Cruz-Urbe et al., 2003); Elands Bay Cave (EBC) (Klein and Cruz-Urbe, 1987; Parkington, 1988, in press); Elandsfontein Bone Circle (EFTBC) (Inskeep and Hendey, 1966; Klein, 1983); Hoedjies Punt 1 (HDP1) (Klein, 1983; Berger and Parkington, 1995; Stynder et al., 2001; Butzer, 2004; Matthews et al., 2005); Klasies River Main (KRM) (Klein, 1976; Singer and Wymer, 1982; Deacon and Geleijnse, 1988; Deacon, 1989, 1995; Deacon and Shuurman, 1992; Tribolo et al., 2005b); Nelson Bay Cave (NBC) (Klein, 1972a, b; Deacon, 1984; Inskeep, 1987); Redcliff Cave (RDC) (Brain and Cooke, 1967; Cooke, 1978; Klein, 1978a; Cruz-Urbe, 1983); Spreeuwal (SPW) (Avery and Klein, unpublished); and Swartklip 1 (ZW1) (Singer and Fuller, 1962; Hendey and Hendey, 1968; Klein, 1975; Butzer, 2004).

bovids, dentitions and horncores), and it presents parallel numbers for composite categories that also include elements (mainly postcranial bones) that could have come from two or more closely related species. The categories are the genus *Lepus*, the families Hyaenidae, Suidae, and Rhinocerotidae, and five successive size classes among the Bovidae. With respect to the bovid species in Table 1 and Fig. 5, the size classes are: small for klipspringer, grysbok, and steenbok; small-medium for grey duiker, Vaalribbok, gazelle, and the

springboks; large-medium for kudu, gemsbok, “giant hippotragine,” blue antelope, southern reedbuck, hartebeests, bastard hartebeests, and wildebeest; large for eland, “giant hartebeest,” Cape buffalo, and long-horned buffalo (at DFT2); and very large for long-horned buffalo (at all sites except DFT2).

We calculated the MNIs for each composite category as if it comprised only a single species. With regard to the Hyaenidae, for example, the MNI estimates assume that dentitions and limb bones came from one species, even at sites where

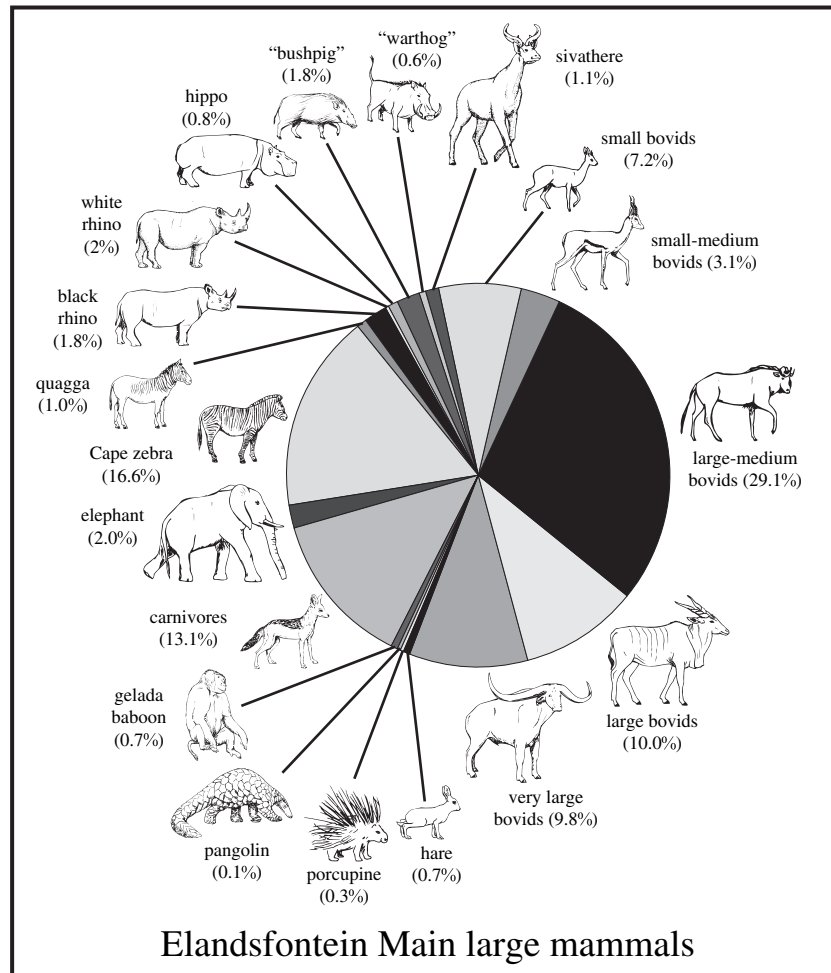


Fig. 4. The relative representation of large-mammal taxa in the EFTM fauna, based on the minimum numbers of individuals (MNI) represented. The percentages were calculated on a total MNI of 712. [Figures 5 and 6](#) illustrate the proportional representation of bovids and carnivores, respectively.

dentitions show that the spotted and brown hyenas were both present. At EFTM, DFT2, Spreeuwal, and Swartklip 1, we could identify some rhinocerotid and bovid postcranial bones to species, at least tentatively, and we have boxed them accordingly in the South African Museum. However, we maintain the composite categories to accommodate specimens we could not identify below the family (or family-and-size) level. The composites also help to compensate for differences in the number of minimally identifiable specimens among samples. The number is particularly high in the fragmented archaeological samples.

The species list for EFTM differs slightly from a previous list (Klein and Cruz-Urbe, 1991) because of taxonomic reassessments. Most important, we have transferred small dentitions previously assigned to “giant hippotragine” to gemsbok. Gemsbok and “giant hippotragine” dentitions differ only in size, and size variation in the EFTM sample suggests that both species are present. Historically, gemsbok were common only in more arid settings, 700 km or more to the north and east (Skinner and Smithers, 1990: 678), although individuals may occasionally have visited the Elandsfontein region (Skead, 1980). The recent recovery of gemsbok at DFT2 and Spreeuwal increases the

likelihood that it also occurred at EFTM, but there is the nagging problem that it is the only EFTM bovid for which horncores are lacking.

Geologic age and assemblage homogeneity

[Table 1](#) and [Figs. 4–6](#) reveal the remarkable diversity of the EFTM fauna, which comprises 48 species of larger mammals (excluding the hominin specimen). This number exceeds not only the number in the other fossil faunas, but also in the historic fauna, which included only 34. The exceptional diversity of EFTM is due partly to the presence of three extralimetary species—pangolin, slender-tailed mongoose (suricate), and civet cat—that are known in the Western Cape only at EFTM, but it is mainly the result of the occurrence of 15 species that have no historic descendants. Four of these—the “Cape zebra,” “giant hartebeest,” southern springbok, and long-horned buffalo—occur in some of the other fossil faunas in [Table 1](#) (and in additional, taxonomically similar assemblages like the one for the Elandsfontein Bone Circle that we have not listed). All four appear to have survived locally until 12–9 ka (Klein, 1984). In the Western Cape, the

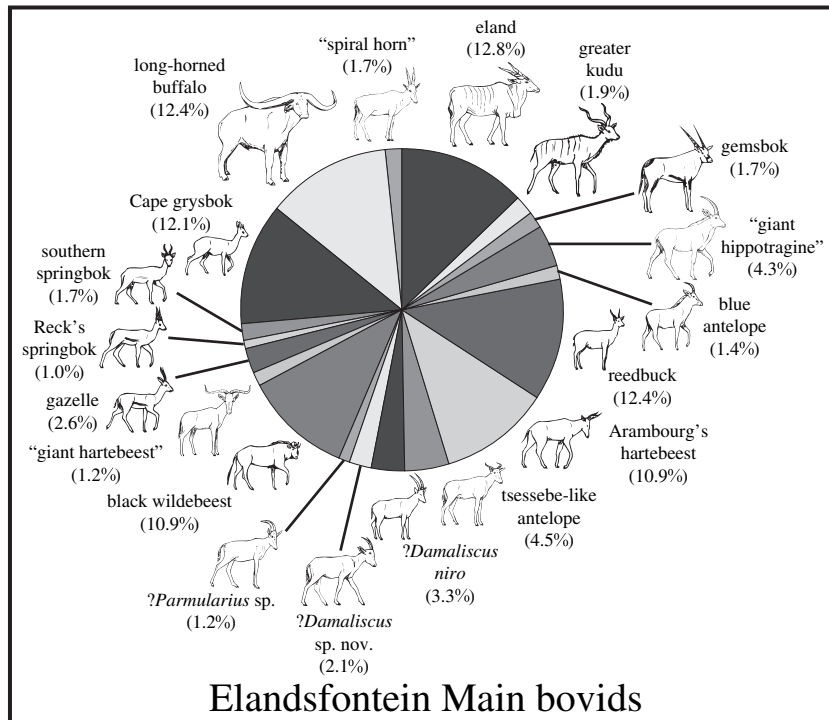


Fig. 5. The relative representation of bovid species in the EFTM fauna, based on the minimum number of individuals (MNI) represented. The percentages were calculated on a total bovid MNI of 421.

remaining 11 extinct species occur only at EFTM, and since the other faunas in Table 1 contain no extinct species that are absent at EFTM, the implication is that the other faunas are much younger. EFTM must thus be significantly older than 270 kyr, the age of the oldest radiometrically dated fauna (from DFT2) among the others. It is probably older than 330 kyr, the minimum age of a fauna with 42 taxa from Lainyamok, Kenya, that is the oldest diverse, directly dated African assemblage to consist entirely of extant forms (Potts and Deino, 1995). Greater precision is impossible, because EFTM itself has provided no material suitable for radiometric dating, and the deposits cannot be linked to any dated external stratigraphy. At present, comparison of the EFTM fauna to radiometrically constrained faunas in eastern Africa provides the most secure foundation for dating.

Based mainly on the bovid species, Klein and Cruz-Uribe (1991) previously concluded that if EFTM occurred in datable geological context in eastern Africa, its age would fall between 700 ka and 400 kyr. Recent east African findings now suggest a somewhat older interval, between roughly 1 Ma and 600 ka. The most useful species for such calculations are those whose presumed ancestors or descendants provide maximum and minimum age estimates, respectively. At EFTM, the two most relevant species are the long-horned buffalo, *Pelorovis antiquus*, which probably descended from *P. oldowayensis*, and the extinct Arambourg's hartebeest, *Rabaticeras*, which probably gave rise to the extant hartebeest genus, *Alcelaphus* (Gentry, 1978, 1990).

The evolution of *P. antiquus* from *P. oldowayensis* occurred subsequent to the formation of Bed IV at Olduvai Gorge,

northern Tanzania. Bed IV was once believed to incorporate the boundary between the Matuyama Reversed Chron and Brunhes Normal Chron at about 780 ka, but it is now thought to be reversed throughout, and it may precede the Jaramillo Normal Subchron between 1.07 and 0.99 Ma (Tamrat et al., 1995). The implication is that *P. antiquus* probably emerged close to or somewhat later than 1 Ma. The earliest-known record of *Alcelaphus* is at Bodo, Middle Awash, Ethiopia, where it is tentatively dated to about 600 ka (Clark et al., 1994; Renne, 2000). The co-occurrence of *Pelorovis antiquus* and *Rabaticeras* thus fixes EFTM between about 1 Ma and 600 ka. This interval is consistent with the presence of eland, *Taurotragus oryx*, which may have evolved from a kudu-like species (*Tragelaphus* sp.) after the emergence of *P. antiquus* (Gentry, 1978, 1990; Gentry et al., 1995), and it is in keeping with the presence of the gelada baboon (*Theropithecus oswaldi*), the extinct suids (*Metridiochoerus andrewsi* and *Kolpochoerus paiceae*), the reedbuck (*Redunca arundinum*), and Reck's springbok (*Antidorcas recki*), all of which are represented by the same or closely related forms at east African sites dated between roughly 1 Ma and 600 ka (Geraads et al., 2004). The age implications of other EFTM taxa are less certain, but there are no species that unquestionably originated after 600 ka.

A major purpose in dating EFTM is to estimate the age of the fossil hominin skull and the associated Acheulean artifacts, but if, for the sake of argument, these are used independently to date the fauna, both suggest an age nearer 600 kyr than 1 Myr. The skull is clearly derived with respect to the 1-myrr-old skulls from Buia, Eritrea (Abbate et al., 1998) and

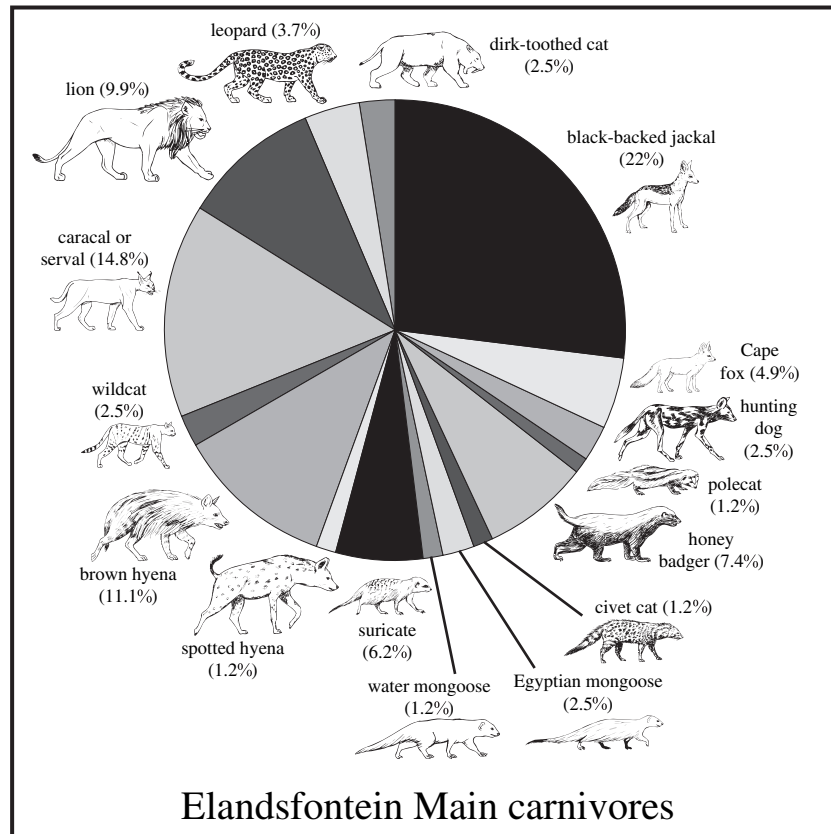


Fig. 6. The relative representation of carnivore species in the EFTM fauna, based on the minimum number of individuals (MNI) represented. The percentages were calculated on a total carnivore MNI of 81.

Daka-Bouri, Ethiopia (Asfaw et al., 2002), or the 970–900-kyr-old fragmentary cranium from Olorgesailie (Potts et al., 2004), all of which more closely fit the concept of *Homo ergaster* or African *H. erectus*. Similarly, the EFTM bifaces tend to be more finely shaped than those from Olduvai Beds II–IV (Leakey and Roe, 1994) or Daka-Bouri (Schick and Clark, 2000), and they are perhaps on a par with those from Bodo (Clark and Schick, 2000).

The circumstances of faunal exposure and recovery at EFTM allow for the possibility, alluded to previously, that the fauna comprises a mix of two or more assemblages, perhaps one that is closer to 1 Ma and one that is closer to 600 ka. This might not only help explain the unusually high species diversity, but also the occurrence of two archaic elements—the sivathere and the dirk-toothed cat—which at 600 ka would be the youngest known African representatives of their lineages. In eastern Africa, sivathere fossils have not been found at any site that postdates 1 Ma (Churcher, 1978; Geraads et al., 2004), while remains of the dirk-toothed cat are unknown after about 1.5 Ma (Arribas and Palmqvist, 1999; Turner and Antón, 2004). The EFTM fauna is tightly associated with the lower (calcareous) duricrust, but it could still mix two or more assemblages if the crust actually comprises crusts of widely different ages exposed in different parts of the site. This possibility may never be conclusively rejected, but fossils of the most abundant ungulate and carnivore

species are scattered widely across the site, and the individual species samples are remarkably homogeneous (Klein, 1982, 1986; Klein and Cruz-Uribe, 1991). None exhibit greater morphological or metrical variability than species samples from other sites where context or direct dating excludes substantial temporal mixture.

Figure 7 shows that this conclusion applies to three common species—the black-backed jackal, the long-horned buffalo, and the Cape grysbok—that are known to have varied significantly in size through Quaternary time. Relative (or intrinsic) variability around the mean is similar between the EFTM samples for each species and the samples from other sites, even though the means for the samples often differ significantly. (In this instance and others below, a statistically significant difference is assumed when the 95% confidence limits for the means of two samples fail to overlap.) A procedure described by Lewontin (1966) revealed only one significant difference (at the 0.05 level or below) in relative variability between an EFTM sample and its counterparts—the EFTM and NBC grysbok.

In advance, it seems unlikely that the fossils of sivathere and dirk-toothed cat happened to come from a portion of the crust that was radically different in age from the crust(s) that provided the bones of jackal, buffalo, grysbok, and other especially common species, and EFTM thus suggests that sivathere and dirk-toothed cat persisted in southern Africa long

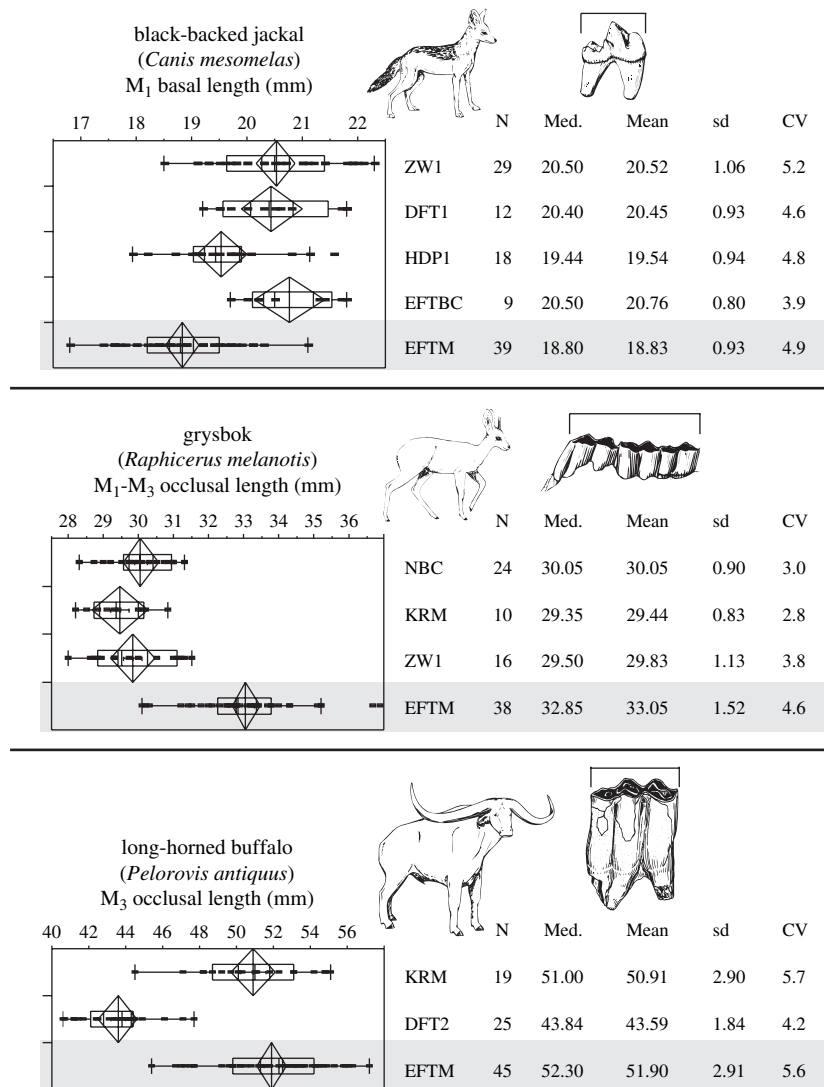


Fig. 7. Box plots describing the length of the lower carnassial (M₁) in black-backed jackals, the lower molar row in Cape grysbok, and the lower third molar (M₃) in long-horned buffalo at EFTM and other sites with sufficient sample sizes for statistical comparison. Table 2 provides background on the other sites. The rectangle in each plot encloses measurements between the 25th and 75th percentiles (= the lower and upper quartiles), the vertical line near the center of the rectangle is the median, and the ends of the horizontal line bisecting the rectangle are 1.5 times the interquartile distance from the lower and upper quartiles, respectively (Sall et al., 2005). The diamond near the center of each plot indicates the mean (vertically) and the 95% confidence limits for the mean (horizontally). Means for which the 95% confidence limits do not overlap are significantly different in the conventional statistical sense. The plots show that the EFTM samples tend to have greater ranges than the others, reflecting larger sample size, but they are similar in the degree of dispersion or packing around the mean or median, even though the mean and median often differ significantly among samples. Stratigraphic context, direct dating, or both show that the other samples represent relatively short time intervals, and the similarity of dispersion argues against the likelihood that EFTM mixes assemblages of widely different ages.

after they had disappeared in eastern Africa. This could not have been predicted in advance, but it is consistent with significant differences between the historic large-mammal faunas of southern and eastern Africa (Grubb et al., 1999). For example, among the extant species listed in Table 1, the dune mole rat, Cape fox, suricate, gray mongoose, brown hyena, mountain zebra, quagga, blue antelope, southern reedbuck, bontebok/blesbok, black wildebeest, Vaalribbok, springbok, and Cape grysbok were restricted to southern Africa (Skinner and Smithers, 1990). The springbok is particularly pertinent because it was common in the early-to-middle Pleistocene of eastern Africa (Gentry, 1978), and if we had only the east African record, we might conclude that springbok became

extinct 400–300 kyr ago. Yet springbok often abound at late Pleistocene sites in southern Africa, and they thrived in the western two-thirds of the subcontinent at the time of European contact.

Within southern Africa, the region at the southwestern corner that includes Elandsfontein was historically further distinguished by a unique climate and biota, with a high degree of endemism (Bigalke, 1979; Cowling and Richardson, 1995). The singular features of the EFTM fauna need imply only that this singularity has great time depth. At least two of the antelope species in Table 1 (?*Parmularius* sp. nov. and the “spiral horn”) have never been reported at any other site, and EFTM is unique among other known African early and

mid-Pleistocene sites for the abundance of “African” elephant (*Loxodonta*) and the absence of Reck’s elephant [*Elephas (Palaeoloxodon) recki*]. The nearest known occurrence of Reck’s elephant is at Kathu Pan, roughly 700 km to the north-east, which has also provided refined Acheulean bifaces recalling those from EFTM (Beaumont et al., 1984). The highly derived molars of Reck’s elephant imply that the Kathu Pan bones and artifacts accumulated after 1 Ma (Klein, 1988), but the fauna overlaps EFTM only to the extent that broadly contemporaneous east African faunas do. The sum of the evidence supports the inference that EFTM stands apart largely because of its geographic position.

Paleoenvironment

The Elandsfontein region currently enjoys a Mediterranean climate with relatively short, cool, wet winters and long, warm, dry summers (Schulze, 1986). Rainfall, which comes primarily between May and September, averages about 300 mm per annum. The average diurnal temperature range is between 8° and 20 °C in July and 15° and 30 °C in January. Soils tend to be nutrient poor and sandy, which means they drain rapidly. In keeping with climate and substrate, before European arrival, the indigenous vegetation consisted of sclerophyllous shrubland or “fynbos” in which the principal plants had hard, tough, leathery, often narrow leaves that are well adapted to prolonged summer drought. The vegetation provided little forage for large browsing or grazing mammals, and excepting occasional black rhinoceros and elephant, rare red hartebeest, and sparse eland, the Elandsfontein region supported no large ungulates (Skead, 1980). The only common ungulates were steenbok and gray duiker, which are small browsers or mixed feeders. The principal nonungulates were hares, porcupine, chacma baboon, aardvark, and a large endemic burrowing rodent, the Cape dune mole rat. Hyraxes were plentiful wherever rocky hills or cliff faces provided crevices or other suitable refuges. The most common carnivores were black-backed jackal, Cape fox, striped polecat, honey badger, Egyptian mongoose, gray mongoose, brown hyena, wildcat, caracal, lion, and leopard. Cape fur seal abounded in the offshore waters.

Regionally, only sites of Holocene age (Global Isotope Stage 1), postdating 12–10 ka, provide faunas like the historic one. Older sites contain assemblages that diverge to various degrees from the historic standard (Klein, 1983). Some sites, such as Hoedjies Punt 1 and nearby Sea Harvest, mix extralimnary species with historic ones, while other localities, such as the Elandsfontein Bone Circle, Duinefontein 1, and Swartklip 1, are dominated by extralimnaries. Among these, greater kudu, reedbuck, black wildebeest, and springbok are especially numerous, and they could thrive only if broad-leaved bush and grasses had spread at the expense of typical fynbos plants. The reedbuck shows further that standing water was widespread. Still other sites, including DFT2 and Spreeuw, add abundant buffalos, zebras, or both to the list of extralimnary species. As discussed below, the sites where buffalo or zebra abound are places where carcasses accumulated on the

margins of marshes or ponds, while the sites where they are rarer are places where hyenas or hominins amassed bones.

In contrast to the fossil herbivores, the fossil carnivore taxa vary little from site to site or time to time, but average individual size within each carnivore species tends to be particularly large at sites where historic ungulates are rare and extralimnary species dominate. In most African carnivores, average individual size increases with distance from the equator (Klein, 1986), and the carnivores, especially the black-backed jackals, from the Bone Circle, Duinefontein 1, and Swartklip 1, were on average larger than any in Africa today. The implication is for site formation under much cooler-than-historic conditions. Average individual carnivore size tends to be smaller at Hoedjies Punt 1 and Sea Harvest, where taxonomic composition implies a less extreme environmental difference from the present. Figure 7 (top) shows that size variation among black-backed jackals at different sites is both conspicuous and statistically significant.

The EFTM fauna anticipates later faunas that are rich in large grazing and browsing ungulates and that lack the most common historic species (especially gray duiker and steenbok). The abundance of reedbuck once again points to standing water, but the sheer diversity of large herbivore species implies an environment without later parallel. Grazers were particularly diverse and included the gelada baboon (a dedicated grammivore), the zebras, the white rhinoceros, both suid species [inferred from the carbon isotope ratio in dental enamel of close east African relatives (Harris and Cerling, 2002)], the “giant hippotragine,” the blue antelope, the reedbuck, all seven alcelaphine antelopes, the gazelle, the springboks, and the long-horned buffalo. Browsers were less diverse, but included sivathere in addition to the greater kudu and black rhinoceros of later sites. The sum of the evidence implies that EFTM samples an interval of exceptionally great vegetational productivity, due mainly to increased moisture. Average individual size in the associated carnivores, particularly the black-backed jackal (Fig. 7), was small, which suggests that increased moisture coincided with relatively mild temperatures.

Arguably, moisture was especially plentiful at EFTM, not only because rainfall was higher but because it extended more into the summer months. At present, the far southerly, near-coastal position of the South Atlantic High pressure cell in summer produces strong southeasterly winds along the coast, and these promote cold-water upwelling that largely precludes summer rainfall in the Western Cape. Analyses of sediments on the continental shelf show that the intensity of upwelling varied in deep time (Little et al., 1996; Pichevin et al., 2005), but so far, the analyses have furnished no evidence for a prolonged interval of reduced summer upwelling that could coincide with the formation of EFTM. Stable-carbon-isotope analysis of the fauna could provide an independent test, since the relatively rare grasses that grow in the Elandsfontein region today are primarily cool-growth-season (C₃) species, and if rainfall extended into summer, warm-season (C₄) varieties would become more common. Stable-carbon-isotope ratios in enamel from a small sample of

EFTM grazers failed to reveal a significant C_4 component in their diets (Luyt et al., 2000), but the sample must be enlarged for a firm conclusion.

The tendency for pre-Holocene faunal samples to deviate from the Holocene condition to one degree or another implies that, so far, no Western Cape site has sampled an interglacial interval that closely resembled the Holocene. In advance, the chances of such sampling were probably limited, since the Holocene appears to have been nearly unique for its warmth and stability. It contrasts particularly with interglacials before 430 ka, which tended to be both longer and somewhat cooler than interglacials afterwards (White, 2004). The bottom line is that the singular climatic conditions of a pre-430-kyr-old interglacial probably explain why EFTM is strikingly different from all known later faunas.

Context and taxonomic composition

The previous sections considered how differences in geologic age and paleoenvironment may account for differences

between the EFTM fauna and others. Figure 8 divides the species in Table 1 among 14 groups to highlight interassemblage differences that reflect depositional context or agent of bone accumulation. In addition to groups whose content is obvious from their labels, Fig. 8 includes the five bovid size categories defined in the section on taxonomy above; the category “hares, hyraxes, etc.,” which groups hedgehogs, hares, dune mole rats, pangolin, baboons, and hyraxes; and two categories for carnivores—“small” for Cape fox, striped polecat, genet, Egyptian mongoose, water mongoose, and slender-tailed mongoose, and “large” for jackal, hunting dog, honey badger, civet cat, hyenas, caracal or serval, lion, leopard, and dirk-toothed cat.

As noted above, the sites in Fig. 8 are composed of three (EFTM, SPW, and DFT2) where bones and artifacts accumulated near the margins of a marsh or pond, one (ZW1) to which they were transported by hyenas, and two (DRS and EBC) to which they were brought by hominins. The hominin sites are deeply stratified archaeological caves. The marsh-edge sites are so far the only ones of their kind to produce significant

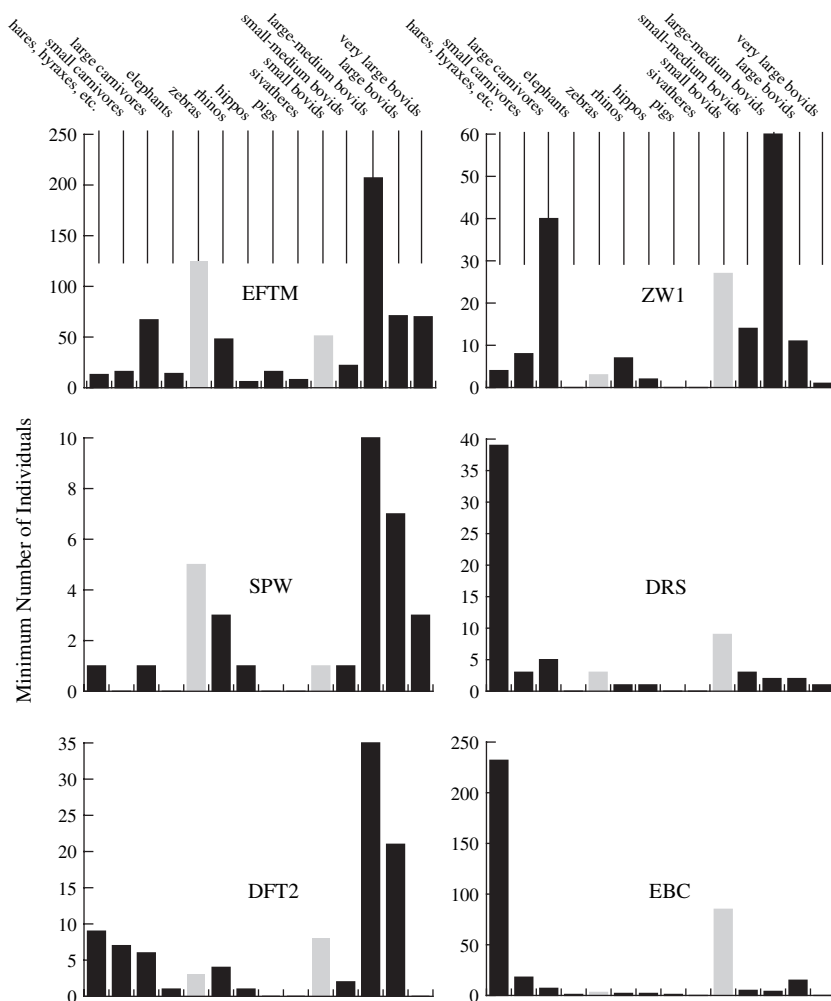


Fig. 8. Histograms comparing the abundance of fourteen taxonomic groups at Elandsfontein Main (EFTM), Spreeuwal (SPW), Duinefontein 2 (DFT2), Swartklip 1 (ZW1), Diepkloof Rock Shelter (DRS), and Elands Bay Cave (EBC). The groups include all the species listed in Table 1. The fifth and tenth bars from the left (for zebras and small bovids) have been dimmed to facilitate interhistogram comparisons.

faunal samples in the Western Cape, but there are four additional hyena dens, and seven additional deeply stratified archaeological caves (Klein, 1983; Parkington, 1990, 2003; Klein et al., 2004). In regard to the proportionate representation of the categories in Fig. 8, the other dens and archaeological sites closely resemble their counterparts in the figure, and they could be used to draw the same conclusions. The conclusions would in fact remain the same if we employed dens and archaeological sites from anywhere in southern Africa.

The category “hares, hyraxes, etc.” includes dune mole rats only for the hyena den and the archaeological caves because most mole rats in the marsh-edge sites probably died in burrows that postdate the fossil occurrences. Excavations at DFT2 repeatedly revealed such burrows emanating from above the fossil horizon (Cruz-Uribe et al., 2003). Dune mole rats feed on plant tissues they encounter in their tunneling and they are thus unlikely to burrow into fissure or cave fills. Neither the den nor the archaeological caves exhibit traces of burrows created by dune mole rats.

Figure 8 supports the following points:

- (1) The three marsh-edge sites are the richest in zebras, large bovids, and very large bovids. At DFT2, where the sample was systematically excavated, these animals are especially well-represented by vertebrae and other axial parts, and the parts commonly occur in anatomical or near-anatomical order (Cruz-Uribe et al., 2003). Surviving surface scatters at EFTM (Fig. 9) suggest a similar pattern, and axial elements are also abundant in the Spreeuwal sample. The sum suggests that each marsh-edge site was a place where large animals died and their carcasses were subsequently disarticulated. Bone damage (discussed below) indicates that hominins played little or no role in the disarticulation and that carnivores were more important.
- (2) The marsh-edge sites and the Swartklip 1 hyena den share an abundance of large-medium bovids. At DFT2 and Spreeuwal, large-medium bovids are again especially well-represented by axial parts, and they probably represent individuals who died on the spot. Based on similarity in geomorphic context, the same is likely for EFTM. In contrast to DFT2, the Swartklip 1 den is relatively rich in large-medium-bovid appendicular parts, especially limb bones, and their epiphyses are often marked or even removed by chewing (Klein, 1975). Greater resistance to destructive chewing could explain why large-medium-bovid parts outnumber small and small-medium parts at Swartklip 1, while greater transportability could explain why they are much more common than large and very large parts. Transport limitations probably also explain why large- and very-large-bovid parts at Swartklip 1 (and other den sites) come mainly from young individuals (Cruz-Uribe, 1991). Adult elements are much more common at the marsh-edge sites.
- (3) The Swartklip 1 hyena den is especially rich in large carnivores. All carnivore species that probably existed nearby are represented, but black-backed jackals dominate, probably because they are especially likely to interact with



Fig. 9. Top: A scatter of large bovid vertebrae exposed by deflation at Elandsfontein Main. Bottom: A scatter of large bovid vertebrae exposed by excavation at Duinefontein 2.

hyenas at carcasses. Among the remaining sites, EFTM has provided the most large-carnivore remains, and jackals again dominate. This could reflect especially frequent carnivore interactions near carcasses, or it could mean that a portion of the EFTM fauna derives from deflated hyena dens.

- (4) The archaeological sites resemble each other and differ from the other sites in the abundance of smaller mammals, meaning mainly “hares, hyraxes, etc.” and small bovids. At EFTM and Spreeuwal, the paucity of hare/hyrax-sized animals may reflect relatively unsystematic recovery, but they are scarcely more abundant in the excavated sample from DFT2, except when the intrusive dune mole rats are included. The archaeological pattern of greater small-mammal abundance spans the MSA and LSA, from perhaps 115 ka (at DRS) to near the time of historic contact (at EBC). It partly reflects the tendency for archaeological caves to occur in rocky settings that hyraxes require, and hyraxes are prominent in most southern African archaeological caves. However, the pattern probably also reflects a tendency for Stone Age foragers to focus on ground game like hyraxes and to abandon many large-mammal elements at butchery sites. If Fig. 8 included

tortoises, the archaeological emphasis on ground game would be more apparent.

Skeletal-part representation

The nonsystematic procedures that were used to recover most of the EFTM bones almost certainly favored the most conspicuous and most readily identifiable elements. Klein and Cruz-Urbe (1991) argued that the bias was least likely to affect skeletal-element representation in the larger species, and they showed that the abundance of different elements within the large-medium, large, and very large bovid categories correlated positively with bone density and negatively with food value. In the absence of density and food-value estimates for any of the EFTM bovids, they used estimates of density and food value for close relatives provided by Lyman (1984, 1985) and Metcalfe and Jones (1988), respectively. Grayson (1988) proposed that a positive correlation with density implies selective destruction of softer bones, while a negative correlation with food value suggests selective removal of more nutritious parts. Since the correlation with density was particularly strong at EFTM, Klein and Cruz-Urbe (1991) concluded that selective destruction played a larger role than selective transport (removal) in shaping the fossil assemblage.

This conclusion may be correct, but subsequent excavations at DFT2 uncovered bovid vertebrae in much greater numbers than they occur in the existing EFTM collection, and vertebrae are among the parts that the EFTM field collectors are most

likely to have neglected since they can be difficult to identify to species. Our most recent sorting and recording showed that vertebrae are as rare or rarer for the EFTM zebras, rhinoceroses, elephants, and hippopotamus. Scapulae and pelvises are rarer still, particularly compared to their abundance at Duinefontein 2. We now believe that skeletal-part representation at EFTM is probably too biased for detailed analysis, and we present numbers only to aid specialists who might be contemplating a comparative taxonomic study. Table 3 lists the NISPs and MNIs for the taxonomically most diagnostic (and the most abundant) elements in the five bovid size classes, and Table 4 provides analogous numbers for the five most common nonbovid taxa. Klein and Cruz-Urbe (1991) presented numbers by bovid species, and we can furnish specialists with element lists, including museum catalog numbers, for any EFTM taxon.

Tables 3 and 4 show that horncores dominate the bovid samples, but dentitions are most common overall, followed by long bones and the calcaneum and astragalus. These are precisely the parts on which field collectors would focus if they were concerned mainly with ready identification to species, but they include the parts that usually provide the largest MNI estimates in more systematically recovered species samples. Thus, the summary MNIs in Table 1 and Figs. 4–6 are surely accurate enough to support the inferences we have drawn on geologic age, paleoenvironment, and the effects of depositional context on taxonomic composition. In addition, field collection at EFTM probably differed little from the explicitly selective collecting that is common at ancient east

Table 3
Skeletal-part representation in the five bovid size classes at EFTM

Element	Small		Small-medium		Large-medium		Large		Very large	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Frontlet (Horncores)	61	35	31	22	340	207	90	58	36	27
Maxilla	83	20	5	4	271	51	55	14	164	37
Mandible	166	51	22	11	396	107	103	23	270	52
Atlas	4	4	1	1	31	26	29	24	46	33
Axis	2	2	2	2	45	44	23	22	39	38
Scapula	5	3	2	2	39	21	26	15	31	16
Proximal humerus	1	1	0	0	33	16	6	3	22	14
Distal humerus	3	2	0	0	180	91	69	30	92	41
Proximal radius	2	1	1	1	86	43	49	23	60	30
Distal radius	2	2	0	0	99	51	51	27	54	32
Proximal ulna	1	1	0	0	36	11	22	6	31	7
Distal ulna	0	0	0	0	0	0	0	0	8	6
Proximal metacarpal	3	2	2	2	63	35	33	16	98	48
Distal metacarpal	5	3	1	1	77	34	91	43	155	65
First phalanges	23	4	7	2	38	5	22	4	113	17
Pelvis	9	4	5	2	40	9	32	8	37	13
Proximal femur	4	3	2	1	19	10	13	7	24	12
Distal femur	3	2	2	1	57	25	43	19	38	13
Proximal tibia	8	5	3	3	59	30	8	5	22	10
Distal tibia	8	5	2	1	110	55	60	30	72	35
Calcaneum	10	5	2	1	49	28	153	71	113	47
Astragalus	12	7	6	3	46	23	124	59	142	70
Proximal metatarsal	4	2	2	1	89	54	30	14	101	54
Distal metatarsal	4	3	5	3	95	42	98	44	120	53

The NISP is the number of identifiable specimens, and the MNI is the minimum number of individuals from which they must come. The list excludes those parts that field collectors are most likely to have overlooked.

Table 4

Skeletal-part representation in black-backed jackals, elephant, Cape zebra, rhinoceroses, and hippopotamus at EFTM

Element	Jackal		Elephant		Cape zebra		Rhinoceros		Hippopotamus	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Maxilla	93	20	67	9	672	93	115	22	28	4
Mandible	84	22	79	14	477	67	130	22	43	5
Atlas	5	5	9	6	0	0	0	0	0	0
Axis	6	6	2	2	2	2	1	1	0	0
Scapula	1	1	8	4	1	1	2	2	0	0
Proximal humerus	7	2	9	4	9	3	10	4	1	1
Distal humerus	16	8	11	3	65	36	37	15	4	4
Proximal radius	9	6	4	2	41	20	52	26	1	1
Distal radius	7	5	2	2	59	34	20	11	2	1
Proximal ulna	16	9	2	1	21	12	29	4	1	1
Distal ulna	5	1	2	2	3	2	18	7	2	1
Proximal metacarpal	23	3	15	2	82	46	90	18	21	3
Distal metacarpal	22	4	11	2	89	38	92	16	21	4
First phalanges	6	1	8	1	117	31	6	1	1	1
Pelvis	0	0	9	3	3	2	4	3	0	0
Proximal femur	11	6	10	5	27	11	11	5	3	2
Distal femur	8	5	15	6	25	12	8	3	0	0
Proximal tibia	1	1	3	2	32	15	20	9	3	3
Distal tibia	8	5	4	3	59	39	46	24	8	5
Calcaneum	9	5	22	13	122	65	85	48	10	6
Astragalus	7	4	13	8	225	118	91	48	8	5
Proximal metatarsal	14	2	8	1	108	54	71	12	24	3
Distal metatarsal	14	2	10	1	145	66	63	10	23	4

The NISP is the number of identifiable specimens, and the MNI is the minimum number of individuals from which they must come. The list excludes those parts that field collectors are most likely to have overlooked.

African open-air fossil localities, as specified, for example, for the Konso early Pleistocene lakeside locality in southern Ethiopia (Suwa et al., 2003). This means that relative-abundance estimates for EFTM can probably be compared directly to those calculated for the east African sites.

Bone damage

The EFTM bones are mostly weathered, but rarely beyond stage 1 in the progressive five-stage scheme proposed by Behrensmeier (1978). The implication is for quick burial or relatively dense shade. Weathering is often restricted to one surface, which was presumably the one exposed to the elements. Sphecid (digger) wasp tunnels occur on 185 postcranial bones, which therefore must have been buried long before mineralization. Some sphecids prefer moister substrates than those near Elandsfontein today, but others burrow in loose dune sand (Bohart and Menke, 1976).

We address bone damage primarily for what it says about hominin involvement in the EFTM fauna. Milo (1994) microscopically examined the surfaces of all of the available limb bones and larger tarsals of large-medium bovids (1092 specimens) and large bovids (516 specimens) and found that 2% and 5%, respectively, exhibited porcupine gnaw marks, 1.8% and 1.4% exhibited carnivore-tooth marks, and only 0.7% and 0.2% bore stone-tool marks. Tool marks were not only rare, but mostly ambiguous. In sharp contrast, a similar microscopic analysis by Milo (1994, 1998) found that tool marks were abundant and far outnumbered both porcupine- and carnivore-tooth

marks on the bovid bones from the MSA occupation layers at the Klasies River Main caves.

The 1608 EFTM bones that Milo studied microscopically included about 18% of the (8834) elements on which tool marks could be reasonably expected. Microscopic analysis is extremely time-consuming, and Milo's sample was surely large enough to suggest that an extended analysis would not produce radically different results. In addition, in our experience with MSA and LSA archaeological faunas, many tool and tooth marks are obvious to the naked eye (e.g., Cruz-Urbe and Klein, 1994), and our macroscopic examination of the EFTM bones that Milo didn't study produced numbers similar to his. We found 90 (=1.2% of 7226) specimens with apparent carnivore-tooth damage and none with unambiguous tool marks. This stands in sharp contrast to the situation at Klasies River Cave 1 and other regional MSA and LSA camp sites, where macroscopically conspicuous tool marks are abundant and they significantly outnumber carnivore-tooth marks. The rarity of tool damage at EFTM suggests that, despite the abundance of Acheulean tools, the tool-makers played little role in the bone accumulation, and we conclude that the bone-artifact association originated mainly from natural mortality near a water source that independently attracted hominins and other large mammals.

The rarity of tool-marked bones at EFTM is noteworthy because it implies that local Acheulean people acquired few of the available large mammals, whether by scavenging or hunting. It is difficult to determine whether EFTM represents an Acheulean rule or the exception because there are few

similar “death” or “carcass” sites where Acheulean people would have obtained bones (as opposed to sites where they might have amassed them), and fewer yet that have been analyzed for bone damage. At most sites for which damage numbers are available, including DFT2, South Africa (Klein et al., 1999; Cruz-Uribe et al., 2003); Hoxne, England (Stopp, 1993); Cagny l’Épinette, France (Dibble et al., 1997); Torralba and Ambrona, Spain (Shipman and Rose, 1983; Villa et al., 2005); and ‘Ubeidiya, Israel (Gaudzinski, 2004a, b), tool-marked bones are no more common than at EFTM, and a reasonable inference again is that local Acheulean people had little impact on the associated large-mammal community. The overall incidence of tool-marked bones is also low at Boxgrove, England, but one unit (4b) produced numerous bones with cut marks and impact fractures, mostly from a single horse (*Equus przewalskii*) that was apparently butchered on the spot (Parfitt and Roberts, 1999). Incompletely reported damage observations from the broadly contemporaneous (400-kyr-old), non-Acheulean locality at Schöningen, Germany (Thieme, 1997, 1998; Roebroeks, 2001), may imply horse butchery on a wider scale. Five wooden spears from Schöningen provide the firmest available evidence that hominins actively hunted during the Acheulean interval, but they do not show how successful the hunters may have been.

Independent of bone damage, limited Acheulean ability to obtain large mammals could be inferred from the relatively low level of Acheulean technology and from the likely small size of Acheulean populations. The issue then is whether the frequency of tool-marked bones at EFTM-like death or carcass sites can inform on this ability. Minimally, for a compelling answer, we need quantified bone-damage observations from a much larger number of sites to establish both the average frequency of tool-marked bones and the extent to which the frequency varies. We probably also need greater consensus on the recognition of tool marks. Experts, perhaps especially those who rely on microscopy, often disagree on identification criteria, and their tool-mark estimates can thus differ significantly (Lupo and O’Connell, 2002). Part of the problem, stressed for key European sites (Gaudzinski, 1999), is that cut marks can be difficult to distinguish from striations produced by trampling or sediment compaction, and impact fractures produced by stone tools can be difficult to distinguish from fractures produced by hyena teeth. The separation often depends less on mark form than on sedimentary context, as at Boxgrove, where the most obviously tool-marked bones come from fine-grained, low-energy deposits in which natural abrasion is unlikely to have produced cut-mark mimics.

If it is eventually shown that tool-marked bones tend to be rare at Acheulean or Acheulean-age death or carcass sites, and if limited Acheulean ability to obtain large mammals is accepted as the probable reason, then it would follow that tool-marked bones should, on average, be more common in comparable MSA or LSA death or carcass sites. Unfortunately, if such sites exist, they remain unreported, in contrast to well-known MSA and LSA cave occupations. Tool-marked bones usually abound in such caves, and their abundance probably implies active hunting. In itself, this does not mean that

MSA and LSA hominins hunted more successfully than their predecessors, but LSA hominins almost certainly did, based on their more sophisticated technology and on indications of greater population density (Klein, 2001).

Mortality

Context provides no indication of a flash flood, veldt fire, sustained drought, or comparable catastrophe at EFTM, and death was probably mainly by attritional factors such as predation, accidents, and endemic disease that disproportionately affect the very young and the old. This expectation can be tested against the age profiles for the two most abundant EFTM species—the long-horned buffalo and the Cape zebra.

Klein (1982) noted that large-ungulate fossil samples usually contain many fewer very young animals than either catastrophic or attritional mortality would produce, and young buffalo and zebra are both remarkably rare at EFTM. Recovery bias is an unlikely explanation since juvenile skulls and the jaws of large animals are conspicuous and easy to identify to species. Juvenile remains are equally scarce in the excavated sample from DFT2, and selective removal or destruction of juvenile bones before or after burial is the best explanation at both EFTM and DFT2. Since bone preservation is excellent at both sites, selective removal before burial was probably more important. On the Serengeti Plain, where mortality in Cape buffalo and Burchell’s zebra (*Equus burchelli*) generally matches the attritional pattern, wildlife biologists rarely encounter very young carcasses, as lions and hyenas consume them quickly and completely (Schaller, 1972). By analogy, carnivore feeding could readily explain the rarity of young buffalo and zebra at EFTM and DFT2. Abundant coprolites document hyena activity at both sites.

Even if EFTM were richer in young buffalo and zebra, the detection of attritional versus catastrophic mortality would still depend on the ratio of prime to postprime adults. Prime (reproductively active) adults tend to dominate all fossil samples because they dominate in life, but some samples contain significantly more postprime individuals than would be expected in live herds, and it is these samples that suggest attritional mortality. Dental wear monitors age in adult buffalo and zebra, and Klein and Cruz-Uribe (1984) advocated the use of molar crown heights to derive individual ages, using a quadratic model that Spinage (1972, 1973, 1976) proposed for estimating age from crown height in Burchell’s zebra, Grant’s gazelle (*Gazella granti*), and other hypsodont east African ungulates. Klein et al. (1983) and Pike-Tay et al. (2001) found that this model adequately predicted age from molar-crown height in Yellowstone elk (*Cervus elaphus*) and caribou (*Rangifer tarandus*), respectively.

However, the estimation of age from crown height is complicated because it requires three parameters—the age at which a permanent tooth erupts, its initial unworn crown height, and the age at which its height approaches zero. Age at zero crown height is particularly hard to estimate, and for any given species, it will clearly vary among successive molars (Steele, 2006). Here we employ a simpler, alternative

analytic procedure that requires only an estimate of initial crown height. This can usually be determined directly in large samples, and the ratio of individual crown height to initial height is a dimensionless measure of individual age. The distributions of such ratios can thus be directly compared among samples, even when the samples represent different species. When the average ratio in one sample is significantly larger than the average in another, the implication is that the first sample is richer in younger animals.

The Yellowstone elk suggest a way to use the crown-height ratios (hereafter referred to as relative crown heights) to identify samples in which postprime adults are especially common. The elk sample includes 226 specimens that were human-hunted and aged from tags that were attached near birth, as well as 96 that were wolf-killed and aged from incisor cementum annuli (Steele, 2005). Hamlin et al. (2000) showed that incisor annuli closely track age in recent elk, and we thus regard the ages of the wolf-killed elk as “known.” Figure 10

(top) presents the distribution of ages within the two subsamples. Young elk are underrepresented in each because human hunters focused on antlered animals, while wolves fully consumed the carcasses of their youngest prey. With this in mind, in paleoecological terms, the age profile of the human-hunted sample is broadly catastrophic and the profile of the wolf-killed sample is broadly attritional.

Figure 10 (bottom) presents the relationship between the relative crown heights of M_1 and M_3 and relative age in the composite elk sample. Relative age is defined as known age divided by potential longevity, estimated at 276 months from the known-age elk sample itself. The figure shows that, when M_1 crown height approaches zero, individuals tend to be about half way through their potential lifespan, and the human-hunted sample suggests that few survive beyond this point. Wolf predation, as presented in Fig. 10 (top), is one reason why. Individuals of the closely related or conspecific European red deer also rarely survive after their M_1 s are

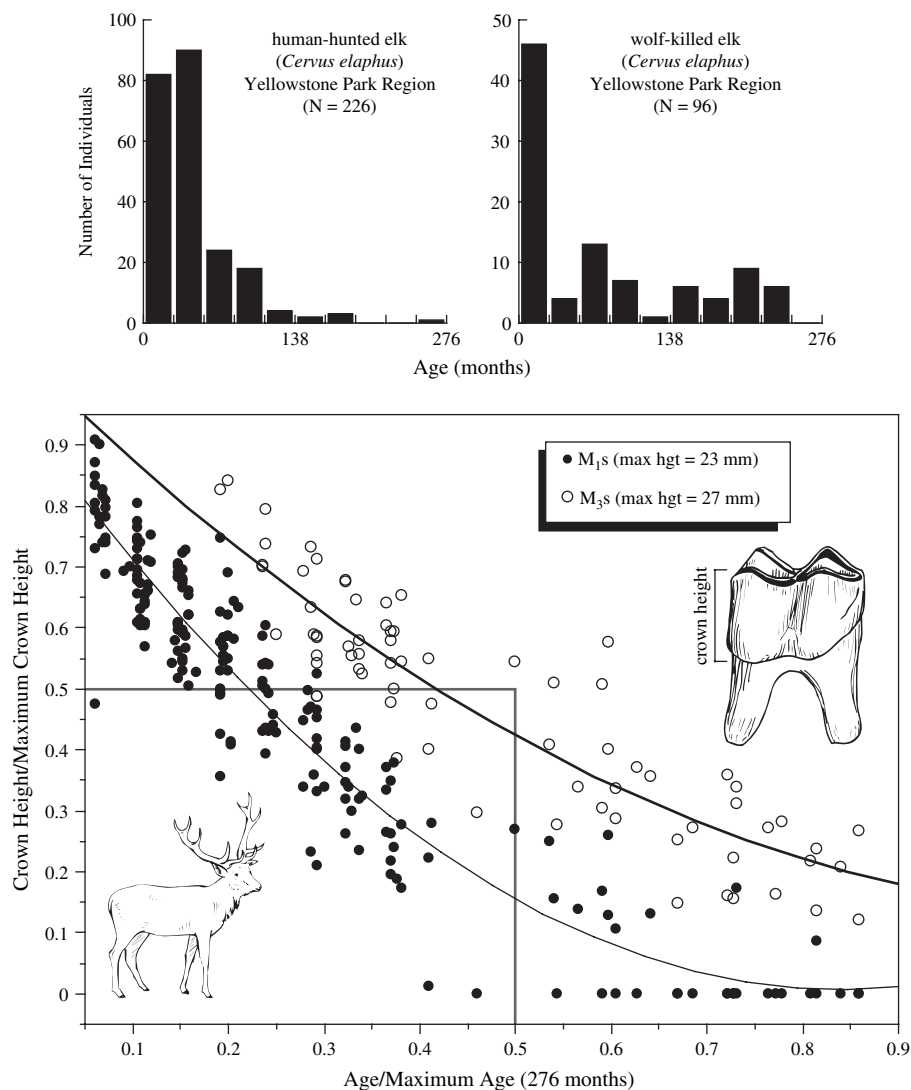


Fig. 10. Top: The ages of elk in human-hunted and wolf-killed samples of Yellowstone elk (Steele, 2005). Bottom: Relative M_1 and M_3 crown heights (crown heights/unworn crown height) versus relative age in the composite elk sample. The thinner and thicker curves mark the least-squares quadratic regression of relative crown height on relative age for M_1 and M_3 , respectively.

worn away (Mitchell et al., 1977). Reproductive activity declines at this point, and the associated age (= half of potential lifespan) is thus a maximum estimate for the division between the prime and postprime adult categories. Figure 10 further shows that, when M_1 height approaches zero, M_3 height tends to be reduced by about half. This is important, as elk and other ungulate M_1 s can be difficult to distinguish from M_2 s, particularly when they are worn, and for age estimates, we and other specialists thus often rely on M_3 s. We do this here, and from Fig. 10 (bottom), we conclude that attritional mortality is implied when average M_3 crown height in an ungulate sample is less than or equal to half of its initial value.

Figure 11 presents box plots that describe relative M_3 crown heights in the human-hunted and wolf-killed Yellowstone elk; relative M_3 crown heights in the long-horned buffalo from EFTM, DFT2, and the Klasies River Main MSA caves; and relative M^3 crown heights in the Cape zebra from EFTM, horse from the Ambrona and Torralba Acheulean sites in Spain, and Burchell's zebra from the MSA layers of

Redcliff Cave in Zimbabwe. The abundance of maxillary or mandibular M_3 s in the EFTM samples determined which to employ. The caption to Fig. 7 explains the box plot format.

Figure 11 shows that using the 0.5 average crown-height criterion, the two elk subsamples divide as expected between a more “catastrophic” one resulting from human hunting and a more “attritional” one resulting from wolf predation. There is some variation among the samples of long-horned buffalo, but the EFTM sample meets attritional expectations, and its apparent difference from the more equivocal DFT2 sample is not statistically significant. (The 95% confidence limits for the means overlap). The Klasies River Main sample resembles the one from EFTM, and it suggests that the Klasies hunters focused their attention on older, more vulnerable buffalo. It could even mean that they mainly scavenged buffalo since postprime carcasses are the ones they were most likely to encounter in the veldt.

The equid samples differ more sharply from one another, but only the one for Burchell's zebra from Redcliff Cave

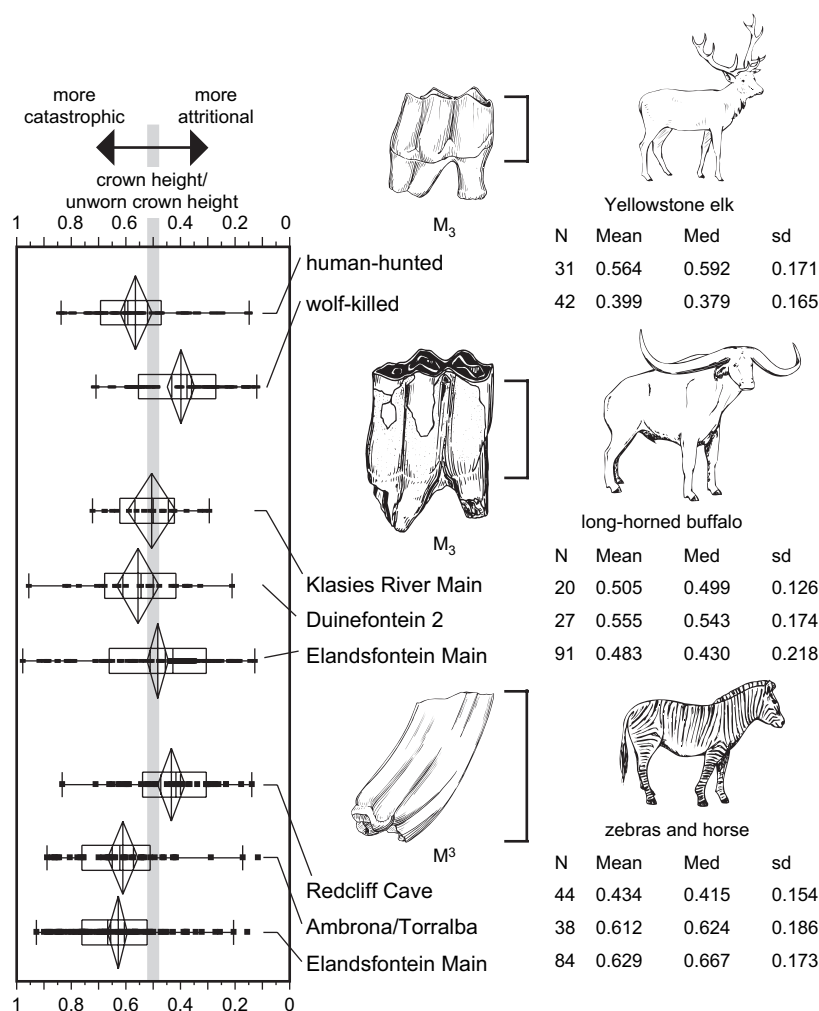


Fig. 11. Box plots describing relative crown height in human-hunted and wolf-killed Yellowstone elk; in long-horned buffalo from the Klasies River Main Middle Stone Age caves, Duinefontein 2, and Elandsfontein Main; and in Burchell's zebra from Redcliff Cave, Eurasian wild horse from Torralba and Ambrona, and Cape zebra from Elandsfontein Main. Table 2 provides background information on the African sites. Excavations by Howell and Freeman [Freeman, 1994; Howell et al., 1996 (1991)] provided the composite Torralba/Ambrona sample. The caption to Fig. 7 explains the box plot format.

unquestionably suggests attritional mortality. It could mean that, like their Klasies contemporaries, the MSA inhabitants of Redcliff focused on older, weaker prey or even that they often scavenged dead zebra. More relevant here, however, is that, unlike the EFTM buffalo sample, the one for Cape zebra departs from “attritional” expectations, and the same difference emerges when age profiles estimated from crown heights are compared (Klein, 1982). The explanation for the Cape zebra profile is unclear, but the horse sample from Torralba/Ambrona is also not attritional, which suggests a role for species ecology and depositional setting. Like the EFTM zebra bones, the Torralba/Ambrona horse bones accumulated on the margins of a shallow marsh or lake (Butzer, 1965), and bone damage suggests that local Acheulean hominins played a minimal role in the process (Shipman and Rose, 1983; Villa et al., 2005).

The kudu and black wildebeest samples from DFT2 diverge even more sharply from attritional predictions (Cruz-Uribe et al., 2003), and considered with the EFTM zebra sample, they serve as a reminder that mortality need be attritional only in aggregate, not in every context. Site-formation specifics, including season of death, may also produce variation among catastrophic mortality profiles (Lubinski, 2001), especially ones that represent one-time events. In short, the interpretation of mortality in fossil samples depends not just on the actualistic observations that underlie the catastrophic and attritional models, but also on the interactive effects of species socioecology and depositional setting. Kurtén (1983) and Lyman (1987) have made this point before, and Barnosky (1985) has applied it to explain the idiosyncratic mortality profile of late Pleistocene Irish elk (*Megaloceros giganteus*) from Balleybetagh Bog, Ireland.

Summary and conclusion

The taxonomic composition of the EFTM large-mammal assemblage implies an age of between 1 million and 600 thousand years ago, while the hominin skullcap and the refined Acheulean bifaces favor a time closer to 600 ka. The morphologic and metric homogeneity of species samples gathered from across the site suggest that EFTM samples a single large-mammal community, as opposed to two or more communities of widely different ages. If this is accepted and an age near 600 kyr is correct, the EFTM sivathere and dirk-toothed cat would represent the latest records of their lineages. Their late survival could reflect the position of EFTM near the extreme southwestern tip of Africa in a region that was distinct historically for its climate and highly endemic flora and fauna.

Geomorphic context indicates that the EFTM bones accumulated at a time when the water table intersected the surface, producing ponds or marshes in shallow depressions. Higher interglacial sea level, greater precipitation, or both could have been responsible, and the small average size of individual carnivores, particularly black-backed jackals, points to mild temperatures. The sum of the evidence places site formation during one of the mid-Pleistocene interglacials before 430 ka that were longer and somewhat cooler than later ones.

Based on freshly exposed bone scatters at EFTM and on their similarity to the excavated scatters at DFT2, the EFTM bones probably come mainly from carcasses of animals that died nearby. Since the site preserves no evidence for a flash flood, veldt fire, sustained drought, or other catastrophe, mortality was probably mainly attritional. However, age-at-death analyses for the two most common species—the long-horned buffalo and the Cape zebra—confirm this only for the buffalo. The failure of the zebra to conform serves as a reminder that mortality needs to be attritional only in aggregate and that the interaction of depositional context and species socioecology can produce departures. As a hypothesis that can be partly tested with observations from other EFTM-like sites, we suggest that the zebra age profile reflects species-specific individual or group behavior near a water hole.

Despite the abundance of Acheulean bifaces and associated flake tools, few of the EFTM bones exhibit unequivocal stone-tool damage, and we conclude that local Acheuleans played little role in the bone accumulation. Tool-marked bones also appear to be uncommon at other Acheulean or Acheulean-age carcass or death sites, and pending observations from a larger sample of such sites, a possible interpretation is that Acheulean-age hominins obtained only a small proportion of the available large mammals, whether by hunting or scavenging.

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