QUATERNARY RESEARCH 36, 94–119 (1991)

Environmental, Ecological, and Paleoanthropological Implications of the Late Pleistocene Mammalian Fauna from Equus Cave, Northern Cape Province, South Africa

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Received October 30, 1989

The late Pleistocene deposits of Equus Cave, northern Cape Province, South Africa, have provided more than 30,000 taxonomically identifiable mammal bones from 48 species. Context, associations, and features of the bone assemblage implicate brown hyenas as the main accumulators. The fauna is significant mainly because (1) it supplements previous evidence that regional climate was cooler and possibly also somewhat moister during part(s) of the late Pleistocene, but deviated less from the historic norm than in areas farther south; (2) it shows that Bond's springbok, which became extinct in the early Holocene, differed from the surviving common springbok not only in important morphological respects but also in reproductive pattern; and (3) it sustains earlier suggestions that an abundance of carnivores, a paucity of small hard bones, an increase in the cranial/postcranial ratio with species size, and exclusively attritional mortality profiles are features that tend to differentiate assemblages accumulated by brown hyenas from those accumulated by people. In addition, pending firmer dating, the fragmentary human fossils from Equus Cave may support an exclusively African origin for anatomically modern humans. © 1991 University of Washington.

INTRODUCTION

Equus Cave, South Africa, has provided one of the largest Pleistocene faunal samples in the world. Geologic context and taxonomic composition imply a late Pleistocene age, while context, taxonomic composition, bone damage, and associated objects indicate that brown hyenas were the main accumulators. So far, only the human remains and statistics on carnivore size have been published (Grine and Klein, 1985; Klein, 1986a). Our purpose here is to summarize the implications of the fauna for (1) late Quaternary environmental change in southern Africa; (2) the ecology and behavior of key species, including especially the brown hyena and the very abundant, extinct Bond's springbok; and (3) the differences between fossil assemblages accumulated by hyenas and those accumulated by Stone Age people.

THE SETTING OF EQUUS CAVE

Equus Cave (approximately 27°37′S, 24°37′E) is located on the Gaap Escarpment at Norlim (formerly Buxton), near Taung in the northern Cape Province of South Africa (Fig. 1, bottom). The escarpment is a 275-km-long, Precambrian dolomite cuesta that trends SW to NE between 27°07′ and 29°10′S on the southeastern margin of the Kalahari Desert and separates the Gaap Plateau on the northwest from a lowerlying planar surface dipping toward the Vaal

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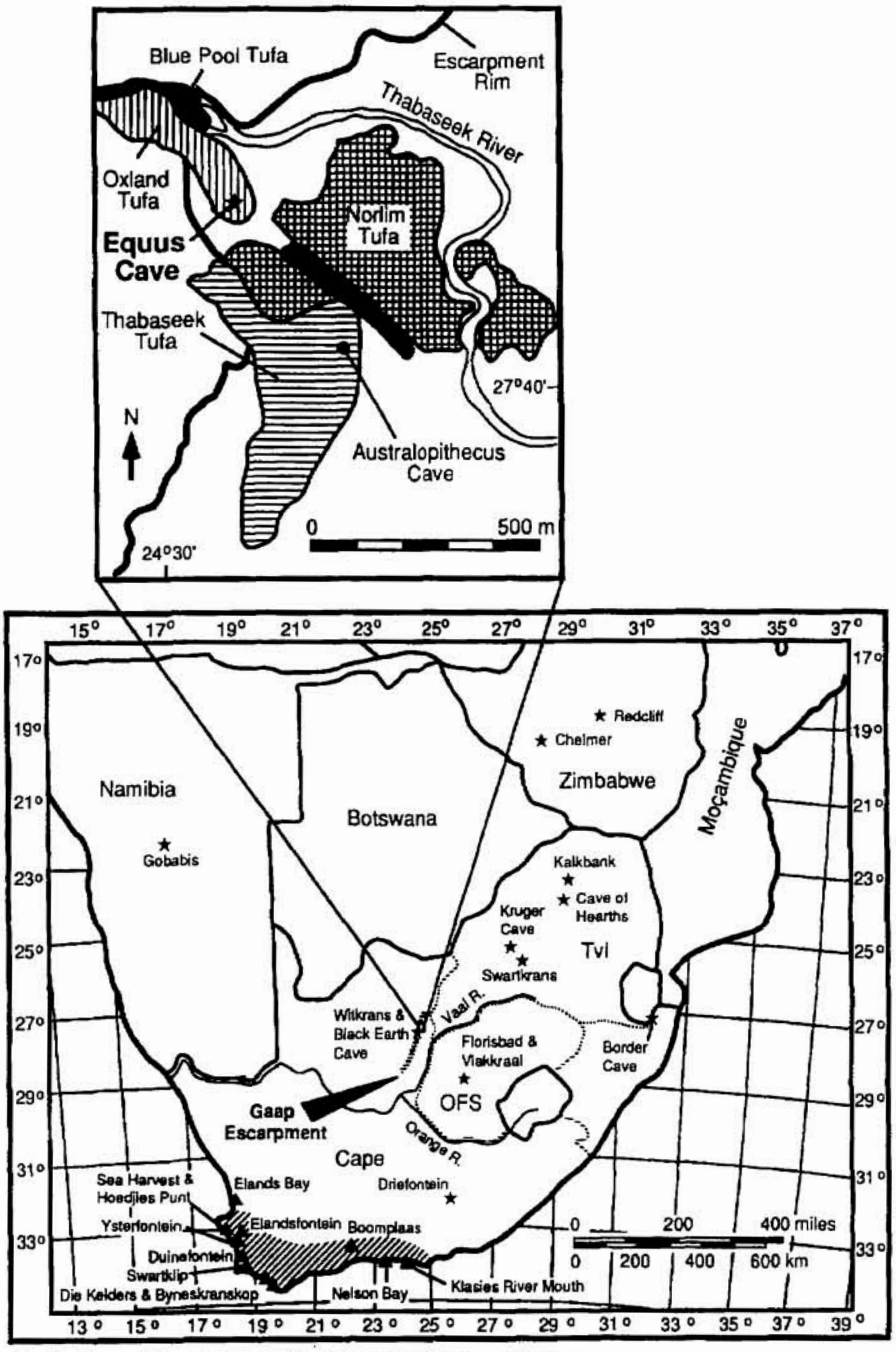

FIG. 1. Bottom: Map showing the approximate locations of the sites mentioned in the text. Stars designate sites where Bond's springbok has been found, and hatching indicates the southern and southwestern Cape region where it is unknown and probably never occurred. Top: Equus Cave and the various tufa bodies developed at Buxton-Norlim (partly after Butzer, 1974, Fig. 3).

River on the southeast. Its face averages 70–120 m high and is mantled at several places with sheets or lobes of tufa (freshwater limestone). These originated from the evaporation of carbonate-charged spring waters, arguably in times of accelerated spring discharge (Butzer *et al.*, 1978; Butzer, 1984) or under conditions no moister than the present (Partridge, 1985). They are particularly well developed in the

Norlim area, where Peabody (1954) and Butzer (1974, 1984; Butzer *et al.*, 1978) have identified four major generations, known (from oldest to youngest) as the Thabaseek, Norlim, Oxland, and Blue Pool/Channel tufas. The tufa bodies contain caves, including one inside the Thabaseek Tufa that provided the first specimen of *Australopithecus africanus* (Dart, 1925). Equus Cave occurs inside the much younger Oxland Tufa, approximately 500 m northwest of the australopithecine cave (Fig. 1, top).

The climate of the Gaap Escarpment is semiarid, with no water surplus at any season. The winters (May to October) are cool and very dry, while the summers (November to April) are hot and punctuated by short, violent storms that provide 95% of the total yearly rainfall. Precipitation near Equus Cave varies from less than 100 to over 1000 mm per annum with an average of about 425 mm (Climate of South Africa, 1954; U.S. Department of Commerce, 1966–1967). Historically, the regional vegetation was dominated by grasses with scattered acacia thorn trees in a community known as "Kalahari Thornveld" (Acocks, 1953) or perhaps more descriptively as acacia grassland. The indigenous fauna must be reconstructed from scattered early travelers' reports (Skead, 1980), but it is clear that grazers predominated, including especially mountain reedbuck and vaalribbok on the escarpment itself and blue wildebeest, Cape hartebeest, blesbok, roan antelope, common springbok, Burchell's zebra, and warthog on the plains above and below. Browsers were certainly less prominent overall, but giraffes fed on the acacias scattered over the plains, and greater kudu and grey duiker found both browse and cover in patches of bush that were concentrated on and adjacent to the escarpment. The most abundant mixed grazer/browser was steenbok, with eland a distant second. The most plentiful nonungulate herbivores were rock hyrax, springhare, Cape hare, scrub hare, porcupine, and baboon. The principal carnivores were lion, leopard, caracal, serval, wild cat, cheetah, brown hyena, spotted hyena, Cape hunting dog, black-backed jackal, and silver fox. The plains ungulates and perhaps also some of the carnivores were probably migratory—during the drier (winter) season, many probably moved away from the Gaap Plateau above the escarpment, perhaps mainly to the valleys of the Vaal River and its tributaries on the undulating plain below.

EXCAVATION, STRATIGRAPHY, AND ANTIQUITY OF THE EQUUS CAVE FILL

Peabody (1954, Fig. 7) was the first to record fossils at Equus Cave, and his mention of an *Equus* tooth gave the site its name. Beaumont and Shackley undertook the first systematic excavations in 1978, and Beaumont extended them in 1982. Commercial quarrying of the tufa had partially destroyed the cave before excavation, and large blocks from the collapsed roof had to be removed from the exposed deposit. A grid of squares 1 m on a side was then laid down (Fig. 2), and the excavation proceeded according to arbitrary 7.5-cm-deep levels or "spits" within four poorly defined natural stratigraphic units, called (from top to bottom) 1A, 1B, 2A, and 2B (Fig. 3).

The uppermost unit, 1A, is a layer of grayish-brown sandy loam up to 50 cm thick, lying unconformably on unit 1B below. Units 1B through 2B comprise a conformable series of mainly reddish-brown, subhorizontal sandy loams with lenses of tufa grit. Unit 2A is differentiated from 1B above and 2B below primarily by an abundance of large, partially corroded tufa (roof) fragments, accompanied by some carbonate cementation of the enclosing sands. In thickness, 1B varies from 30 to 50 cm, 2A from 60 to 70 cm, and 2B from 60 to 80 cm. The origin of the reddish sands is largely, if not entirely, eolian (Shackley, personal communication, 1982).

The entire sequence is rich in animal bones, and 1A also contains typical Later

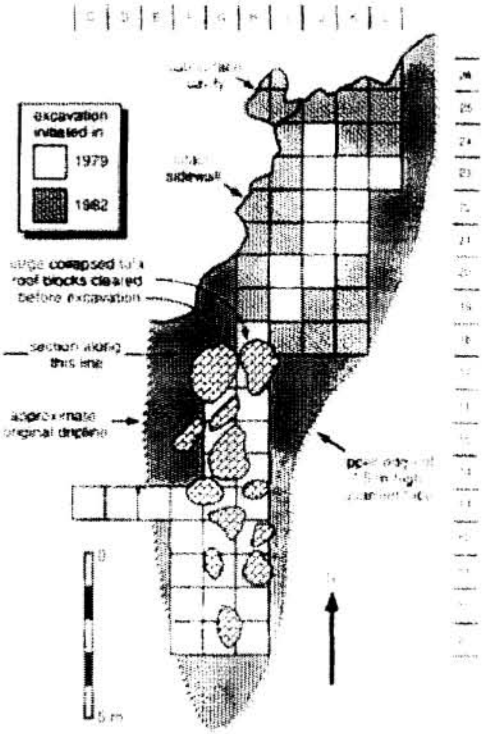

FIG. 2. Floorplan of Equus Cave.

Stone Age bone points. Two radiocarbon dates—2390 ± 60 yr B.P. (Pta-2452) on charcoal from near the middle of 1A and 7480 ± 80 yr B.P. (Pta-2495) on ostrich eggshell from near its base—indicate that 1A dates from the Holocene (Vogel *et al.*, 1986). The geologic antiquity of units 1B through 2B is much less certain. Occasional artifacts of Middle Stone Age (MSA) aspect, particularly in 2B (Beaumont *et al.*, 1984), suggest that 1B–2B are older than 30,000–40,000 yr B.P., the upper limit of the MSA elsewhere in southern Africa (Volman, 1984). However, organic residues extracted from bones in the upper part of 2B have been dated to 16,000 ± 160 yr B.P. by radiocarbon (J. C. Vogel, unpublished data). If this dating is valid, it would imply that the MSA artifacts are derived (washed in). Perhaps equally likely, the dated samples have been contaminated by younger carbon, and the antiquity of the 1B–2B sequence may be indicated more accurately by its geomorphic context.

The position of 1B–2B within the Oxland Tufa show that they postdate the outer portion of this tufa, dated by ionium (^{230}Th) to about 230,000 yr B.P. (Vogel and Partridge, 1984). In addition, Butzer *et al.* (1978) argue that they antedate the development of a manganiferous patina that covers the Blue Pool Tufa I and that is older than 32,700 yr B.P. Butzer (1984) has further suggested that the dissolution and initial filling of Equus Cave reflect the same accelerated spring discharge that produced Blue Pool Tufa I, which began to form perhaps 103,000 yr B.P. according to U-series dating (Vogel and Partridge, 1984). In sum, circumstantial, geomorphic evidence suggests that units 1B–2B were deposited sometime between 103,000 and 32,700 yr B.P., either in the latter part of the last interglaciation (oxygen-isotope stage 5) or in the early to middle part of the last glaciation (isotope stages 4 and 3).

In what follows, we often treat layers 1B, 2A, and 2B as if they were a single unit. This is partly because they are totally conformable and partly because layer-by-layer analyses not presented here suggest no major differences in their faunal contents.

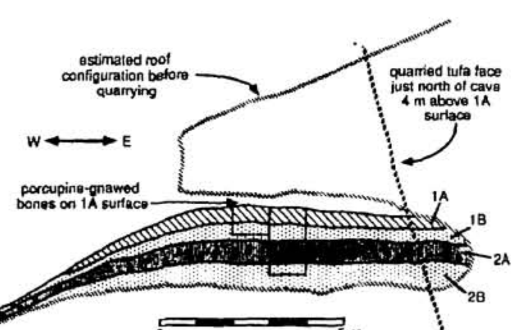

FIG. 3. Profile along the south wall of strip 18 at Equus Cave.

PALYNOLOGY

Equus Cave has provided little pollen, except in hyena coprolites that occur throughout. The pollen spectra from coprolites in unit 1A imply vegetation broadly similar to the historic Kalahari Thornveld, while spectra in coprolites from units 1B through 2B indicate far more open vegetation with many fewer trees, particularly relative to grasses and composites (Scott, 1987). Tree pollen is especially rare in coprolites from 2B, where the total spectrum suggests much cooler conditions, up to 4°C below the present average. As discussed below, a cooler climate is also implied by the 1B–2B fauna. The pollen further implies greater effective moisture, though this could reflect simply reduced evaporation under cooler temperatures. The pollen evidence is not helpful in resolving the dating uncertainty, because cooler conditions are in keeping with either the tentative 16,000 yr B.P. date for 2B or with the geomorphic argument bracketing the entire 1B–2B sequence between 103,000 and 32,700 yr B.P. In the latter case, the pollens would mean that 1B–2B accumulated either within the earlier part of the last glaciation, sometime between 75,000 and 32,700 yr B.P. or within the pronounced cool phase (isotope substage 5b) that interrupted the last interglaciation between about 94,000 and 84,000 yr B.P.

GENERAL CONDITION AND COMPOSITION OF THE BONE ASSEMBLAGE

The Equus Cave bones are very friable and highly fragmented, partly from predepositional events and partly from profile compaction and postdepositional leaching. Some additional fragmentation occurred during excavation and transport from the site, but many pieces still remain readily identifiable to skeletal part and taxon. The overwhelming majority come from macromammals (hedgehog/hyrax-size or larger) on which we focus here. In addition, there are occasional bones from micromammals (small rodents, insectivores, and bats), birds, reptiles, amphibians, and fish. The micromammals and birds will be reported by D. M. Avery and G. Avery, respectively. No specialist has studied the reptile, amphibian, and fish bones, but among them we recognized specimens from snake(s), tortoise(s), monitor lizard (*Varanus* sp.), and crocodile (*Crocodylus niloticus*). The crocodile bones come mainly from layers 1B–2B, where, like the pollen and the macromammals, they may reflect moister-than-historic conditions. However, only five pieces are involved, and it is conceivable that they came from the Harts River, about 8 km away, where crocodiles may have occurred historically.

Among the macromammal bones, we identified approximately 10% or 32,343 to skeletal part and taxon. Whenever possible, besides taxon, for each part we also recorded degree of completeness, side, and/or state of epiphyseal fusion. Following the procedures laid out in Klein and Cruz-Uribe (1984), we then used these data to calculate both the number of identifiable specimens (NISP) for each taxon and the minimum number of individuals (MNI) from which the specimens must have come. Table 1 presents the summary NISPs and MNIs for each taxon, while Figures 4–6 show the proportional representation of each taxon based on its MNI.

Because the bones are highly fragmented and often come from species that are osteologically very similar, many specimens were identifiable only to superspecific categories. The most numerous problematic bones were bovid postcranial fragments, which we could assign only to size categories—small, small-medium, large-medium, and large (see Table 1 caption). The NISPs and MNIs for bovid species are thus based exclusively on cranial elements (teeth and horncores), while those for size categories include both these and all postcranial bones. Other distinctions we often could not make were between Cape fox and bat-eared fox, brown hyena and spotted hyena, wildcat and black-footed cat, and leopard and cheetah. The lumping of bones from each species pair is reflected in the composite categories in Table 1, which include

TABLE 1. THE NUMBER OF IDENTIFIABLE SPECIMENS (NISP)/THE MINIMUM NUMBER OF INDIVIDUALS (MNI) PER LARGE MAMMAL SPECIES AND STRATIGRAPHIC UNIT AT EQUUS CAVE

	Undiff. 1	1A	1B	2A	2B	1B–2B
Erinaceus frontalis, hedgehog	—	—	—	2/1	1/1	3/2
Leporidae gen. et sp. indet. hare(s)	22/2	27/3	43/5	52/4	110/9	205/16
Pedetes capensis, springhare	4/1	5/1	17/3	9/1	2/1	28/4
Hystrix africaeaustralis, porcupine	3/1	9/2	13/2	19/2	68/6	100/7
Papio ursinus, chacma baboon	15/3	62/6	39/3	47/4	12/2	98/7
Homo sapiens, people	—	3/1	2/1	3/1	4/1	9/1
Canis mesomelas, black-backed jackal	41/3	262/15	497/15	1122/41	4314/165	5838/217
Vulpes chama, Cape fox	9/2	44/5	55/8	88/13	408/50	543/65
Otocyon megalotis, bat-eared fox	1/1	3/2	8/2	16/2	75/9	99/11
Cape fox/bat-eared fox	26/2	161/5	225/8	419/13	1512/52	2156/67
Lycaon pictus, Cape hunting dog	5/1	—	13/2	25/4	88/11	126/16
Mellivora capensis, honey badger	—	1/1	1/1	8/3	18/4	27/4
Aonyx capensis, clawless otter	—	—	4/2	6/2	35/5	45/8
Genetta sp., genet	—	—	1/1	2/1	4/1	7/2
Atilax paludinosus, water mongoose	—	—	—	—	5/1	5/1
Herpestes ichneumon, Egyptian mongoose	—	5/2	—	—	1/1	1/1
Cynictis penicillata, yellow mongoose	3/1	2/1	12/2	19/2	52/3	83/5
Suricata suricatta, suricate	—	—	—	1/1	—	1/1
Crocuta crocuta, spotted hyena	—	2/1	11/2	29/4	128/13	168/19
Hyaena brunnea, brown hyena	3/1	35/5	58/8	151/11	492/41	701/54
Brown hyena/spotted hyena	4/1	41/6	83/9	214/13	737/47	1034/58
Felis libyca, wildcat	2/2	4/4	9/3	18/4	60/10	87/14
Felis nigripes, black-footed cat	—	1/1	1/1	—	1/1	1/1
Wildcat/black-footed cat	3/2	15/4	42/3	47/4	106/10	195/14
Felis caracal, caracal	1/1	4/1	16/1	86/4	278/8	380/12
Panthera leo, lion	—	—	8/1	15/2	62/4	85/5
Panthera pardus, leopard	—	3/2	6/2	14/2	45/7	65/11
Acinonyx jubatus, cheetah	—	—	1/1	1/1	1/1	3/2
Leopard/cheetah	—	3/2	14/3	27/2	65/7	106/12
Orycteropus after, aardvark	—	1/1	10/3	3/1	5/1	18/3
Procavia capensis, rock hyrax	37/2	121/8	44/6	65/11	120/17	229/32
Equus burchelli, Burchell's zebra	13/2	37/3	163/12	389/14	1341/44	1893/62
Equus capensis, "Cape zebra"	—	—	16/2	41/4	169/9	226/12
Diceros bicornis, black rhinoceros	—	—	2/1	5/2	14/3	21/3
Hippopotamus amphibius, hippo	—	—	—	1/1	4/1	5/1
Phacochoerus aethiopicus, warthog	6/2	21/5	31/5	37/5	115/14	183/23
Giraffa camelopardalis, giraffe	—	—	—	—	1/1	1/1
Taurotragus oryx, eland	—	3/2	2/2	6/1	20/2	20/4
Tragelaphus strepsiceros, greater kudu	—	2/1	9/3	8/3	26/5	43/9
Hippotragus sp. indet., roan or sable antelope	—	3/1	22/7	36/5	51/7	109/13
Kobus leche, lechwe	—	—	10/2	29/4	90/9	129/12
Redunca fulvorufula, mountain reedbuck	15/2	29/6	57/9	109/13	402/44	568/60
Pelea capreolus, vaalribbok	3/2	14/3	17/3	73/10	221/20	316/30
Connochaetes gnou and/or *Alcelaphus buselaphus*, black wildebeest/red hartebeest	12/2	21/4	101/12	209/16	698/64	1008/79
Megalotragus priscus, "giant hartebeest"	—	—	1/1	9/2	18/6	28/8
Damaliscus dorcas, blesbok	6/1	7/2	50/6	240/18	824/69	1121/88
Connochaetes taurinus, blue wildebeest	—	4/2	11/3	44/7	125/16	180/19