

Indications of habitat association of *Australopithecus robustus* in the Bloubank Valley, South Africa

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ABSTRACT

Establishing the habitat preferences of early hominin taxa is a necessary, though difficult, requirement for understanding the interaction between environmental change and hominin evolution. The environments typically associated with *Australopithecus robustus* have been reconstructed as predominantly open grasslands situated within a habitat mosaic that included a more wooded component with a nearby perennial water source. Most studies have concluded that the open grassland component represents the habitat preference of the hominins. In this study we investigate indicators of habitat association of *A. robustus* that are preserved in the animal paleocommunities represented in a series of fossil cave infills in the Bloubank Valley of South Africa, including Swartkrans, Sterkfontein, Kromdraai, and Coopers. Testing for conditions of isotaphonomy reveals a potential bias relating to depositional matrix and perhaps accumulating agent, though such a bias has not unduly influenced the taxonomic composition the assemblages. Correspondence analysis of census data from modern African nature reserves demonstrates that carnivore predation patterns are indicative of animal communities, which in turn are representative of habitats. As a result, modern census data are used to document patterns of habitat preference of large herbivores, thus allowing assignment of fossil taxa to a series of broadly defined habitat categories. Correspondence analysis of fossil assemblages reveals that the abundance profile of *A. robustus* is most similar to that of woodland-adapted taxa. In addition, fluctuations in the relative abundance of taxa assigned to the broad habitat categories reveal a significant negative correlation between *A. robustus* and open grassland-adapted taxa, indicating that the more grassland-adapted taxa there are in a given assemblage, the fewer hominins there tend to be. Thus, it appears that the open grasslands that comprise the majority of the paleoenvironments associated with *A. robustus* do not necessarily indicate the habitat preference of the hominins. Rather, it would appear that in addition to being dietary generalists, *A. robustus* were also likely to have been habitat generalists.

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Introduction

The dolomitic cave infills of the former Transvaal in South Africa have long been known as significant hominin fossil repositories. Apart from Taung in the North West Province and Makapansgat in the Northern Province, all of the early hominin-bearing caves are located in or near the Bloubank Valley, Krugersdorp District, Gauteng Province (approx. 26°00'S, 27°45'E). Vegetation in the Bloubank Valley is a type of false grassveld known as the central variation of the Bankenveld (Acocks, 1988: 113). A false grassveld is a relatively open grassland with summer rains averaging approximately 750 mm and frosty winters that result in particularly sour,

wiry grasses that become relatively unpalatable in winter. Trees are mainly restricted to river courses and around the openings of solution cavities and sinkholes. Although the fossil cave infills of the Bloubank Valley area are currently poorly temporally constrained, several deposits have revealed large and well-documented faunal assemblages associated with the hominin taxon *Australopithecus robustus*. To date, *A. robustus* fossils have been recovered from six discrete localities in the Bloubank Valley area, though only four of these localities (Sterkfontein, Kromdraai, Swartkrans, Coopers), comprising eight distinct faunal assemblages, have produced sufficiently large and/or well-documented samples to be included in this analysis (Table 1).

In his initial announcement of *A. robustus*, Broom (1938) concluded that these hominins inhabited an environment much like that of the present Bloubank Valley. He went on to suggest that *A. robustus* lived "...among the rocks and on the plains" (Broom,

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Table 1
Faunal assemblages examined in this study with probable age estimates^a

Site	Member/deposit	Abbreviation used in text	Age estimate
Sterkfontein	Member 5, Oldowan Infill	ST5OL	1.7–2.0
		Kromdraai	
Kromdraai	Kromdraai A	KA	1.5
		Kromdraai B	KB
Swartkrans	Member 1, Lower Bank	SKLB	1.7
		Member 1,	SKHR
	Hanging Remnant		
	Member 2	SKM2	1.5
Coopers	Member 3	SKM3	1.5
		Coopers D	COD

^a Faunal assemblage data for ST5OL from Pickering (1999). See text for derivation of age estimates.

1943: 79), though he later allowed the possibility that the environment might have been somewhat wetter and more vegetated in the past (Broom and Robinson, 1952). Examining the mammalian faunas associated with the Transvaal hominins, Cooke (1952, 1963) agreed that they indicated an environment analogous to that of the area today, supporting Broom's interpretation of the robust australopiths as open plains dwellers. Robinson (1963) speculated that the expansion of open grassland habitats through the Plio-Pleistocene was a significant evolutionary factor propelling many of the adaptive developments seen in the robust australopiths, in particular in relation to alterations in dentition and cognitive capacities.

More recent studies have utilized significantly augmented faunal assemblages from the Bloubank Valley area to reconstruct an environment for *A. robustus* that was predominantly an open to lightly wooded grassland (Vrba, 1975, 1976, 1980, 1985a,b; Brain, 1981a; Brain et al., 1988; Shipman and Harris, 1988; McKee, 1991; Denys, 1992; Avery, 1995, 2001; Watson, 2004), perhaps with a nearby edaphic grassland (Reed, 1997; Reed and Rector, 2006), though one study has suggested a mesic, closed woodland for Member 1 of Swartkrans (Benefit and McCrossin, 1990). Although relatively open grasslands are primarily indicated, several of these studies have concluded that these grasslands were part of a larger habitat mosaic that included a woodland component with a nearby perennial water source (Brain et al., 1988; Avery, 1995; Reed, 1997; Watson, 2004). Given the probable linkage between environmental and evolutionary change in the hominin lineage (Robinson, 1963; Foley, 1987), disentangling which portions of the environmental mosaic can be associated with *A. robustus* is an important albeit difficult endeavor.

Paleoecological analyses of *A. robustus* localities generally operate under the reasonable assumption that the relatively open grassland environments that are typically reconstructed represent the habitat preference of the hominins. However, the close geographical and perhaps temporal proximity of the South African cave infills has caused some to question whether this type of environment really does represent the habitat preference of the hominins (Shipman and Harris, 1988; White, 1988; Wood and Strait, 2004). Nevertheless, the association between *A. robustus* and open grassland habitats remains a persistent component of our current understanding of the paleoecology of this species.

The aim of the present study is to investigate whether any indicators of habitat association of *A. robustus* are preserved in the faunal assemblages of the Bloubank Valley area. Owing to the potentially significant influence of biasing factors, such as accumulating agent and depositional environment, strict taphonomic control is of the utmost importance. Therefore, particular attention is paid to testing for isotaphonomic conditions between the assemblages. In this study we document fluctuations in the abundance of *A. robustus* relative to a series of ecologically sensitive taxa whose habitat preferences are used to model the ecological

composition of *A. robustus*' surrounding animal paleocommunity. Habitat preferences for these fossil taxa are established via comparison with animal communities from a series of modern African nature reserves. Reliance on death assemblages to model once-living animal communities can be problematical, though studies have demonstrated close correspondence between the two (Behrensmeyer et al., 1979; Reed, 1997). In this paper we further investigate the association between modern carnivore assemblages and animal community composition to test whether animals tend to die where they live, and thus whether carnivore-derived assemblages can be used to model animal communities and, in turn, environments.

Materials and methods

Faunal assemblage data were recorded for the *A. robustus*-bearing deposits of Swartkrans Members 1–3 (SKLB, SKHR, SKM2, SKM3), Kromdraai B (KB), Coopers D (COD), and Sterkfontein Member 5-Oldowan Infill (ST5OL). Although no hominins have been recovered from Kromdraai A (KA), for comparative purposes it is included in this analysis as it has produced a large and well-documented faunal assemblage. Kromdraai A and B represent distinct depositional units, probably derived from significantly different time periods. Based on the fauna from Kromdraai A, a date of approximately 1.5 million years of age (Ma) is evident (White and Harris, 1977; Delson, 1984). Using a single magnetic reversal, and assuming a faunal age between 1.5–2.0 Ma, Thackeray et al. (2002) suggest that Kromdraai B is at least 1.9 Ma. The presence of a relatively complete *Hexaprotodon protamphibius* cranium (Vrba, 1981), a taxon which disappears in East Africa by approximately 1.9 Ma, supports such a magnetostratigraphic age. The site of Swartkrans has produced the largest concentration of specimens attributable to *A. robustus*. The geology of the site has been well-documented, and comprises four separate hominin-bearing faunal assemblages extracted from three discrete members (Brain, 2004). The earliest of the Swartkrans deposits is Member 1, which has been divided into two separate subdeposits. The Lower Bank of Member 1 represents the oldest of the Swartkrans assemblages, biostratigraphically dated to approximately 1.7 Ma (de Ruiter, 2003; Brain, 2004). Its companion deposit, the Hanging Remnant, has been biostratigraphically dated to about 1.6 Ma (White and Harris, 1977; Delson, 1984; Vrba, 1985a; de Ruiter, 2003; Brain, 2004), a date that accords well with an ESR estimate of 1.63 Ma (Curnoe et al., 2001). Although ages as young as 1.0 and 0.7 Ma have been proposed for Members 2 and 3 of Swartkrans, respectively (Vrba, 1995), these deposits are more consistent with a date of approximately 1.5 Ma in terms of biostratigraphy (White and Harris, 1977; Delson, 1984; de Ruiter, 2003; Brain, 2004). The Oldowan Infill of Sterkfontein Member 5 has been dated to approximately 1.7–2.0 Ma (Kuman and Clarke, 2000). The abundant suids and bovids derived from Coopers D indicate an age estimate of 1.6–1.9 Ma (Berger et al., 2003), consistent with a recent U-Pb date of approximately 1.62 Ma (Steininger et al., 2008).

We have arranged the fossil deposits into what we consider to be the most probable chronological sequence: KB-ST5OL-COD-SKLB-SKHR-SKM2-SKM3-KA (see Table 1 for abbreviations used in the text). All of these assemblages were examined by us with the exception of ST5OL. This latter deposit was analyzed by Pickering (1999) using data collection techniques consistent with those employed for the current study. Data collection involved a manual overlap approach as recommended by Bunn (1982, 1986) to document both the minimum number of elements (MNE) and the comprehensive minimum number of individuals (cMNI: Pickering, 1999) in each assemblage. Details of the procedure are presented in de Ruiter (2004). In short, the technique involves a specimen-by-specimen comparison of fossils to obtain the most accurate

approximation of the number of skeletal elements and individuals as possible. This is accomplished by laying out all specimens of a particular skeletal element and/or taxonomic group on a large table (or floor), and comparing them individually to determine whether they are likely to have come from a single element or animal. In cases where large numbers of specimens are involved (e.g., bovid dentitions, bovid postcrania) samples were subdivided into nonoverlapping dental wear stage categories or body size groupings before proceeding with specimen-by-specimen comparisons.

Although early collection procedures at Kromdraai were highly selective (Broom, 1951), later excavations (Brain, 1981b; Vrba, 1981; Berger et al., 1994) adopted a complete fossil recovery strategy. The same biased collection procedure is true of early work in the Hanging Remnant of Member 1 and Member 2 of Swartkrans in the late 1940s (Broom, 1951), though complete recovery practices were exercised in subsequent excavations under the direction of C.K. Brain (Brain, 1981b, 2004). In particular, Brain's in situ excavations of uncalcified and decalcified sediments in the Lower Bank of Member 1, Member 2, and Member 3 of Swartkrans were so precise that they allowed a workable GIS to be constructed (Nigro et al., 2003). Excavations at Coopers D (Berger et al., 2003) and in the Oldowan Infill of Member 5 at Sterkfontein (Kuman and Clarke, 2000) have employed total recovery excavation procedures since these respective operations were inaugurated. Such consistent fossil collection procedures minimize the potential influence of different sampling strategies on assemblage composition.

Testing for taphonomic bias

The aim of this study is to investigate the habitat association of *A. robustus* in relation to its surrounding animal paleocommunity. This amounts to examining a biological signal that we assume is reflected in estimates of taxonomic abundance. However, biological responses to differing environmental conditions, as mirrored in taxonomic abundance data, can be masked by taphonomic factors (Badgley, 1986; Bobe et al., 2002). Such factors must be controlled for in any comparative analysis of fossil assemblages if meaningful interpretations are to be drawn. The potential biases introduced as a result of bone accumulating agent and depositional matrix have been well-documented in the South African cave infills (Brain, 1981b). Our approach is to first determine whether there is evidence of taphonomic bias(es), and then assess the potential impact of any recognized taphonomic bias(es) on assemblage composition.

A variety of bone-collecting agents have been implicated in the accumulation of the South African cave infills (Brain, 1981b; Pickering, 1999; de Ruiter and Berger, 2000; de Ruiter, 2004; Newman, 2004; Pickering et al., 2004, 2007). Carnivore prey acquisition tends to be highly selective (Pienaar, 1969; Wilson, 1981; de Ruiter and Berger, 2001), resulting in potentially biased bone accumulations. However, it is likely that the South African assemblages are the result of the combined operation of multiple agents intermittently utilizing the caves over long timespans (Brain, 1980). Bone surface modifications provide direct evidence for the involvement of bone-accumulating agents, including hominins, carnivores, and rodents (Brain, 1981b; Pickering, 2002; Newman, 2004). The presence of culturally modified materials, such as stone and bone tools, can likewise serve as an indication of a hominin accumulating agent. Coprolites can be used to implicate specific donors, typically hyenas (Pickering, 2002). Additionally, the ratio of carnivores to ungulates has been cited as a reliable indicator of carnivore involvement in an accumulation, specifically that of brown hyenas (Brain, 1981b; Cruz-Urbe, 1991; Pickering, 2002).

The relative destruction of bones by carnivores is taxonomically mediated, with accumulators such as hyenas doing more damage to carcasses than collectors such as leopards (Brain, 1981b;

Blumenschine and Marean, 1993). Relative levels of fragmentation are also affected by differences in depositional matrix, which will in turn impact the taxonomic identifiability of fossil materials. In the South African cave infills fossils are derived from three principal depositional matrices. Hard breccia deposits are heavily calcified sediments cemented together into a solid mass, requiring labor intensive manual or chemical preparation (KA, KB, SKHR). Uncalcified sediments are those which were never cemented by calcium carbonate (SKLB). Decalcified sediments are breccia deposits where the cementing calcium carbonate has been leached out by the activities of tree roots, leaving loose soil and fossils behind (SKM2, SKM3, COD, ST5OL). Marean (1991) recommended examining the completeness of ungulate compact bones (carpals, tarsals, lateral malleolus of the fibula) to determine the relative severity of postdepositional fragmentation in faunal assemblages, creating what he termed the completeness index. The procedure involves assigning a completeness value (percentage complete) to ungulate compact bones lacking evidence of bone surface modification, summing these completeness values, and dividing by the NISP of compact bones. Marean (1991) suggested that completeness values be computed per bone and per body size class. However, in several of the South African fossil deposits carpals and tarsals are not common, and division into skeletal element and body size groupings often produced particularly small sample sizes. In order to facilitate comparison of assemblages using a maximum of available fossil material, the completeness index was computed amalgamating all ungulate body sizes and compact bones.

Given the potential for taphonomic biases arising via accumulating agent and depositional matrix, it is of particular importance that we investigate the impact of any taphonomic overprint that might be evident. Skeletal part representation has long been considered to be a useful indicator of potential taphonomic overprinting in faunal assemblages (Voorhies, 1969; Behrensmeier, 1991; Bobe and Eck, 2001; Bobe et al., 2002), as changes in the proportional representation of skeletal elements between deposits would likely signal the existence of a taphonomic bias. We therefore compare the relative abundance of a selection of skeletal elements that span a range of transportability, destructibility, and carnivore attraction in order to test for isotaphonomic conditions across assemblages. The particular skeletal elements examined include cranial, dental, and postcranial remains, incorporating both fore- and hind limb elements. They represent a variety of different shapes and structural densities, and thus include a range of potential taphonomic influences. In order to evaluate the statistical significance of differences in the relative abundance of skeletal elements, 95% confidence intervals were constructed based on the formula:

$$p \pm 1.96 * \text{SQRT}[(p*q)/(n-1)],$$

where p is the proportion of a given skeletal element, q is equal to $1-p$, and n represents the total sample size (Buzas, 1990).

A final test for isotaphonomic conditions utilizes chord distance (CRD), a measure of faunal dissimilarity, to compare the taphonomic and taxonomic composition of the assemblages (Ludwig and Reynolds, 1988; Bobe et al., 2002). Chord distance measures emphasize relative proportions of categories over absolute abundances (Ludwig and Reynolds, 1988), making them particularly useful for comparing assemblages comprised of varying sample sizes. Chord distance values are computed between assemblage j and assemblage k by the formula:

$$\text{CRD}_{jk} = \text{SQRT}[2(1 - \text{ccos}_{jk})]$$

$$\text{with } \text{ccos}_{jk} = \frac{\sum^S (X_{ij} * X_{ik})}{\text{SQRT}[\sum^S X_{ij}^2 \sum^S X_{ik}^2]}$$

where X_{ij} represents the abundance of the i^{th} taxon or skeletal element in the j^{th} assemblage, X_{ik} represents the abundance of the i^{th} taxon or skeletal element in the k^{th} assemblage, and S is the total number of taxa or skeletal elements common to the two assemblages. Chord distance values range from zero for assemblages with

identical composition, to the square root of 2 (≈ 1.414) for assemblages with nothing in common. These values will allow us to explore whether there is any link between taphonomic conditions and taxonomic abundance across assemblages, or if the two factors vary independently.

Taxonomic abundance and faunal change

After controlling for taphonomic factors, taxonomic abundance data are used to test for biological responses of animal paleo-communities to changes in environmental conditions over time in the Bloubank Valley. Several studies have documented the utility of taxonomic abundance data for signaling environmental or climatic changes, as responses of animal communities to external alterations are more likely to be reflected in fluctuations in relative abundance than in speciation or extinction events, in particular at local scales (Bobe and Eck, 2001; Bobe et al., 2002; Alemseged, 2003). While fluctuations in taxonomic abundance in faunal assemblages can elucidate patterns of change in paleoenvironments, this is not to say that taxonomic abundance in a given fossil assemblage reproduces the actual composition of the original paleocommunity. Nonetheless, differences in proportional representation of mammalian taxa can be used to investigate changes in paleocommunity composition over time (Klein, 1980; Bobe and Behrensmeier, 2004).

Sample size varies significantly across the assemblages examined in this study, potentially confounding analyses based on taxonomic abundance (Magurran, 1988; Bobe and Eck, 2001). Rarefaction analysis is a technique for estimating the number of species expected in a given assemblage if all assemblages were of equal size (Magurran, 1988), thereby allowing us to detect the presence of sample size biasing. We test for the relative influence of sample size on animal paleocommunity composition by documenting species richness and species evenness in each of the assemblages. Species richness is a measure of the number of species in an assemblage relative to sample size. For this study we use the Fisher's log series (α) as our measure of species richness; Fisher's log series (α) allows a goodness-of-fit test (χ^2) to determine if there is a significant difference between observed and expected species distributions. Species evenness is a measure of the relative dominance of the most abundant species in an assemblage, since assemblages characterized by one or a few very common animals are differently distributed than assemblages where many species exist in similar abundances. We use the Berger-Parker index as our estimate of species evenness to estimate the impact of variations in abundance within assemblages; Berger-Parker values are typically presented as reciprocal values ($1/d$), such that greater values indicate less dominance of the most common species in an assemblage.

For this study we focus on the predominantly herbivorous taxa from the Bloubank Valley sites, including representatives of the Cercopithecidae, Equidae, Suidae, and Bovidae, in relation to the Hominidae (Table 2). Most of these herbivorous taxa are dependent on the relative distribution of the vegetation that forms the basis of their diet (Jarman, 1974; Skinner and Smithers, 1990; Estes, 1991). The habitat dependence of these various taxa means that they tend to be particularly responsive to fluctuations in vegetational distribution, which in turn are influenced by such climatic factors as temperature and moisture levels. As such, they provide a useful proxy for prevailing environmental conditions, in particular relating to changes in these conditions over time. Because of their higher trophic position, carnivores tend to have wide habitat tolerances (Skinner and Smithers, 1990; Estes, 1991). Owing to this, they are unlikely to aid in resolving habitat structure in the fossil assemblages; therefore, they are excluded from this analysis. Because of the likelihood of differing taphonomic histories, smaller

Table 2

Comprehensive minimum numbers of individuals of mammalian families recovered from the breccia cave infills examined in this study. Taxonomic families in bold are included in this analysis (see text for details)

Taxonomic family	Fossil deposit								Total
	KB	ST5OL	COD	SKLB	SKHR	SKM2	SKM3	KA	
Bovidae	14	33	88	70	182	150	139	149	825
Cercopithecidae	39	8	20	18	70	27	30	28	240
Procaviidae	1	5	6	29	31	19	24	16	131
Hominidae	6	2	2	9	58	8	6	0	91
Equidae	1	3	2	4	8	17	9	31	75
Felidae	4	2	13	8	18	8	9	8	70
Canidae	4	2	7	5	7	14	15	12	66
Hyaenidae	4	1	7	4	17	12	9	6	60
Leporidae	2	0	12	10	0	7	9	3	43
Suidae	1	2	10	2	7	8	2	3	35
Viverridae	2	4	7	1	1	6	11	2	34
Hystricidae	0	0	4	2	3	2	3	1	15
Mustelidae	1	0	1	2	0	2	2	0	8
Giraffidae	0	0	2	0	1	2	1	0	6
Pedetidae	0	0	2	2	0	1	1	0	6
Hippopotamidae	1	0	0	1	1	1	1	0	5
Elephantidae	0	0	0	2	1	0	1	0	4
Orycteropodidae	0	0	0	1	0	1	1	0	3
Manidae	0	0	0	1	0	0	1	0	2
Total	80	62	183	171	405	285	274	259	1719

mammals, such as the Hyracoidea, Rodentia, and Lagomorpha, are not included. Very rare animals (i.e., those with fewer than eight individuals in the eight combined assemblages) are excluded owing to their rarity: Elephantidae, Giraffidae, Hippopotamidae, Orycteropodidae, and Manidae. A total of 24,211 specimens were identified to skeletal part and taxonomic family, representing a minimum of 1,266 individuals animals included in the subset of materials analyzed in this study. These combined individuals represent approximately 74% of the 1,719 macromammals recorded in the respective assemblages (Table 2), thus encompassing the majority of available faunal information.

Animal census data from a series of 33 African nature reserves are utilized to document the habitat preferences of modern herbivores (Table 3). Species are grouped into genera for the primates, equids, and suids, and into tribes for the bovids. Census data are taken from original published reports wherever possible, and represent as accurate a compendium of animal abundance information as is possible for the reserves included. We conducted a correspondence analysis to examine the association between taxa and habitats in the modern nature reserves to document the relationship between taxonomic abundance and habitat preference. Correspondence analysis is a visual ordination technique designed to graphically display relationships between variables. Utilizing data arranged in bivariate contingency tables, correspondence analysis visually displays clusters of points representing similar, closely related variables, while dissimilar variables appear farther apart from each other (Greenacre and Vrba, 1984; Greenacre, 2007). For instance, when applied to animal communities or faunal assemblages, taxa are grouped with the localities in which they are well-represented, while at the same time each locality is grouped with the taxa which are prominent in it. The resulting clusters of similar variables are interpreted by examining their spread across each axis in search of the underlying features that unite them.

Employing a taxonomic uniformitarian argument, fossil relatives of modern taxa are assumed to have similar habitat preferences as their modern counterparts as determined via correspondence analysis. Isotopic (Sponheimer, 1999; Sponheimer et al., 1999, 2003; Luyt, 2001; Harris and Cerling, 2002), dental microwear (El-Zaatar et al., 2005), and ecological functional morphological (Reed, 1997; Sponheimer et al., 1999) evidence is used to test this assumption. For instance, specimens of *Metridiochoerus*

Table 3

Census data for modern African game parks and modern carnivore kill data

Country	Game Park	<i>Papio</i>	<i>Chlorocebus</i>	<i>Equus</i>	<i>Phacochoerus</i>	<i>Potamochoerus</i>	Alcelaphini	Antilopini	Aepycerotini	Tragelaphini	Reduncini	Bovini	Hippotragini	Neotragini	Cephalophini	Source
Benin	Pendjari	4,000	500	0	5,000	0	4,224	0	0	100	13,281	5,815	2,325	0	4,633	Milligan et al., 1982; Sayer and Green, 1984
Botswana	Chobe	331	0	2,121	170	0	854	0	868	320	539	3,773	1,185	1,135	0	Kabajja, 2005
Botswana	Makgadikgadi	0	0	15,640	0	0	3,155	4,668	296	592	0	0	0	477	0	Kabajja, 2005
Botswana	Kgalagadi	0	0	0	0	0	8,102	4,814	0	15,487	0	0	0	6,382	1,678	Kabajja, 2005
Botswana	Moremi	2,205	0	1,674	1,542	0	4,343	0	18,615	1,111	12,332	40,160	232	43	0	Kabajja, 2005
Burkina Faso	Arli	1,890	100	0	2,960	0	1,916	0	0	800	8,500	650	1,920	0	2,240	Green, 1979
Burkina Faso	Deux Bale	0	0	0	74	0	453	0	0	198	227	40	1,200	0	651	Milligan et al., 1982
Burkina Faso	Po	0	0	0	187	0	543	0	0	108	290	248	777	0	482	Milligan et al., 1982
Cameroon	Waza	0	0	0	200	0	605	10	0	0	13,277	0	223	0	0	Esser and Van Lavieren, 1979
Cameroon	Bouba Ndjida	1,500	250	0	2,196	0	6,988	0	0	1,100	7,046	2,000	4,356	0	5,400	Van Lavieren and Bosch, 1977; Van Lavieren and Esser, 1979
Central African Republic	Saint-Floris	0	0	0	50	0	3,022	0	0	0	3,224	1,813	504	0	0	Milligan et al., 1982
Democratic Republic Congo	Virunga	0	0	0	603	35	1,199	0	0	53	5,797	7,402	0	0	1	Bourlière, 1963
Ethiopia	Omo	0	0	983	8	0	2,093	646	0	950	0	404	0	0	3	Baba et al., 1982
Gabon	SW Gabon	0	70	0	0	5020	0	0	0	1,820	420	3,570	0	0	3,710	Prins and Reitsma, 1989
Ivory Coast	Comoe	3,000	2,000	0	0	1500	8,000	0	0	1,000	7,510	450	1,000	0	13,000	Geerling and Bokdam, 1973
Kenya	Lake Nakuru	50	25	0	20	0	0	250	260	22	1,135	27	0	12	3	Kutilek, 1974
Kenya	Masai Mara	0	0	12,000	1,000	0	20,000	12,500	5,000	650	750	4,000	0	200	50	Darling, 1960
Kenya	Nairobi	165	22	1,929	230	0	3,977	690	655	91	143	0	0	4	2	Bourlière, 1963; Foster and Kearney, 1966; Foster and Coe, 1968
Namibia	Tsumeb	1,500	50	106	1,984	0	3,738	293	271	6,313	0	0	0	400	280	Joubert and Mostert, 1975
Namibia	Etosha	0	0	14,000	1,500	0	4,600	12,000	0	2,500	0	0	296	500	250	Joubert and Mostert, 1975; Greenacre and Vrba, 1984
Niger	W	0	0	0	2,130	0	1,440	0	0	240	6,120	4,140	2,850	0	0	Milligan et al., 1982
Nigeria	Kainji	0	0	0	1,200	0	2,500	0	0	950	4,800	275	2,200	0	1,525	Ayeni, 1980; Milligan et al., 1982
Nigeria	Yankari	171	14	0	113	0	74	0	0	6	175	37	67	0	3	Afolayan and Ajayi, 1980; Milligan et al., 1982
South Africa	iMfolozi	4,202	140	1,426	5,521	0	4,307	0	4,894	16,447	3,927	3,195	0	937	715	Mentis, 1970; Taylor, 1998
South Africa	Kruger	10,000	5,000	14,400	5,000	500	13,750	0	153,000	8,395	5,335	10,614	1,587	5,500	1,300	Pienaar et al., 1966; Pienaar, 1969; Schaller, 1972; Greenacre and Vrba, 1984
South Africa	Mkuzi	500	50	0	0	0	1,397	0	9,394	533	69	0	0	6	4	Greenacre and Vrba, 1984
South Africa	Timbavati	500	0	980	287	0	3,044	0	8,569	821	302	0	0	0	0	Hirst, 1969
Tanzania	Tarangire	0	0	2,500	400	20	1,600	300	3,100	530	270	1,400	10	280	0	Lamprey, 1962

(continued on next page)

Table 3 (continued)

Country	Game Park	<i>Papio</i>	<i>Chlorocebus</i>	<i>Equus</i>	<i>Phacochoerus</i>	<i>Potamochoerus</i>	Alcelaphini	Antilopini	Aepycerotini	Tragelaphini	Reduncini	Bovini	Hippotragini	Neotragini	Cephalophini	Source
Tanzania	Lake Manyara	500	0	255	95	0	675	0	150	50	37	2,097	0	0	0	Mwayalosi, 1977;
Tanzania	Ngorongoro	400	200	4,500	0	0	16,635	5,235	0	214	120	661	0	0	0	Prins and Douglas-Hamilton, 1990
Tanzania	Serengeti	8,700	5,000	280,000	17,000	0	455,000	190,000	65,000	9,500	5,500	50,000	5,000	0	0	Kruuk, 1972;
Zambia	Kafue Flats	0	0	1,200	0	50	3,000	0	0	213	37,620	250	250	0	0	Schaller, 1972;
Zimbabwe	Hwange	1,000	0	1,900	400	0	2,630	0	8,000	5,450	1,250	13,000	2,500	3,000	2,000	Estes and Small, 1981
																Kruuk, 1972;
																Schaller, 1972;
																Greenacre and Vrba, 1984; Sinclair and Arcese, 1995
																Sheppe and Osborne, 1971
																Dasmann and Mossman, 1962;
																Greenacre and Vrba, 1984
Modern bone-accumulating agent data																
Nossob	porcupine den	0	0	0	0	0	14	40	0	0	0	0	0	5	2	Brain, 1981b
Makgadikgadi	brown hyena den	0	0	12	0	0	7	5	0	0	0	0	0	2	1	Lacruz and Maude, 2005
Kruger	spotted hyena den	0	0	27	4	1	18	0	111	24	1	28	0	1	0	Skinner et al., 1986
Kruger	spotted hyena kills	0	0	1	1	0	21	0	110	24	25	2	0	1	0	Pienaar, 1969
Kruger	brown hyena kills	7	0	8	1	0	7	0	49	80	46	2	4	0	1	Pienaar, 1969
Kruger	leopard kills	11	0	8	12	11	9	0	789	40	39	3	0	22	14	Pienaar, 1969
Londolozi (Kruger)	leopard kills	2	7	0	5	0	0	0	77	9	1	0	0	2	17	Le Roux and Skinner, 1989
Tai Forest	leopard kills	0	9	0	0	2	0	0	0	0	0	0	0	0	82	Zuberbuhler and Jenny, 2002
Ngorongoro	spotted hyena kills	0	0	54	0	0	206	21	0	0	0	1	0	0	0	Kruuk, 1972
Serengeti	leopard kills	1	0	1	0	0	17	114	0	2	20	0	0	0	0	Schaller, 1972
Serengeti	hyaena kills	0	0	68	4	0	169	157	1	2	1	3	0	0	0	Kruuk, 1972

exhibit isotope values indicating significant C₄ resources in its diet (Harris and Cerling, 2002), similar to modern *Phacochoerus*. As a result, *Metridiochoerus* is assigned to a grassland category (ecological assignments detailed below). In cases where modern census data are unavailable, we again assume a taxonomic uniformitarian argument. For instance, gelada baboons are unknown in any of the modern nature reserves included in this study. However, the dietary preference of the extinct taxon *Theropithecus oswaldi* indicates a predominantly grassland-based diet, similar to modern *Theropithecus* (Lee-Thorp et al., 1989). In this case, *Theropithecus*, like its living descendants, is assigned to the grassland category.

Modern carnivore predation patterns are examined in order to test the association between animal communities and death assemblages. Data on bone accumulations of modern carnivores are limited, and most published reports are derived from areas exhibiting considerable human disturbance. We therefore rely on two carnivore lairs located in areas evincing minimal human disturbance to investigate whether death assemblages mirror the habitats from which they are recovered (Table 3). We also examine the composition of a modern porcupine den, as these rodents are known to be proficient bone accumulators (Brain, 1981b). In addition, modern leopard and hyena kill data from the Serengeti, Ngorongoro, Kruger, and Taï Forest national parks are examined to test if carnivore predation patterns are reflective of the animal communities from which they are drawn. Although these modern carnivore predation patterns do not represent discrete faunal assemblages, the resultant skeletal remains can nonetheless provide us with valuable ecological information (e.g., Behrensmeyer et al., 1979).

The habitat preferences of the modern herbivores are used to assign the select fossil taxa (minus the hominins) from the Bloubank Valley sites to a series of broadly defined habitat categories in order to investigate the ecological composition of the faunal assemblages. Fluctuations in the relative abundance of *A. robustus* are investigated to document the correlation between numbers of hominins and numbers of animals assigned to habitat categories. The intent is not to search for any temporal patterning across assemblages, but rather to investigate whether there is a consistent relationship between *A. robustus* and any particular habitat category.

Results

Taphonomic conditions

In order to search for evidence relating to particular accumulating agents, details of a series of taphonomic indicators are presented in Table 4. The total NISP presented in Table 4 relates only

to those specimens that are identifiable to skeletal part and taxonomic family. Hominin produced damage is rare; the large number of hominin modified materials in SKM3 includes 270 bone fragments bearing evidence of burning (Brain and Sillen, 1988). The stone tools found in all of the deposits are indicative of hominin activity, though it is not possible to determine whether these materials were deposited within the cave itself or in the catchment area immediately surrounding the cave (Butzer, 1984; Pickering, 1999). Carnivore damage is evident in all deposits, though such indications are infrequent (typically less than 5% of the respective assemblages). Rodent gnawed bones, although rare, also reveal some level of contribution from these bone collectors. Coprolites are present in several of the assemblages, indicating that carnivores (probably hyenas) were active in the immediate vicinity of the caves. The carnivore to ungulate ratio also indicates that carnivores were involved in the accumulations, pointing to hyenas as accumulators of at least some portion of the material.

When completeness index values are computed as a measure of fragmentation (Table 5), there is no appreciable difference between decalcified and uncalcified sediments in terms of bone destruction. As a result, for this study they are considered together as a unit. A *t*-test ($t = 3.25$, $p = 0.02$, $df = 5$) reveals a significant difference in the levels of fragmentation between hard breccia and uncalcified/decalcified breccia. It appears that hard breccia-derived fossils tend to be less fragmented than uncalcified/decalcified breccia-derived fossils. These differing levels of fragmentation are likely to influence the relative identifiability of fossil remains.

Skeletal element abundance data are presented in Table 6, and Fig. 1 illustrates the relative abundance of these skeletal elements across the faunal assemblages. Because of the likelihood of differing taphonomic histories for very small animals, only data from body size class II, III, and IV individuals (based on Brain, 1981b) are included. Although not strongly indicated, the pattern that emerges from the skeletal part distributions confirms some level of bias relating to depositional matrix. In broad terms, hard breccia-derived assemblages, in particular SKHR, tend to have too many craniodental remains and too few postcranial remains relative to the uncalcified/decalcified assemblages. Since taxonomic identification depends on fossil preservation and extraction, in particular of the more diagnostic craniodental elements, this difference represents a potentially important taphonomic bias. Isolated teeth show a relatively even distribution across the assemblages ($\chi^2 = 5.99$, $p = 0.54$), while all other elements display relatively uneven distributions. Since isolated teeth account for the bulk of the faunal material in each assemblage, thus forming the basis of most taxonomic identifications, their relatively even distribution might mitigate the potential taphonomic bias relating to depositional matrix. Nonetheless, it is apparent that depositional matrix

Table 4
Taphonomic indicators diagnostic of bone accumulating agents^a

	Fossil deposit							
	KB	ST5OL	COD	SKLB	SKHR	SKM2	SKM3	KA
Stone tools	4	483	50	62	1	132	73	45
Hominin-modified bone	0	1 (0.03)	0	13 (0.22)	0	31 (0.37)	375 (5.96)	0
Carnivore-modified bone	14 (0.28)	174 (4.66)	121 (1.59)	131 (2.17)	45 (0.47)	72 (0.86)	197 (3.13)	36 (1.95)
Rodent-gnawed bone	1 (0.02)	6 (0.16)	13 (0.17)	22 (0.36)	6 (0.06)	24 (0.29)	41 (0.65)	5 (0.27)
Coprolites	4 (0.08)	0	2 (0.03)	59 (0.98)	0	8 (0.10)	0	6 (0.32)
Carnivore:carnivore+ungulate ratio	0.49	0.19	0.26	0.21	0.18	0.20	0.23	0.13
Total NISP (identifiable specimens)	4985	3731	7574	6040	9583	8416	6293	1847

^a The stone tool category excludes debitage and naturally occurring stone. Hominin modified bone includes cut- and hammerstone percussion-marked bones and bones with probable traces of burning, regardless of the potential author(s) of these traces. Numbers in parentheses indicate percentage of total NISP of taxonomically identifiable fossils recovered from each deposit. Carnivore-modified bone includes bones with tooth markings and with evidence of gastric etching. Carnivore coprolites are considered to be highly diagnostic of hyena activity (Pickering, 2002). A carnivore:carnivore+ungulate ratio of 0.20 or greater is generally considered to be indicative of carnivore, probably hyena, activity (Cruz-Uribe, 1991; Pickering, 2002), though lower values do not necessarily exclude hyenas as accumulating agents (Lacruz and Maude, 2005). Data on hominin modified bones for ST5OL from Pickering (1999) and for SKLB, SKM2 and SKM3 from Pickering et al. (2007).

Table 5
Depositional matrix and associated completeness index values (based on Marean, 1991) for the assemblages included in this study^a

Deposit	Breccia type	Completeness index
KA	hard	0.81
KB	hard	0.78
SKHR	hard	0.82
SKLB	uncalcified	0.72
SKM2	decalcified	0.76
SKM3	decalcified	0.65
ST5OL	decalcified	nd
COD	decalcified	0.71

^a Completeness index computed by assigning percentage completeness values to ungulate compact bones, and dividing the summed completeness value by the total NISP of compact bones in an assemblage.

presents a potentially significant bias; therefore, it is necessary to test whether there is any linkage between taphonomic conditions and taxonomic identification.

In order to test for the impact of taphonomic bias(es) introduced as a result of accumulating agent and/or depositional matrix, chord distances were computed for pairs of assemblages using taxonomic abundance (Table 7) and skeletal element abundance data (Table 6) from the Bloubaank Valley assemblages; chord distance values are presented in the bottom rows of these respective tables. In addition, because of the current uncertainty over age estimates in the South African cave infills, we have produced a matrix of chord distances (Table 8) that can be consulted should there be a significant change in the age assessment of any particular site. However, we would note that current efforts at dating the robust australopith sites using radiogenic isotopes do not contradict the arrangement of the deposits as listed in this study (e.g., Steininger et al., 2008). Because isolated teeth represent such a preponderance of skeletal elements, the possibility exists that they are masking more subtle taphonomic signals in the skeletal part data. We therefore compute chord distance values between pairs of assemblages both with and without isolated teeth included as a category. Removing the isolated teeth from consideration results in greater chord distance differences between assemblages, particularly for SKHR and KA (Fig. 2). Both of these assemblages were recovered exclusively from a hard breccia matrix, likely influencing their respective taphonomic compositions. However, when we correlate the taphonomic chord distances with isolated teeth against the chord distances without isolated teeth, we see that there is a strong, significant correlation between them (Spearman's $r_s = 0.96$, $p = 0.00$). In other words, although the removal of isolated teeth results in greater apparent taphonomic dissimilarity, the relative ranking of the assemblages remains effectively unchanged, indicating a broadly commensurate level of change across all the assemblages.

Table 6
Abundance of a selection of skeletal elements (MNE) for body size II, III, and IV individuals in each of the faunal assemblages (body size categories based on Brain, 1981b)^a

	Fossil deposit								Total
	KB	ST5OL	COD	SKLB	SKHR	SKM2	SKM3	KA	
Maxilla	7	0	17	10	172	14	23	65	308
Mandible	23	11	50	28	261	31	92	137	633
Isolated teeth	176	265	425	389	657	279	700	524	3415
Humerus	12	25	39	41	37	44	87	30	315
Radius	17	21	34	23	26	22	58	16	217
Metacarpal	16	23	47	23	27	24	55	13	228
Femur	10	12	34	15	36	12	27	33	179
Tibia	10	17	31	20	25	15	43	12	173
Metatarsal	21	20	54	42	27	17	99	17	297
Astragalus	10	24	44	45	33	24	50	15	245
Chord distance (teeth included)		0.114	0.105	0.087	0.381	0.344	0.090	0.217	
Chord distance (teeth excluded)		0.470	0.332	0.284	0.967	0.836	0.340	0.766	

^a Chord distance values presented in the last two rows are computed for assemblages with isolated teeth included in the analysis and isolated teeth excluded (see text for details). Chord distance values are calculated between pairs of sites and are listed for the site at the head of the column and the site in the column to the left.

Taxonomic chord distances demonstrate that faunal turnover between assemblages was considerable, with a peak reached between KB and ST5OL, two assemblages with little in common in terms of relative faunal representation (Fig. 2). In spite of this marked taxonomic difference, there is little difference in taphonomic conditions between KB and ST5OL, in particular when isolated teeth are included in the chord distance computation. At the same time, the greatest taphonomic chord distance is seen between SKLB and SKHR, though the taxonomic chord distance between these assemblages is relatively low; both are derived from Member 1 of Swartkrans, representing uncalcified and hard breccia deposits, respectively. It would thus appear that the difference in taphonomic chord distance values can be attributed to depositional matrix. There is no correlation between taxonomic chord distances and taphonomic chord distances either with (Spearman's $r_s = 0.29$, $p = 0.54$) or without (Spearman's $r_s = 0.11$, $p = 0.82$) isolated teeth included, confirming that taphonomic and taxonomic chord distance values are not linked. In other words, taxonomic and taphonomic chord distance values vary independently. These data demonstrate that although a taphonomic bias likely exists relating to depositional matrix and perhaps bone accumulating agent, such biasing has not consistently influenced the taxonomic composition of the assemblages in any particular direction. In the absence of a consistent taphonomic bias, we conclude that taxonomic abundance data from the assemblages represent reasonable reflections of original animal paleocommunity composition and, therefore, fluctuations in taxonomic abundance across the assemblages can be interpreted as animal community responses to changing environmental conditions.

Taxonomic and ecological composition

Sample size can have an impact on estimates of taxonomic abundance, and in the case of the assemblages examined in this study there is a significant correlation between cMNI and the number of species counted in an assemblage (Spearman's $r_s = 0.78$, $p = 0.02$; data from Table 9). Rarefaction analysis generates a series of curves for the respective assemblages if they are artificially reduced (rarefied) in size to that of the smallest assemblage. In this case, all of the assemblages are rarefied to the size of ST5OL at 48 individuals, resulting in plots comprised of predicted numbers of species relative to the numbers of individuals counted in each assemblage (Fig. 3). The largest assemblage, SKHR, plots close to the majority with an estimated 14 species when it is reduced to 48 individuals. The two smallest assemblages, ST5OL and KB, appear to have fewer recognized species than the majority of the assemblages, while SKM2, the second largest assemblage, includes more species than might be expected. Although these latter sites do

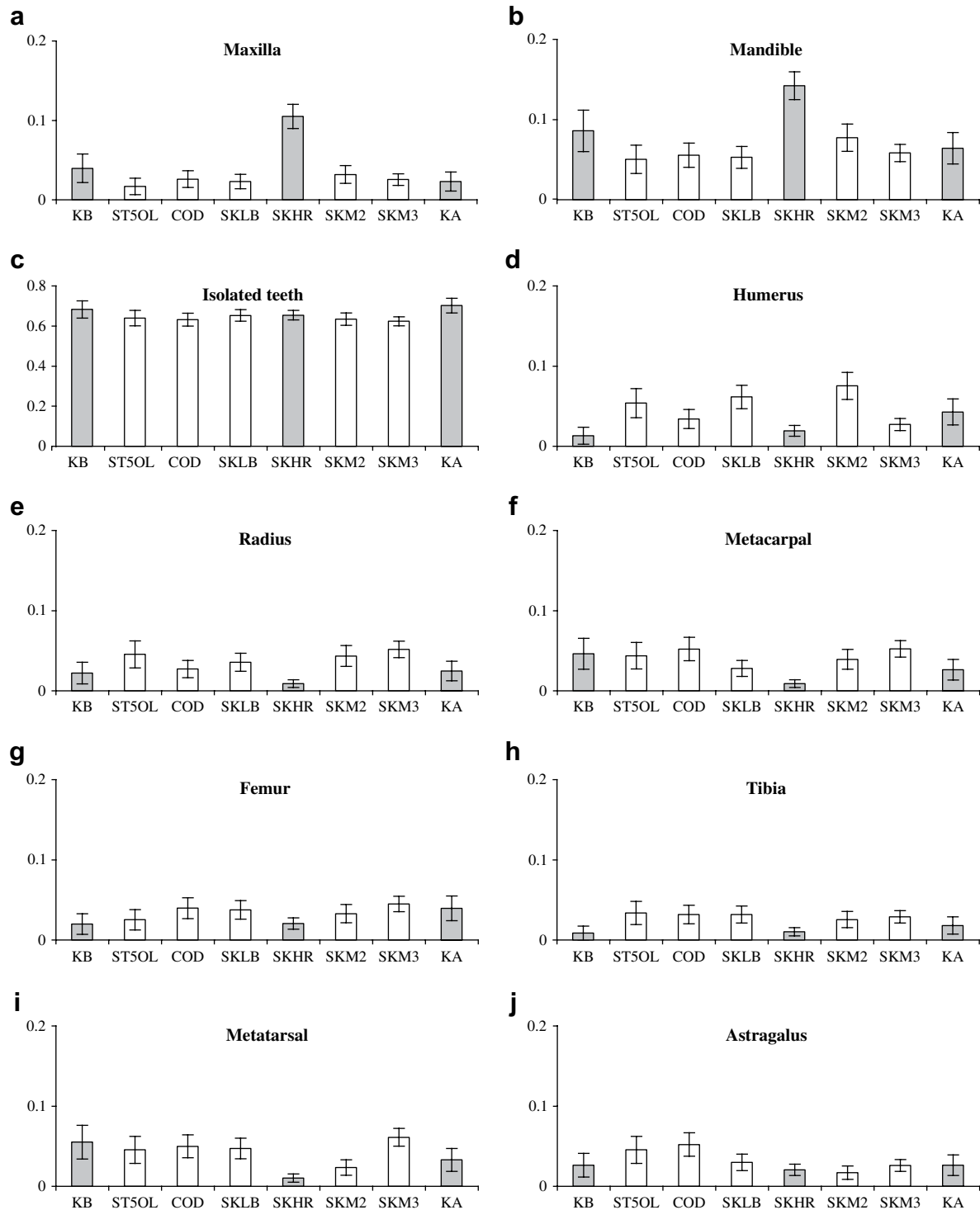


Fig. 1. Relative abundances of a selection of skeletal elements for body size II, III, and IV individuals in each of the assemblages. Values are calculated from MNE data in Table 6. Binomial error bars indicate 95% confidence intervals. Shaded boxes denote hard breccia assemblages; unshaded boxes denote uncalcified/decalcified assemblages.

separate out from the majority of the assemblages, the difference is not large; therefore, it is unclear how great an impact sample size might have on the taxonomic composition of the assemblage. Notwithstanding, because sample size appears to be linked to the number of species identified, it is necessary to examine the influence of sample size on the ecological composition of the assemblages.

Species diversity indices allow us to document the ecological composition of assemblages (Ludwig and Reynolds, 1988;

Magurran, 1988), to test whether these assemblages are reasonable reflections of coherent animal communities. To investigate species richness we use Fisher's log series (α); values are presented in Table 9. There is no significant correlation between cMNI and Fisher's log series (α ; Spearman's $r_s = 0.19$, $p = 0.65$), suggesting that larger sample sizes do not necessarily result in significantly richer (i.e., more speciose) faunal assemblages. Turning to the goodness of fit test (χ^2) for the Fisher's log series (α), none of the assemblages shows an observed distribution that significantly

Table 7
Comprehensive minimum numbers of individuals (cMNI) of the select mammalian taxa from the Bloubank Valley cave infills with reconstructed habitat associations^a

	Fossil deposit								Associated habitat
	KB	ST5OL	COD	SKLB	SKHR	SKM2	SKM3	KA	
<i>Australopithecus robustus</i>	6	2	2	9	58	8	6	0	–
<i>Papio hamadryas robinsoni</i>	18	0	12	12	30	20	23	1	woodland
<i>Papio angusticeps</i>	14	0	0	0	0	0	0	15	woodland
<i>Papio (Dinopithecus) ingens</i>	0	0	0	1	17	1	0	0	woodland
<i>Gorgopithecus major</i>	2	0	0	0	0	0	0	10	woodland
<i>Theropithecus oswaldi</i>	0	1	8	4	16	2	7	0	grassland
Small papionin	0	7	0	0	7	0	0	2	woodland
<i>Cercopithecoides williamsi</i>	5	0	0	1	0	4	0	0	woodland
<i>Equus burchelli</i>	1	3	1	0	0	9	1	7	grassland
<i>Equus capensis</i>	0	0	1	3	6	7	7	23	grassland
<i>Eurygnathohippus lybicum</i>	0	0	0	1	2	1	1	1	grassland
<i>Phacochoerus</i> sp.	1	0	0	1	0	7	1	1	grassland
<i>Metridiochoerus andrewsi</i>	0	2	10	1	7	1	1	2	grassland
<i>Megalotragus</i> sp.	0	0	3	3	7	4	4	4	grassland
<i>Connochaetes cf. taurinus</i>	5	1	15	23	48	19	33	13	grassland
Medium-sized alcelaphine	0	6	18	11	37	24	19	28	grassland
<i>Damaliscus</i> sp.	0	18	7	7	20	29	17	56	grassland
<i>Antidorcas marsupialis</i>	0	3	18	13	0	19	28	0	grassland
<i>Antidorcas recki</i>	3	0	12	0	12	3	5	18	grassland
<i>Antidorcas bondi</i>	2	0	0	3	33	0	0	9	grassland
<i>Gazella</i> sp.	1	0	0	5	7	5	14	0	grassland
<i>Oreotragus oreotragus</i>	0	1	0	1	1	3	1	0	woodland
<i>Raphicerus campestris</i>	0	2	2	1	1	7	4	1	woodland
<i>Ourebia ourebi</i>	0	0	0	0	0	3	0	0	closed/wet
<i>Syncerus</i> sp.	1	0	0	2	2	2	3	3	woodland
<i>Simatherium kohllarseni</i>	0	0	1	0	0	0	0	0	woodland
<i>Pelorovis</i> sp.	0	0	0	0	0	1	0	0	woodland
<i>Taurotragus oryx</i>	1	2	1	0	0	1	2	3	woodland
<i>Tragelaphus strepsiceros</i>	0	0	3	0	7	6	2	6	woodland
<i>Tragelaphus scriptus</i>	0	0	2	0	0	4	0	1	woodland
<i>Hippotragus</i> sp.	0	0	2	0	3	9	4	2	closed/wet
<i>Kobus cf. leche</i>	0	0	0	0	0	1	1	0	closed/wet
<i>Redunca arundinum</i>	0	0	0	0	1	0	0	1	closed/wet
<i>Redunca fulvorufula</i>	1	0	2	0	0	0	0	0	grassland
<i>Pelea</i> sp.	0	0	2	1	3	10	2	4	grassland
Total	61	48	122	103	325	210	186	211	
Chord distance		1.385	1.066	0.616	0.629	0.832	0.498	0.983	

^a The last row for each column gives the chord distances computed from taxonomic abundance data. Chord distance values are calculated for pairs of sites and are listed for the site at the head of the column and the site in the column to the left. See text for derivation of associated habitats.

varies from expected. Likewise, there is no significant relation between cMNI and the Berger-Parker index (Spearman's $r_s = 0.52$, $p = 0.18$). This latter point suggests that increases in sample size do not necessarily produce faunal assemblages that are more evenly distributed in terms of species dominance. These diversity data combine to demonstrate that although there is a relationship between sample size and the number of species in an assemblage, there is no indication that increasing sample size unduly influences the ecological composition of the assemblages.

Results of a correspondence analysis of the taxonomic abundance of large herbivores from a series of modern African nature reserves are presented in Fig. 4 (data from Table 3). Three distinct clusters representing three habitat types are evident. The first is

a clustering of taxa and parks from closed or wet habitats, including *Potamochoerus*, Cephalophini, Reduncini, and Hippotragini. This cluster groups together animals that require very dense vegetational coverage [*Potamochoerus*, Cephalophini (i.e., tree coverage of greater than 40% of available land surface)] with those requiring somewhat less coverage (Reduncini, Hippotragini) in the form of thick stands of tall grasses and sedges at water's edge. These taxa are all linked by their need for a permanent, ample water supply. For the purpose of this study they are all grouped together into a single habitat category (closed/wet), as they are consistently associated in modern nature reserves (see also Alemseged, 2003). The second clustering represents parks predominated by woodlands that are characterized by tree coverage of 20–40% of available

Table 8
Matrix of chord distances computed between pairs of assemblages for taphonomic (upper right) and taxonomic (lower left) data^a

Deposit	KB	ST5OL	COD	SKLB	SKHR	SKM2	SKM3	KA		
KB	–	0.114	0.064	0.104	0.331	0.112	0.065	0.198	Taphonomic chord distances	
ST5OL	1.385	–	0.105	0.067	0.414	0.105	0.118	0.271		
COD	1.129	1.066	–	0.087	0.350	0.103	0.071	0.227		
SKLB	1.029	1.106	0.616	–	0.381	0.092	0.086	0.245		
SKHR	1.016	1.110	0.866	0.629	–	0.344	0.344	0.171		
SKM2	1.101	0.800	0.639	0.610	0.832	–	0.090	0.214		
SKM3	1.058	1.039	0.521	0.303	0.808	0.498	–	0.217		
Taxonomic chord distances	KA	1.253	0.649	0.993	1.052	1.026	0.755	0.983		–

^a Note: values in bold are those presented in Tables 6 and 7; taphonomic chord distances based on skeletal part data including isolated teeth.

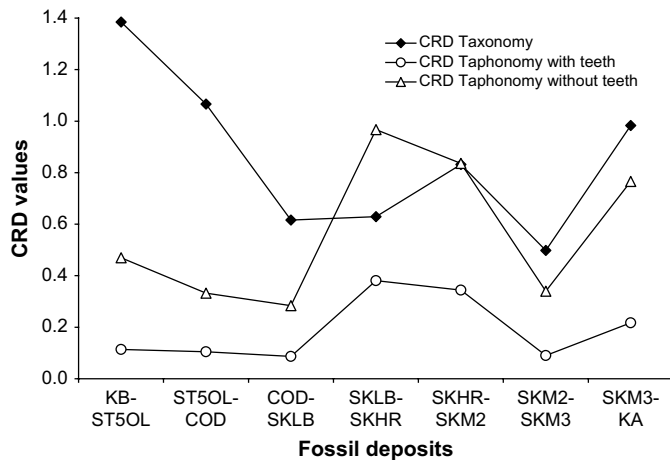


Fig. 2. Plots of chord distances between pairs of assemblages for taphonomic (Table 6) and taxonomic (Table 7) data. Correlation of taphonomic chord distances with and without isolated teeth (Spearman's $r_s = 0.96$, $p = 0.00$) indicates strong similarity between the two sets of data. Correlation of taphonomic and taxonomic chord distances reveals no significant relationship (Spearman's $r_s = 0.29$, $p = 0.54$). The lack of correlation between taphonomic and taxonomic chord distances indicate that fluctuations in taxonomic abundance vary independently of changes in taphonomic conditions.

land surface. This group includes such taxa as *Papio*, *Chlorocebus*, *Phacochoerus*, and the bovid tribes Tragelaphini, Bovini, Neotragini and Aepycerotini. The particularly high numbers of *Aepyceros* in the closely geographically-spaced Kruger, Timbavati, and Mkuzi parks pull them away from the remaining woodland parks, though all three nonetheless represent woodland habitats. The final clustering represents open grassland parks and taxa, typified by relatively sparse tree coverage of less than 20% of available land surface, and ranging from bushy grasslands to open savannas. This grouping includes *Equus*, the Alcelaphini, and the Antilopini. The close clustering evident in this latter group indicates that the abundance profiles of these taxa are notably similar across modern nature reserves.

Data on modern carnivore kill patterns, modern carnivore dens, and the porcupine den from Table 3 are inserted into the correspondence analysis presented in Fig. 4 as supplementary points. This insertion of supplementary points is a standard procedure in correspondence analysis whereby additional row values can be subsequently incorporated to demonstrate where they plot in the computation, but without influencing the outcome of the original analysis. When these supplementary points are added it is apparent that the carnivore predation patterns are strongly indicative of their surrounding habitats, as are the bone accumulations from the two modern lairs. The porcupine den is also strongly representative of its surrounding habitat. In all cases, the environment that would be reconstructed from these modern data corresponds closely with the actual environmental setting. As a result, we conclude that carnivore kill data are representative of the taxonomic composition

Table 9
Measures of species richness and species diversity^a

	Fossil deposit							
	KB	ST5OL	COD	SKLB	SKHR	SKM2	SKM3	KA
cMNI	61	48	122	103	325	210	186	211
# species	14	12	20	20	22	29	24	23
Fishers log series (α)	5.69	5.14	6.80	7.40	5.33	9.12	7.34	6.57
χ^2 value	4.17	4.23	2.72	3.82	4.35	2.79	5.71	3.82
p-value	0.38	0.38	0.61	0.43	0.50	0.59	0.34	0.56
Berger-Parker index	3.39	2.67	6.78	4.48	5.60	7.24	5.64	3.77

^a The Fisher's log series (α) computation allows for a goodness of fit test; χ^2 and probability values are presented with the α values.

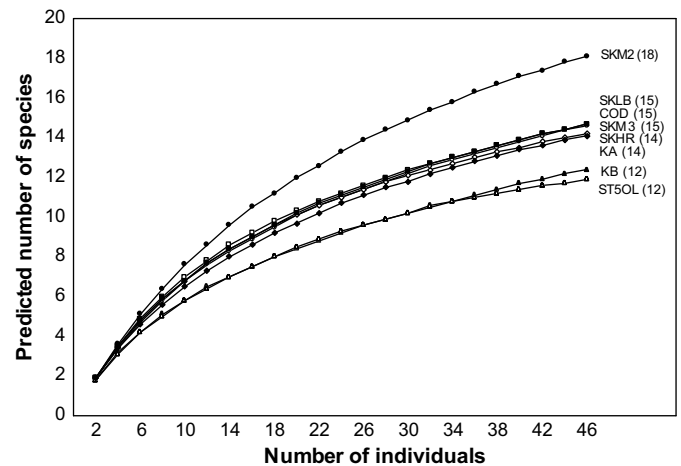


Fig. 3. Rarefaction curves computed for the assemblages examined in this study. Rarefaction analysis predicts the number of species that might be present if sample sizes of all assemblages are artificially standardized to that of the smallest assemblage (ST5OL). KB and ST5OL have relatively smaller assemblages, and SKM2 has a relatively larger assemblage, compared to the remaining deposits. Values in parentheses after site names indicate the predicted number of species per assemblage.

of the surrounding animal communities, and that these data can be used to reconstruct habitats at this scale of analysis.

Taxonomic abundance data for the select large mammals from the Bloubaank Valley fossil assemblages are presented in Table 7. All fossil specimens employed in this analysis were identifiable to at least the level of the genus with two exceptions. First, the category 'small papionin' is comprised of individuals that have been variously identified as *Parapapio*, *Cercocebus*, and perhaps even *Lophocebus*, as it is difficult to reliably identify these small primates (Frost and Delson, 2002). Second, the category 'medium-sized alcelaphine' consists of fossils that might be referred to a variety of taxa, including *Parmularius*, *Beatragus*, *Rabaticeras*, and larger-bodied species of *Damaliscus*. Since many of these medium-sized alcelaphine species are diagnosed based on horn cores, and since horn cores are poorly represented in the South African cave infills, more precise taxonomic identification is presently not possible. As a result, they are counted as a single taxonomic category, likely resulting in an underestimate of the actual numbers of individuals if more than one medium-sized alcelaphine species was originally deposited in a given assemblage. The three habitat groupings recognized in Fig. 4 are applied to the *A. robustus*-bearing faunal assemblages to test the ecological composition of the animal paleocommunities, with the inferred habitat preferences provided in Table 7. The mountain reedbuck (*Redunca fulvorufula*) is re-assigned to the grassland category, as it does not share the extreme water dependence of the remaining Reduncini. The oribi (*Ourebia ourebi*) prefers a more closed/wet habitat than other Neotragini. Apart from these two taxa, the remaining bovids show strong correspondence in ecological requirements at the tribal level.

The numbers of individuals from the fossil assemblages assigned to each of the three habitat categories were summed (data from Table 7) and a correspondence analysis performed (Fig. 5). In this analysis, the habitat categories were analyzed together, with *A. robustus* values inserted as supplementary points so that they would not influence the outcome of the habitat separation. There does not appear to be any temporal trend in the ordering of the fossil deposits along either axis. KB plots as a distinct outlier along axis 1, a positioning which is strongly influenced by the large number of primates in this assemblage. The category 'closed/wet' plots as an outlier along axis 2, though it remains closely aligned with the 'grassland' category along axis 1; notwithstanding, it is apparent that none of the fossil assemblages group with the

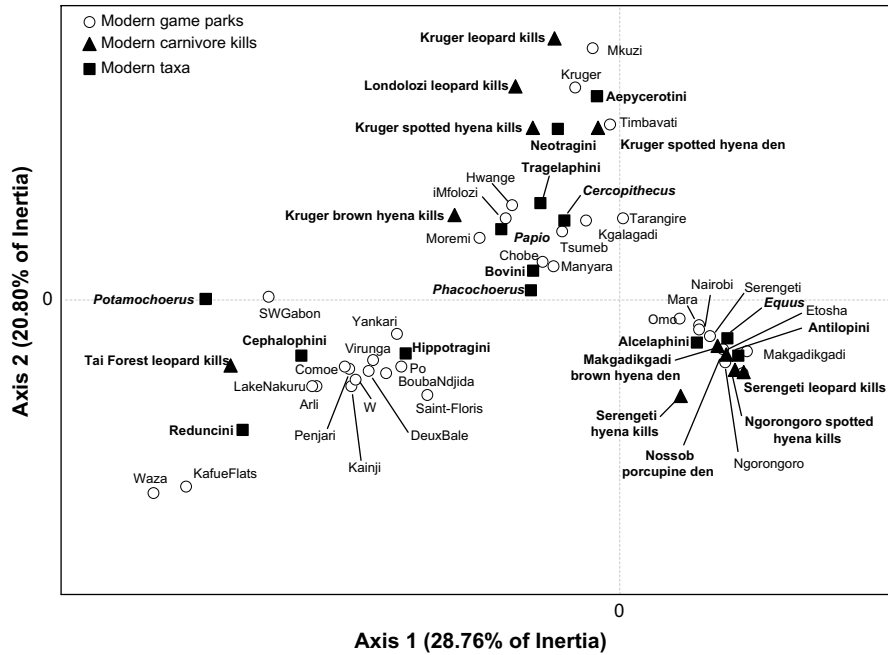


Fig. 4. Correspondence analysis of modern nature reserve census counts and associated carnivore kill data (data from Table 3). Modern carnivore kill data were inserted as supplementary points so as not to influence the outcome of the analysis. The geographically closely-spaced Kruger, Timbavati, and Mkuzi parks all have very high numbers of impala (*Aepyceros melampus*), pulling them away from the remaining woodland habitat parks; nonetheless, all three are comprised of woodland habitats.

‘closed/wet’ category. Most of the assemblages group nearest to the ‘grassland’ category, and farther away from the ‘woodland’ category. This relative positioning is especially apparent along axis 1, which accounts for approximately 80% of the inertia (variance) in the data. This proximity of fossil assemblages to the ‘grassland’ category is consistent with the majority of reconstructions of the paleoenvironment typically associated with *A. robustus*. However, when *A. robustus* values are inserted as supplementary points, it is evident that the hominins plot closer to the ‘woodland’ category, a grouping that is inconsistent with a close association between the hominins and a grassland habitat. Instead, these data demonstrate that ‘woodland’ taxa share the most comparable abundance profile relative to the hominins. In other words, the relative representation of *A. robustus* is most similar to the relative representation of ‘woodland’ taxa across the assemblages.

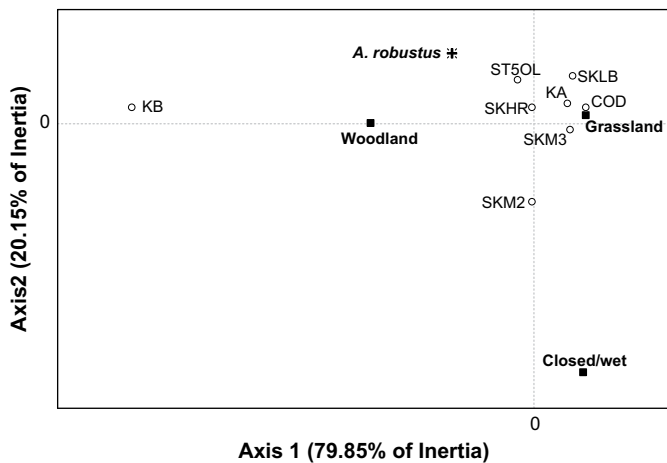


Fig. 5. Correspondence analysis of habitat categories derived from the faunal assemblages examined in this study (data from Table 7). *A. robustus* values were inserted as supplementary points so as not to influence the outcome of the analysis. The close proximity of *A. robustus* and the ‘woodland’ category along axis 1 demonstrates that the abundance profile of *A. robustus* is most similar to that of the ‘woodland’ category.

The relative abundance of taxa assigned to the three habitat categories was computed (data from Table 7) and plotted (Fig. 6). The proportions of taxa representing the three habitat categories tend to be relatively consistent across the assemblages, with three principal exceptions. First, the fauna represented at KB is dramatically different from that seen in the other assemblages, with an abundance of woodland-adapted taxa and a relative paucity of grassland-adapted taxa. Second, there is a slight underrepresentation of grassland taxa in SKHR, relating to the abundance of hominins from this assemblage. Third, although they are not common, SKM2 has significantly more taxa indicative of a closed/wet habitat than the remaining assemblages. Apart from these departures, there are no significant differences in terms of the relative representation of fauna adapted to the various habitat categories over time. Excluding KB, grassland-adapted taxa clearly predominate, generally representing greater than 60% of animals in a given assemblage; woodland taxa are moderately well-represented, typically accounting for slightly more than 20% of animals. These data are in accordance with paleoenvironmental reconstructions indicating predominantly grasslands for the fossil cave infills.

Correlating the proportions of *A. robustus* with proportions of taxa assigned to the different habitat categories, we see a strong, statistically significant, negative association between the hominins and the ‘grassland’ category ($r_s = -0.86$, $p = 0.007$; Table 10). At the same time there are only weak, insignificant correlations with the ‘woodland’ and ‘closed/wet’ categories. The significant, negative correlation between *A. robustus* and grassland-adapted taxa indicates that the more grassland animals there are in a given assemblage, the fewer hominin individuals there tend to be. Although these correlations do not clearly indicate the habitat preference of the hominins, they do demonstrate an inverse relationship between the hominins and grassland-adapted fauna. We interpret this to mean that although they lived in environments predominantly characterized by open grasslands, they were not closely tied to such environments, thus the predominant environmental signal does not necessarily indicate a habitat preference for the robust australopiths.

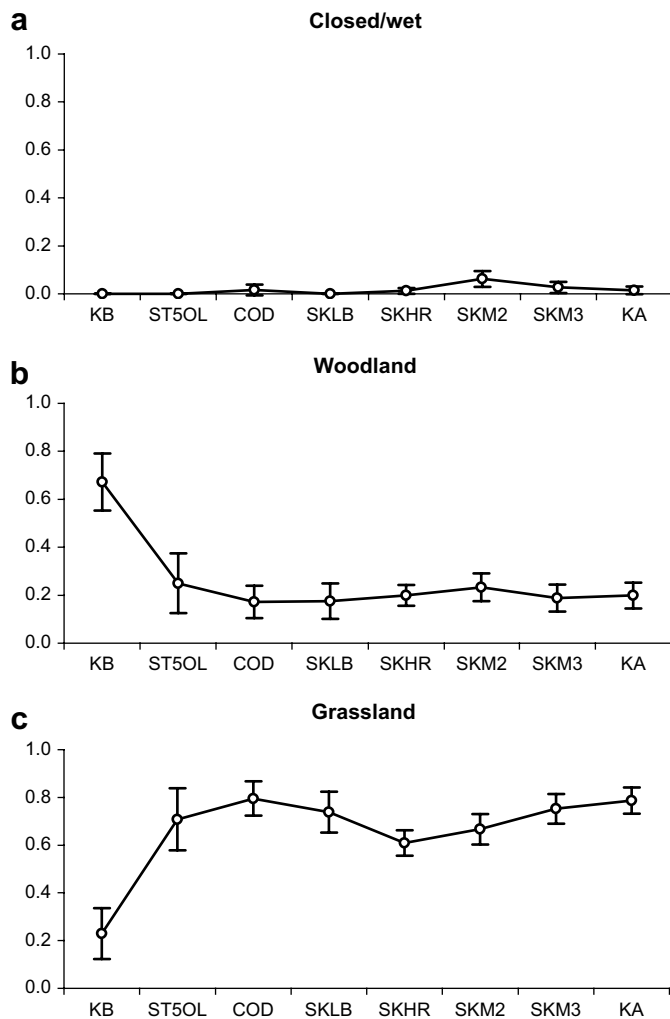


Fig. 6. Relative abundance of taxa assigned to the three habitat categories utilized in this study. Values are calculated from cMNI data in Table 7. Binomial error bars indicate 95% confidence intervals.

Discussion

Taphonomic data implicate a variety of bone accumulating agents in each of the fossil assemblages, including carnivores, rodents, and hominins. In addition, the relative influence of abiotic factors such as slopewash cannot be discounted, as significant numbers of bones would have been mobilized into the caves from their surrounding catchment areas (Butzer, 1984). However, none of these lines of evidence are sufficient to implicate a predominant, or consistent, bone accumulating agent across the assemblages. Moreover, the time-averaged nature of the fossil cave infills enhances the likelihood that numerous different agents were involved over time. Consequently, it is apparent that a variety of accumulating agents were active in the vicinity of the caves during

the time they were open to the surface. As Brain (1980: 107) has pointed out, “any cave which has been open for thousands of years is likely to have had bones brought to it in a variety of different ways”. We assume that the combined impact of numerous agents over long spans of time minimized the idiosyncratic influence of any individual accumulating agent in the fossil assemblages. Since there is no consistent taphonomic pattern relating to accumulating agent, we further assume that any taphonomic biases introduced as a result of bone accumulating agents had an approximately equivalent impact across assemblages, as no one assemblage appears to have been significantly more biased relative to the others.

Testing for conditions of isotaphonomy does, however, reveal a bias relating to depositional matrix. Fossils from hard breccia deposits appear less fragmented than fossils from uncalcified/decalcified deposits, and are characterized by an overabundance of craniodental remains. This results in a potentially significant bias relating to identifiability of specimens, as it is the craniodental remains that form the bulk of specific taxonomic assignments. This difference is influenced by the relative difficulty encountered when manually preparing fossils out of hard breccia, in particular fragmented postcranial specimens that are often not removable (pers. obs.). However, since taxonomic identification is based principally upon craniodental remains and since the most common skeletal elements (isolated teeth) are relatively evenly distributed across assemblages, we conclude that this taphonomic bias has not irretrievably masked the underlying biological signal relating to animal paleocommunity composition. Indeed, in terms of chord distances, there is no relationship between taphonomic conditions and taxonomic composition. This indicates that taxonomic representation varies independently of taphonomic conditions. We interpret this to mean that changes in taxonomic abundance over time do indeed signal animal paleocommunity responses to alterations in environmental conditions, allowing us to investigate fluctuations in animal paleocommunity composition in the Bloubank Valley.

The faunal assemblage from KB consistently stands out as unique relative to the other Bloubank Valley cave infills. Brain (1981b) suggested that KB had been collected by large carnivores, while Vrba (1981) concluded that the cave represented a death trap for ungulates and primates that were then opportunistically scavenged by visiting carnivores. The notable prevalence of primates in this assemblage might indicate some form of accumulation bias, perhaps a situation that rendered primates particularly susceptible to incorporation in the assemblage (e.g., a specialized predator of primates). The small numbers of carnivore modified bones and coprolites do not aid in resolving this issue, and a high level of comminution of bones has potentially obscured indications of bone surface modification (Brain, 1981b). While the high number of primates in and of itself is insufficient to implicate a specialized primate predator, the high carnivore:ungulate ratio does imply significant carnivore activity. However, the dissimilar taxonomic composition of KB is not coupled with a notable taphonomic difference, thus the unique nature of this assemblage cannot be solely a result of taphonomic bias. We therefore hypothesize that KB samples a paleoenvironment that was unlike that seen in the other

Table 10
Relative abundance values (proportions) of select mammalian taxa assigned to habitat categories^a

	Fossil deposit								Spearman's r_s	p-level
	KB	ST5OL	COD	SKLB	SKHR	SKM2	SKM3	KA		
<i>A. robustus</i>	0.10	0.04	0.02	0.09	0.18	0.04	0.03	0.00	–	–
Closed/wet	0.00	0.00	0.02	0.00	0.01	0.06	0.03	0.01	–0.59	0.13
Woodland	0.67	0.25	0.17	0.17	0.20	0.23	0.19	0.20	0.48	0.23
Grassland	0.23	0.71	0.80	0.74	0.61	0.67	0.75	0.79	–0.86	0.007*

^a Spearman's r_s correlation coefficients are computed for each category compared to *A. robustus*. Probability value with an asterisk (*) is statistically significant.

deposits; more research is required to confirm this suggestion, preferably with an augmented faunal assemblage.

Results of the correspondence analysis of modern nature reserves demonstrate groupings of taxa and habitats that are consistent with those of previous correspondence analyses (Greenacre and Vrba, 1984; Alemseged, 2003), even though we utilize a different set of nature reserves and census counts, and include taxa not previously incorporated (Cercopithecidae, Equidae, Suidae). In their bone transect study in the Amboseli National Park, Behrensmeyer et al. (1979) determined that bone distributions of certain taxa did not match their live census data. However, at the grosser scale of our analysis, we do see close correspondence between modern carnivore kill data and animal community composition. This includes both data from bone accumulations as well as animal kill data from a series of different carnivorous agents. These results indicate that animals do tend to die where they live, thus it would appear that carnivore-produced bone accumulations are broadly representative of animal communities, which in turn are good indicators of environment.

Taxonomic abundance data demonstrate that the paleoenvironments of all but KB can be reconstructed as predominantly open grasslands. The preponderance of grassland-living taxa in the majority of the Bloubank Valley assemblages is in agreement with paleoecological analyses that reconstruct a predominantly open and relatively arid environment with nearby edaphic grasslands for *A. robustus* (Vrba, 1975, 1976, 1980, 1985a,b; Brain, 1981a; Brain et al., 1988; Shipman and Harris, 1988; McKee, 1991; Denys, 1992; Avery, 1995, 2001; Reed, 1997; Watson, 2004; Reed and Rector, 2006). The results of this study differ, however, in that they indicate that these open grasslands do not reflect the habitat preference of the hominins. Although *A. robustus* is consistently associated with open grassland environments, they exhibit a strong, statistically significant, negative relationship with the taxa that occupy this habitat. In other words, the more open grassland-adapted taxa there are in an assemblage, the fewer hominins there are in that assemblage. Such a conclusion contrasts with the notion of *A. robustus* as an open grassland specialist.

If the unique nature of the fauna from KB is not exclusively the result of taphonomic bias, the predominantly wooded environment that is indicated by this assemblage might, in fact, represent a habitat favored by the hominins. However, because correlations between the hominins and the remaining habitat categories are insignificant, statistical support for an actual habitat preference remains elusive. One line of evidence that does support a woodland habitat preference for *A. robustus* is the correspondence analysis that groups the hominins more closely with this particular habitat. The proximity of *A. robustus* to the 'woodland' category along axis 1 in Fig. 4 indicates that this is the category with the most comparable abundance profile relative to the hominins. In other words, the relative representation of *A. robustus* is most similar to the relative representation of 'woodland' taxa across the assemblages. Although not conclusive, this close association between *A. robustus* and the 'woodland' category is suggestive that the conditions that were sufficient for woodland-adapted animals were also favored by the hominins.

Several studies of the isotope chemistry of *A. robustus* dental enamel have demonstrated a preponderance of C₃ resources, indicative of a principally forest- or woodland-based diet (Lee-Thorp et al., 1994; Sponheimer et al., 2005, 2006a,b). This isotopic evidence is supported by studies of enamel microwear patterns that demonstrate consumption of hard food items, such as seeds and nuts, that are typically associated with forest-based food sources (Grine, 1986; Grine and Kay, 1988). At the same time, isotopic analysis has demonstrated that a significant proportion of *A. robustus*' diet was comprised of C₄ grass-based resources, accounting for an average 35% of the diet, perhaps in the form of

fallback foods (Sponheimer et al., 2005, 2006b). Although isotope data for sedges, termites, and numerous African mammals exist (Sponheimer et al., 2003, 2005), there is currently little data regarding the isotopic composition of other potential fallback foods, such as underground storage organs, in Africa. Nonetheless, the hominins appear to have preferred a forest-based diet, though they were also capable of consuming sometimes considerable amounts of resources extracted from the surrounding grasslands that comprised the major portion of the habitat mosaic.

The patterns of habitat utilization documented in this study present us with several potential ecological implications. It is possible that the assemblages are time-averaged, and that the hominins have been artificially lumped in death alongside taxa that they might never have encountered in life. This would imply that the hominins were itinerant occupants of the area, present during the rarer occasions when conditions were particularly favorable (expanded woodlands), and absent when conditions were unfavorable (expanded grasslands). However, the environmental mosaics reconstructed for several of the deposits indicate a variety of habitats, including woodlands potentially capable of sustaining hominin populations (Brain et al., 1988; Avery, 1995; Reed, 1997; Watson, 2004). The likelihood therefore exists that the hominins were habitat generalists capable of living in a variety of environments, but perhaps preferring woodlands over the less-favored grasslands when conditions were sufficient. As large-bodied, mobile, intelligent apes, the hominins would have been able to respond to environmental oscillations by altering their behavioral patterns in numerous ways. Among the apes, hominins are unique in their capacity to modify their diet to consume significant quantities of C₄-based resources (Sponheimer et al., 2005). In fact, *A. robustus* is marked by the ability to dramatically alter its dietary behavior on both seasonal and interannual scales (Sponheimer et al., 2006b). The capacity to subsist on less-favored dietary items likely allowed the hominins to survive periods of resource stress by resorting to fallback foods that might be unavailable to other occupants of the area, as well as by altering their population densities.

Summary and conclusions

The aim of this study was to investigate whether any indicators of the habitat association of *A. robustus* were preserved in the faunal assemblages of the Bloubank Valley of South Africa. Notwithstanding evidence of limited taphonomic biasing relating to depositional matrix and perhaps accumulating agents, it appears that these potential biases have not unduly influenced the ecological composition of the faunal assemblages. Correspondence analysis of census data from a series of modern nature reserves displayed the habitat preferences of a select group of large mammal taxa, in turn allowing assignment of fossil taxa from the Bloubank Valley assemblages to a series of broadly defined habitat categories. Subsequent correspondence analysis of the faunal assemblages reveals that *A. robustus* has an abundance profile most similar to the 'woodland' habitat category, meaning that the relative representation of the hominins corresponds most closely to that of woodland-adapted taxa. Additionally, the strong, negative correlation that is evident between *A. robustus* and grassland-adapted taxa contrasts with reconstructions of these hominins as open grassland habitat specialists. Rather, our admittedly limited dataset from a small number of closely spaced fossil localities nonetheless suggests that *A. robustus* was a habitat generalist. These data, coupled with recent evidence demonstrating a highly generalized diet, indicate that the commonly held perception that the specialist adaptations of *A. robustus* doomed it to extinction in the face of fluctuating environmental conditions during the Plio-Pleistocene requires rethinking.

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