

Faunal Assemblage Seriation of Southern African Pliocene and Pleistocene Fossil Deposits

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ABSTRACT Fossil assemblages from the Pliocene and Pleistocene of southern Africa were seriated in order to give a better idea of their relative chronology. Time-sensitive mammals were selected for calculation of the Faunal Resemblance Index among 17 site units. On the basis of a logistical seriation and subsequent site analysis, the following sequence of sites was deemed most probable: Makapansgat Member 3, Makapansgat Member 4, Taung Dart deposits, Sterkfontein Member 4 and Taung Hrdlička deposits, Sterkfontein Member 5 (in part) and Kromdraai B, Kromdraai A and Swartkrans Member 1, Swartkrans Member 2, Swartkrans Member 3, Plovers Lake, Cornelia, Elandsfontein Main Site, Cave of Hearths Acheulian levels, Florisbad and Equus Cave and Klasies River Mouth. © 1995 Wiley-Liss, Inc.

Associations of the early hominid fossils with a wealth of Pliocene and Pleistocene fauna from southern Africa provide vital clues to the past environments and evolutionary processes that shaped human evolution. Due to the nature of the cave deposits in which these ancient assemblages are typically found, where absolute geochronological dating techniques are inhibited, the absolute and even relative temporal positions of these sites have proved difficult to ascertain. Nevertheless, it is of pivotal importance in studies of mammalian evolution, and particularly in paleoanthropological research, to establish a chronology with which we can assess the evolutionary roles of the varied fauna found in southern African cave deposits.

Understanding the timing of deposition in southern African hominid fossil sites is of continuing importance, as illustrated by the influence dates have on interpretations of hominid phylogeny and theories of the causes of evolution. For example, the proposed late date for the type specimen of *Australopithecus africanus* from Taung, at circa 1 mya (Partridge, 1973, 1982, 1985; Vogel

and Partridge, 1983; Vogel, 1985) led to the suggestion that the Taung child may have been close to the hypodigm of *A. robustus* (Tobias, 1973, 1975, 1978; Wolpoff, 1974) or that it represented a derived form of *A. africanus* (Tobias, 1991a,b). Recent faunal dating of Taung (Delson, 1988; Cooke, 1990; McKee, 1993a), placing the site in time closer to Sterkfontein and Makapansgat, opens the possibility that the Taung hominid is a more typical or even primitive representative of *A. africanus*.

Turner (1983, 1990) and Vrba (1985a, 1988, 1992) have argued that changes in global climate during the Pliocene caused mammalian evolutionary changes in Africa. Recently Hill et al. (1992) have suggested that the origin of *Homo* corresponded to these putative climatic changes on the basis of the age of a specimen they feel represents the genus. However, in southern Africa it is

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not clear whether the apparent faunal turnovers seen in the fossil record predate or postdate any climatic change, or whether or not some of the faunal turnovers are indeed real (McKee, 1991, in press). Thus an understanding of cause and effect in mammalian evolution requires at least an understanding of the succession of sites if not the actual age of deposition.

Opportunities to determine the ages of sites by geological dating have been limited by the nature of cave deposits. Sedimentological correlations of sites (Butzer, 1974), nick-point analysis of cave openings (Partridge, 1973), sedimentological rates (Partridge, 1985), and isotopic techniques (Vogel and Partridge, 1983; Vogel, 1985) have provided unsatisfactory results (De Swardt, 1974; Butzer et al., 1978; Tobias et al., 1993; McKee, 1993a). Palaeomagnetic chronologies have given mixed results, with some success at Makapansgat (Brock et al., 1977; McFadden et al., 1979; McFadden, 1980) and Kromdraai (Jones et al., 1986), but few clues at other sites due to the dynamics of cave sediments. Electron spin resonance (ESR) has provided age estimates for various sites, including Border Cave (Grün et al., 1990a), Klasies River Mouth (Grün et al., 1990b), and Sterkfontein (Schwarcz et al., 1993), but these are dependent on assumptions regarding rates of uptake of uranium (Grün and Stringer, 1991). Nevertheless, there is considerable potential in the application of ESR dating with necessary caveats and corroborating evidence from other techniques.

Chronologies based on faunal correlations have thus been the primary means of dating southern African fossil sites. Many attempts have been made (reviewed by McKee, 1993a), but the most relevant work has its cornerstone in the faunal spans delineated by Ewer and Cooke (1964) and Cooke (1967). The oldest of these temporal associations was the Sterkfontein Faunal Span, comprising the *Australopithecus*-bearing deposits of Sterkfontein, Makapansgat, and Taung, as well as the Older Gravels of the Vaal River Basin. The subsequent Swartkrans Faunal Span encompassed deposits from the Sterkfontein extension site (most of which is now

referred to as Sterkfontein Member 5), Swartkrans, and Kromdraai. The Vaal-Cornelia Faunal Span included the Vaal Younger gravels, Elandsfontein (formerly known as Hopefield or Saldanha), and Cornelia, followed by the Florisbad-Vlakkraal Faunal Span encompassing the important *Homo*-bearing sites of Florisbad and Broken Hill.

As progress is made in both excavation and taxonomic identification of southern African fossil fauna, sufficient samples are emerging for the refinement of the early methods that simply recognized faunal spans. Toward this end, biochronologies within taxonomic families have been established for bovids (Vrba, 1975, 1982, 1985b), cercopithecids (Delson, 1984, 1988), carnivores (Hendey, 1974; Turner, 1990), and suids (Harris and White, 1979). A combined picture of all the known mammalian fauna may then be useful in the seriation of individual site units within and between the faunal spans.

There are numerous factors that may lead to similarities or differences of faunal representation in site assemblages that must be considered when attempting to establish biochronologies across taxonomic boundaries. Temporal determinants, those most useful for faunal dating, interplay with other sampling biases so that only a fraction of the total faunal community living at any one time would be represented in a cave deposit. A summary of the key factors that may lead to similarities or differences among faunal assemblages in southern African cave deposits can be found in Table 1.

Although faunal dating may have its limitations due to the complex network of factors that determine site assemblages, it remains as the most reliable tool for determining the sequence of fossil sites in southern Africa. Our objective here is to establish a chronological framework for understanding mammalian evolution in the Pliocene and Pleistocene of southern Africa through the seriation of site units. In order to achieve this with a total mammalian perspective, issues arising from the complicating factors discussed above must be resolved with an appropriate method.

TABLE 1. Factors causing similarities or differences in faunal representation at southern African cave sites

Environmental factors
Faunal community
Floral community
Demography
Climate
Altitude
Terrain
Geographic proximity of sites
Availability of water
Cave size and depth
Taphonomic factors
Taphonomic agents
Bone preservation
Mixing of deposits
Interpretive factors
Selective excavation and preparation
Taxonomic biases
Temporal factors
Origins
Radiations
Extinctions

METHODS AND ASSUMPTIONS

Lists of identified mammalian species and genera were compiled from published literature for 23 Neogene site units (Fig. 1 and Table 2). This amounted to 246 species of 159 genera and 44 families.

It was our primary goal to seriate the sites based on similarities of identified species between site unit assemblages. The initial step is to create a matrix exhibiting the number of identified species shared between each pair of site units (Table 3A); the diagonal from top left to bottom right shows the number of identified species for each site unit. Specific identifications with "cf." or "aff." were included for the analysis, as in Turner and Wood (1993).

The ideally seriated matrix should exhibit an ordering of figures within each row, increasing from left to right toward the diagonal, and decreasing away from the diagonal. In other words, sites closer in time should share a successively greater number of species than more temporally distant sites. The nontemporal factors listed in Table 1, however, severely complicate the ideal, and additional steps are necessary to place the focus of the seriation on the temporal components of the data.

Intrinsic standardization of the data is necessary in order to alleviate the problems engendered by differential sampling; a well

sampled or faunally diverse site is more likely to yield species identified from elsewhere than is a site with a paucity of fauna. Simpson's (1960) Faunal Resemblance Index (FRI) provides a partial solution to the sampling problem and is employed here. For each pair of sites, the FRI is calculated by taking the number of species shared (C) divided by the total number of species found in the smaller sample (N_1), or simply $FRI = C/N_1 \times 100$. These values are displayed in Table 3B. The advantage of the method is that a small sample can exhibit an FRI value comparable to that of a much larger sample, thus standardizing the figures in the matrix. It should be noted, however, that a site with a large sample still has a greater probability of sharing species with other sites and the use of an FRI does not address this issue.

Complications from nontemporal factors of site similarities can cause spurious correlations. For example, a long-lived but ecologically limited species, *Hippopotamus amphibius*, appears at the oldest and youngest sites, but not at sites that span the time in between. Thus the analysis must be limited to the species that are most sensitive to time and not restricted to highly specialized environments.

Evaluation of temporally sensitive species can be a somewhat subjective task. Any criteria used to label a species as time-sensitive must be seen as an underlying assumption of the analysis. For this analysis we established the following objective criteria for identifying such species: (1) The species must occur at more than one fossil site; species known from only one site that show evolutionary relationships to species from other sites can be used as corroborating evidence. (2) The species must not be present throughout the entirety of the sequence (given the assumption of an oldest site). (3) Species that are highly sensitive to local environmental conditions may cause spurious correlations among sites of similar conditions from vastly different times, and thus should be excluded. Known habitat preferences of extant species can be used to infer similar tendencies of the same or related species in the past, but the potential for bias in exclud-

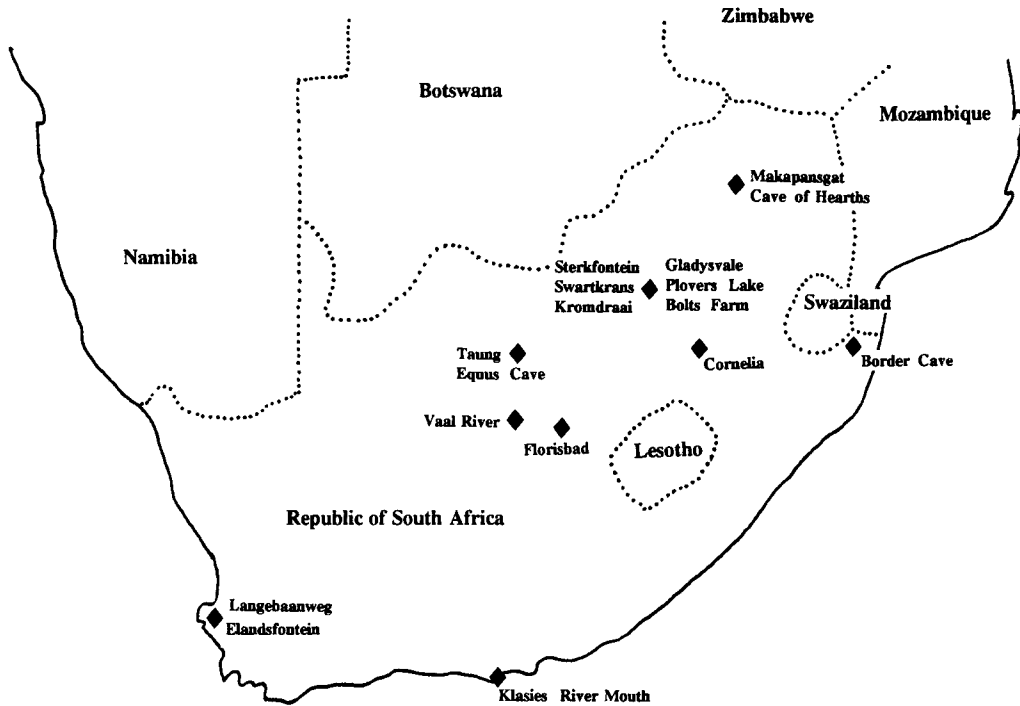


Fig. 1. Map of southern African fossil sites.

ing species on this basis must be acknowledged. Thus species that occur at sites which, on the basis of independent evidence, appear to have been environmentally distinct (e.g., Taung and Makapansgat), were not excluded. It should be remembered that most of the southern African fossil sites are cave deposits that have sampled mammals from a mosaic of local environments.

Virtually all of the 66 time-sensitive species identified using the above criteria showed some degree of irregularity in their appearances at various sites, as they are not free from the factors listed in Table 1. It thus must be assumed that sampling of such species from site units is random with respect to time. The time-sensitive species are listed in Table 4 along with their distribution among the sites used in the analysis. The matrices in Table 5 are based on time-sensitive species alone.

Once time-sensitive species were considered, a number of sites had to be excluded from the analysis due to small sample sizes. The small samples of time-sensitive species

produced unrealistically large FRI values. These sites included Langebaanweg, the Taung Dart Deposits, the Vaal Older River Gravels, and Border Cave. Additional sites were excluded because it was known a priori that fauna from deposits of vastly different time periods were mixed into single assemblages; these sites were Bolt's Farm and Gladysvale (Berger, 1993). It must be acknowledged at the outset, however, that some mixing of fossils may have occurred at other sites with multiple deposits.

Logistical seriation of the sites was based on the matrix of FRI values for time-sensitive species. A computer program was written which tested different site sequences in order to minimize differences among adjacent sites showing "backward steps": figures that decrease in value toward the diagonal are "backward steps" because in an ideal matrix the FRI values should always increase toward the diagonal. This was accomplished by summing the absolute value of differences between adjacent sites in a row showing "backward steps." The site unit or-

TABLE 2. Site units and codes used in Tables 3-5¹

Site unit	Code
Langebaanweg 'E' Quarry	LANG
Makapansgat Member 3	MAK3
Makapansgat Member 4	MAK4
Taung Dart deposits	TAUD
Taung Hrdlička deposits	TAUH
Sterkfontein Member 4	STS4
Sterkfontein Member 5	STS5
Older Vaal River Gravels	VAAL
Bolt's Farm	BOLT
Kromdraai A	KROA
Kromdraai B	KROB
Gladysvale	GLVH
Swartkrans Member 1	SWT1
Swartkrans Member 2	SWT2
Swartkrans Member 3	SWT3
Plovers Lake	PLOV
Cornelia	CORN
Elandsfontein Main Site	EFTM
Cave of Hearths (Acheulian levels)	COHA
Border Cave (MSA levels)	BCVM
Florisbad springs	FLOS
Equus Cave (MSA levels)	EQUU
Klasies River Mouth (MSA I and II levels)	KLAS
Extant species in southern Africa	EXTA

¹Species identified from each site were compiled by one of us (JKM) from the following references: Berger (1993), Brain (1981), Brain and Watson (1992), Brickhill (1976), Brink (1987), Butzer et al. (1974), Churcher (1970), Collings (1972), Collings et al. (1976), Cooke (1978, 1988, 1990, 1991, 1993a,b), Cooke and Wells (1947), de Graaf (1960, 1988), Freedman (1957), Greenwood (1955), Helgren (1979), Hendey (1981), Hooijer (1958), Klein (1976, 1977), Klein et al. (1991), Klein and Cruz-Urbe (1991), McKee (1991, 1993a,c), Randall (1975), Pocock (1987), Skinner and Smithers (1990), Szalay and Delson (1979), Turner (1986), Vrba (1981, 1987a,b), Watson (1993). An unpublished species list was provided by J.F. Thackeray for Plovers Lake.

der producing the minimum sum was deemed the best seriation. As the number of possible seriated orders is a factorial of the number of site units, only 10 sites could be seriated at any one time and the complete sequence was compiled from overlapping seriations. For the overall ordering of the sequences, an a priori assumption was made that sites with fewer extant species were earlier in time.

Use of the method outlined above minimizes the effects of nontemporal factors but is far from foolproof. Initial tests of the process revealed that a number of principles must be imposed on the logistical seriation and interpretation of the matrix. (1) When available, stratigraphic relations among site units must be used. For example, Swartkrans Member 3 must follow Swartkrans Member 2, although this detracts from an ideal sequence of FRI values. (2) Where multiple sequences are possible, each must be treated as tenable. The exclusion of certain

sites often changes the sequence among other sites, and these situations must be scrutinized carefully. However, pencon-temporaneous sites may be expected to seriate in alternating positions. (3) Each site must be considered in light of corroborating evidence from evolutionary sequences of lineages, human artifacts (stone tools, etc.), and absolute dating, whenever such information is available.

RESULTS

The seriation of the FRI values presented in Table 5B led to the following optimum series of 10 sites per run:

- A. MAK4 MAK3 TAUH STS4 STS5
KROB KROA SWT1 SWT3 SWT2
B. MAK3 MAK4 STS4 TAUH KROB
KROA SWT1 SWT2 SWT3 PLOV

These two sequences maintained consistency with the further removal of individuals sites. The position of the Taung Hrdlička assemblage alternated with Sterkfontein Member 4, depending on the inclusion of Sterkfontein Member 5. As discussed below, this may be because of near contemporaneity of the two alternating sites. Although Makapansgat Member 4 was sometimes positioned before Member 3, and Swartkrans Member 3 sometimes seriated before Member 2, forcing the stratigraphic orders in sequence did not affect the relative positions of the other site units.

In the presumed middle of the site sequence, the seriation results were quite consistent and confirmed the relations suggested by sequences A and B above. For example:

- C. TAUH STS5 KROA SWT1 SWT3
SWT2 PLOV CORN EFTM COHA
D. TAUH KROB KROA SWT1 SWT2
CORN EFTM COHA EQUU KLAS

Optimal seriations of the more recent sites produced a more variable picture, depending on the sites used for analysis. The main variants are illustrated by the following sequences:

TABLE 3. List of shared species at southern African site units: (A) absolute frequencies of shared species and (B) faunal resemblance index (FRI)¹

		A																								
LANG	MAK3	MAK4	TAUD	STS4	VAAL	TAUH	BOLT	STS5	KROB	KROA	GLVH	SWT1	SWT2	SWT3	PLOV	CORN	EFTM	COHA	FLOS	EQUU	KLAS	BCVM	EXTA			
34	LANG	4	2	1	3	2	1	2	1	1	2	2	1	1	2	1	1	1	1	0	0	0	0	1		
4	MAK3	51	13	3	24	1	15	13	9	11	15	15	5	6	2	3	6	2	2	7	5	2	2	14		
2	MAK4	13	34	2	14	0	9	12	11	8	9	7	3	3	3	3	1	3	1	3	0	0	0	14		
1	TAUD	3	2	7	3	0	2	2	0	1	2	2	1	1	1	1	0	0	0	0	0	0	0	0		
3	STS4	3	24	14	3	45	0	18	16	20	21	20	9	9	6	1	6	6	4	7	4	1	1	15		
2	VAAL	1	0	0	5	0	2	0	1	1	1	1	2	2	2	2	2	5	1	3	3	1	1	13		
1	TAUH	15	9	2	18	0	33	16	10	13	11	13	13	6	5	5	0	2	5	1	3	3	1	13		
2	BOLT	13	8	2	16	2	31	11	11	15	14	19	9	9	7	4	5	4	4	3	3	1	0	8		
1	STS5	9	12	0	18	0	10	11	31	15	17	11	13	6	8	3	2	6	8	5	6	2	1	17		
1	KROB	11	11	0	16	1	13	11	33	20	9	16	7	7	8	6	2	4	5	2	4	3	0	15		
2	KROA	15	8	1	20	1	11	15	17	20	48	22	25	13	17	12	6	11	9	7	13	10	3	19		
2	GLVH	15	9	2	21	1	13	14	11	9	22	54	20	12	15	12	7	12	10	19	11	8	27	73		
2	SWT1	14	7	1	20	1	13	19	13	16	25	20	46	19	23	9	5	13	7	6	15	10	3	20		
1	SWT2	5	3	1	9	2	6	9	6	7	15	12	19	25	24	8	5	11	3	6	13	6	3	14		
1	SWT3	6	3	1	9	2	5	9	8	8	17	15	23	24	34	10	5	12	5	7	19	9	5	21		
2	PLOV	2	3	1	6	1	5	7	3	6	12	12	9	8	10	24	3	7	8	5	9	5	3	13		
1	CORN	3	1	0	1	2	0	4	2	2	6	7	5	5	5	3	18	11	5	8	6	3	1	6		
1	EFTM	6	1	0	6	2	2	5	6	4	11	12	13	11	12	7	11	40	10	14	19	17	4	26		
1	COHA	2	3	0	6	0	5	4	8	5	9	12	7	3	5	8	5	10	29	9	13	11	6	21		
0	FLOS	0	2	1	0	4	0	1	3	5	2	7	10	6	7	5	8	14	9	22	18	8	4	16		
0	EQUU	7	3	0	7	0	3	6	4	13	19	15	13	19	9	9	6	19	13	18	46	22	10	43		
0	KLAS	5	0	0	4	0	3	1	2	3	10	11	10	6	9	5	3	17	11	8	22	34	9	32		
0	BCVM	2	0	0	1	0	1	0	1	0	3	8	3	3	5	3	1	4	4	6	10	9	15	15		
1	EXTA	14	14	0	15	0	13	8	17	15	19	27	20	14	21	13	6	26	21	16	43	32	15	101		

		B																								
LANG	MAK3	MAK4	TAUD	STS4	VAAL	TAUH	BOLT	STS5	KROB	KROA	GLVH	SWT1	SWT2	SWT3	PLOV	CORN	EFTM	COHA	FLOS	EQUU	KLAS	BCVM	EXTA			
100	LANG	12	6	14	9	40	3	6	3	3	6	6	4	3	8	6	3	3	3	0	0	0	3			
12	MAK3	100	38	43	53	20	45	42	29	33	31	29	30	20	18	8	17	15	7	9	15	15	13	27		
6	MAK4	38	100	29	41	0	27	26	39	33	24	26	21	12	9	13	6	3	10	5	9	0	41			
14	TAUD	43	29	100	43	0	29	29	0	14	29	14	14	14	14	0	0	0	0	0	0	0	0			
9	STS4	53	41	43	100	0	55	52	58	48	44	47	44	36	26	25	6	15	21	18	16	12	7	33		
40	VAAL	20	0	0	0	100	0	40	0	20	20	20	20	40	40	20	40	40	0	0	0	0	0			
3	TAUH	45	27	29	55	0	100	52	32	39	33	39	39	24	15	21	0	6	17	5	9	9	7	39		
6	BOLT	42	26	29	52	40	52	100	35	35	48	45	61	36	29	29	22	16	14	14	10	3	0	26		
3	STS5	29	39	0	58	0	32	35	100	48	55	35	42	24	26	13	11	19	28	23	19	6	7	55		
3	KROB	33	33	0	48	20	39	35	48	100	61	27	48	28	24	25	11	12	17	9	12	9	0	45		
6	KROA	31	24	14	44	20	33	48	55	61	100	46	54	52	50	50	33	28	31	32	28	29	20	40		
6	GLVH	29	26	29	47	20	39	45	35	27	46	100	43	48	44	50	39	30	41	45	41	32	53	50		
4	SWT1	30	21	14	44	20	34	61	42	48	54	43	100	76	68	38	28	33	24	27	33	29	20	43		
4	SWT2	20	12	14	36	40	24	39	24	28	52	48	76	100	96	96	33	28	44	12	27	52	24	20	56	
3	SWT3	18	9	14	26	40	15	29	26	24	50	44	68	96	100	42	28	35	17	32	56	26	33	62		
8	PLOV	8	13	14	25	20	21	29	13	25	50	50	68	96	100	42	100	17	29	33	23	21	20	54		
6	CORN	17	6	0	6	40	6	22	11	11	33	39	38	33	33	42	100	17	29	33	33	21	20	54		
3	EFTM	15	3	0	15	40	6	16	19	12	30	33	33	44	35	29	61	100	34	64	48	50	27	65		
3	COHA	7	10	0	21	0	17	14	28	17	31	41	24	12	17	33	28	34	100	41	45	38	40	72		
0	FLOS	9	5	0	18	0	5	14	23	9	32	45	27	27	32	33	44	64	41	100	82	36	27	73		
0	EQUU	15	9	0	16	0	9	10	19	12	28	41	33	52	56	38	33	48	45	100	65	67	93	94		
0	KLAS	15	0	0	12	0	9	3	6	9	29	32	29	24	26	21	17	50	38	36	65	100	60	94		
0	BCVM	13	0	0	7	0	7	0	7	0	20	53	20	20	33	20	7	27	40	27	67	60	100	100		
3	EXTA	27	41	0	33	0	39	26	55	45	40	50	43	56	62	54	33	65	72	73	93	94	100	100		

¹Site codes are listed in Table 2.

TABLE 4. Time-sensitive mammalian species with site unit occurrences marked by an asterisk¹

	M A K 3	M A K 4	S T S 4	T A U H	S T S 5	K R O B	R O A	S W T 1	S W T 2	S W T 3	P L O V	C O R N	E O T M	C O H A	F L O S	E Q U U	K L A S	E X T A
Artiodactyla																		
<i>Alcelaphus buselaphus</i>														*		*	*	*
<i>Antidorcas australis</i>											*		*					
<i>Antidorcas bondi</i>			*			*	*							*	*	*		
<i>Antidorcas marsupialis</i>								*	*	*					*	*		*
<i>Antidorcas recki</i>		*			*	*	*	*	*	*			*	*		*	*	
<i>Connochaetes gnou</i>												*	*		*	*		*
<i>Damaliscus dorcas</i>															*	*		*
<i>Damaliscus niro</i>												*	*		*			
<i>Hippotragus cookei</i>	*		*															
<i>Hippotragus leucophaeus</i>		*											*				*	*
<i>Makapania broomi</i>	*		*															
<i>Megalotragus priscus</i>											*	*	*	*	*	*		
<i>Oreotragus major</i>	*	*	*	*	*													
<i>Pelea capreolus</i>								*	*	*	*					*	*	*
<i>Pelorovis antiquus</i>												*	*	*	*	*	*	*
<i>Raphicerus campestris</i>								*	*	*						*	*	*
<i>Redunca arundinum</i>								*	*			*	*	*			*	*
<i>Redunca darti</i>	*		*									*	*	*			*	*
<i>Redunca fulvorufula</i>																*	*	*
<i>Simatherium kohlarseni</i>	*	*															*	*
<i>Syncerus caffer</i>																	*	*
<i>Taurotragus oryx</i>								*	*	*	*	*	*	*	*	*	*	*
<i>Tragelaphus strepsiceros</i>								*	*	*	*	*	*	*	*	*	*	*
<i>Kolpochoerus paiceae</i>												*	*					
<i>Metridiochoerus andrewsi</i>									*	*	*		*					
<i>Notochoerus scotti</i>	*	*		*														
<i>Phacochoerus aethiopicus</i>														*	*	*	*	*
<i>Phacochoerus modestus</i>						*	*	*	*	*		*						
<i>Potamochoeroides shawi</i>	*		*															
Carnivora																		
<i>Lycan pictus</i>													*		*	*		*
<i>Vulpes pulcher</i>							*	*										
<i>Dinofelis barlowi</i>	*		*					*										
<i>Homotherium crenatidens</i>	*		*		*	*	*	*		*								
<i>Megantereon cultridens</i>			*		*	*	*	*	*	*								
<i>Panthera pardus</i>			*	*		*	*	*	*	*	*					*	*	*
<i>Chasmaporthetes silberbergi</i>			*	*	*	*	*	*	*	*								
<i>Chasmaporthetes nitidula</i>			*	*	*	*	*	*	*	*								
<i>Hyaena brunnea</i>			*			*	*	*	*	*			*			*	*	*
<i>Pachycrocuta bellax</i>	*		*		*	*	*	*	*	*						*	*	*
<i>Aonyx capensis</i>								*	*	*			*		*	*	*	*
<i>Mellivora capensis</i>													*		*	*	*	*
<i>Atilax paludinosus</i>														*	*	*	*	*
<i>Herpestes ichneumon</i>								*				*	*		*	*	*	*
<i>Suricata suricatta</i>									*	*			*		*	*	*	*
Primates																		
<i>Australopithecus africanus</i>	*	*	*															
<i>Australopithecus robustus</i>						*		*	*	*								
<i>Homo sapiens</i>													*	*	*	*	*	*
<i>Cercopithecoides williamsi</i>	*	*	*	*		*		*										
<i>Papio izodi</i>			*	*														
<i>Papio angusticeps</i>						*	*											
<i>Papio robinsoni</i>						*	*	*	*	*	*							
<i>Papio cynocephalus</i>														*		*	*	*
<i>Parapapio broomi</i>	*	*	*															
<i>Parapapio whitei</i>	*	*	*															
<i>Parapapio jonesi</i>	*	*	*			*	*	*	*	*								
<i>Theropithecus oswaldi</i>								*	*	*			*					
Proboscidea																		
<i>Elephas recki</i>			*		*													
Perissodactyla																		
<i>Equus burchelli</i>					*		*		*	*				*	*	*		*
<i>Equus capensis</i>					*		*	*	*	*	*	*	*	*	*	*		
<i>Hipparion libycum</i>	*						*	*	*	*		*						
Hyracoidea																		
<i>Procavia transvaalensis</i>		*		*			*	*	*	*	*							
Rodentia																		
<i>Mystromys antiquus</i>	*		*	*		*		*										
<i>Proodontomys cookei</i>	*	*	*	*		*	*	*										
<i>Hystrix makapanensis</i>	*							*										
<i>Elephantulus antiquus</i>	*	*	*	*	*	*	*	*										
<i>Myosorex robinsoni</i>	*		*				*	*										

¹Site codes are listed in Table 2.

- E. STS5 KROA SWT1 SWT2 PLOV
CORN EFTM FLOS EQUU KLAS
F. SWT2 SWT1 KROA PLOV CORN
EFTM FLOS COHA EQUU KLAS
G. SWT1 SWT2 SWT3 PLOV KROA
CORN EFTM EQUU COHA FLOS

Because of the high FRI value for Plovers Lake and Kromdraai A, two of the sequences place the latter site after Swartkrans. But note in sequence F that the first three sites are in reverse order from that expected; they seriated correctly among themselves in order to allow for the similarities between Kromdraai A and Plovers Lake.

None of the Middle Stone Age (MSA) sites (Florissbad, Equus Cave, and Klasies) takes consistent positions in the seriation. A close look at the species from the late Pleistocene sites shows why: there are few distinctive faunal trends following the time of Elandsfontein deposition, thus site correlations are somewhat more spurious. Nevertheless, there is consistency in the sequence of Plovers Lake, Cornelia, Elandsfontein, and Cave of Hearths, and one of the MSA sites always comes out as the most recent site. This is illustrated by the following sequence covering the entire time span:

- H. MAK3 TAUH STS4 KROB SWT1
PLOV CORN EFTM COHA FLOS

Site analysis

Makapansgat

Makapansgat Member 3 has long been thought to be the oldest of the southern African fossil sites, and this is borne out by the faunal seriation. Over two-thirds of its species are extinct, and it shares no time-sensitive species with the late Pleistocene *Homo*-bearing sites. The assemblage includes particularly ancient species from East Africa such as the chalicotheriid, *Ancylotherium hennigi*, a primitive buffalo, *Simatherium kohllarseni*, and two primitive suids, *Potamochoeroides shawi* (Bender, 1992) and *Notochoerus scotti* (Cooke, 1993).

Member 4 at Makapansgat has its greatest faunal associations with Member 3, hence their alternating positions in the seriations. Both deposits contain *Australopithe-*

cus africanus as well as the ancient artiodactyls, *Simatherium* cf. *kohllarseni* and *Notochoerus scotti*, and Eisenhart (1974) had noted that the cercopithecids are virtually identical. Makapansgat Member 4 does pick up more extant fauna, but this is largely due to the microfauna from "rodent corner" which may have only a tenuous association with the large mammals in other parts of the cave. Although a stratigraphic separation between the two "members" exists in some parts of the cave, the difference may not have been of a geologically significant time period and Members 3 and 4 may be better viewed as different parts of the same cave exhibiting slightly different taphonomic processes (Maguire et al., 1985).

Taung

Most of the Taung fauna came from the Hrdlička deposits, which have their greatest affiliations with Sterkfontein Member 4. The faunal seriation of the time-sensitive species supports the recently espoused view that the Hrdlička deposits are roughly contemporaneous with Sterkfontein Member 4 (McKee, 1993a). As the association is as strong with Swartkrans Member 1 as it is with Makapansgat Member 3, a slightly later age may be tenable.

The Taung hominid skull, however, probably came from a cave system associated with the Dart deposits, and has been posited to be considerably older than the age represented by the Hrdlička faunal assemblage (McKee, 1993b). There are few time-sensitive species yet known from the Dart deposits, so a faunal age is difficult to ascertain by the seriation method used here. All of the seven species likely to be from the Dart deposits are extinct, and only two time-sensitive species (*A. africanus* and *Parapapio broomi*) occur at other sites, so an age predating Makapansgat is conceivable. On the other hand, the occurrence of four unique, extinct species, as witnessed in the Dart deposits, is not unexpected at a time following deposition at Makapansgat (McKee, 1994). The Dart assemblage, including the type specimen of *Australopithecus africanus*, most likely falls between the times of Makapansgat (Members 3 and 4) and Sterkfontein Member 4 (McKee, 1993a).

Sterkfontein

Sterkfontein Member 4 has been extremely well sampled through 27 years of continuous excavation. As it has yielded considerably more of the late Pliocene fauna known from other Transvaal sites than does Makapansgat, it most likely postdates Makapansgat. However, Sterkfontein Member 4 shares many ancient species with Makapansgat, and thus shows the last appearance of seven time-sensitive species (Table 4), including *A. africanus*.

Member 5 at Sterkfontein marks the first appearance in southern Africa of the genus *Homo* as well as of stone tools. Its strongest faunal affinities are with Sterkfontein Member 4, followed by Kromdraai A. Being that it has lost some of the older species, notably *A. africanus* and *Notochoerus scotti*, it is best placed following the Taung Hrdlička deposits. It does not have as strong an affinity to Swartkrans as does Kromdraai B, so the seriation places Sterkfontein Member 5 before Kromdraai B.

Sterkfontein Member 5 thus falls between two sites with which it has very little in common. There are a number of possible explanations for this. It may have had a distinctly different environment from that of Taung, as it does today, and thus would have more in common with Sterkfontein Member 4. However, it seems to be nearly contemporaneous with Kromdraai B, yet shares fewer than half of all its species, and only 27% of its time-sensitive species with this nearby site in the same valley. This may be attributable to taphonomic considerations in which early *Homo* is a major contributor to the Sterkfontein Member 5 deposit (Vrba, 1975, 1976, 1980; Brain, 1981, 1985; McKee, 1991), but not to Kromdraai which has been viewed as a part death trap and part feeding lair of opportunistic predators (Vrba, 1981; Brain, 1981). Indeed, Kromdraai B has remarkably few bovids, and Sterkfontein Member 5 has a paucity of cercopithecids.

A final possibility for the interpretation of Sterkfontein Member 5, as suggested by Vrba (1985), is that temporally distinct deposits are mixed within the "member." Archaeological evidence from recent excavations (Kuman, 1994) has increased the

likelihood of this interpretation. The time-sensitive species, however, fit conformably within the seriated position of Member 5 (Table 4).

Kromdraai

Kromdraai A and B are most similar to each other, but Kromdraai B, with *Australopithecus (Paranthropus) robustus*, is most likely older. Both units are the same FRI of time-sensitive species with Makapansgat Members 3 and 4, and Kromdraai B has proportionally stronger ties to Sterkfontein Member 4. Kromdraai A, on the other hand, is the first site to show a large increase in the number of extant time-sensitive species as well as those species characteristic of the Cornelia Faunal Span. This is largely due to the increased proportion of bovid species known from the site.

A case could be made for Kromdraai A following Swartkrans Member 1, as suggested by the seriation. This is largely due to the similarity between Kromdraai A and Plovers Lake, but there are other considerations. *Dinofelis pivetaeui* of Kromdraai A is seen to be an evolutionary descendent of *D. barlowi*, known from Swartkrans Member 1 and earlier sites (Cooke, 1991). Swartkrans Member 1 also has stronger faunal ties to Sterkfontein Member 4 and the Taung Hrdlička deposits. On the other hand, Kromdraai A has a strong resemblance to Kromdraai B and Sterkfontein Member 5, and has not yielded as many extant species as Swartkrans Members 2 and 3, so we suggest that on the current evidence it comes just before or very near in time to Swartkrans Member 1.

Swartkrans

The Swartkrans Formation harbors both *A. robustus* and *Homo* together for the first time. Each of the three members share the most species, including time-sensitive species, among themselves, and it has been suggested that they do not span a long period of time (Brain, 1988, 1993; Delson, 1988). However, Member 1 is clearly distinct from the others. It is the last site unit in the seriation to have strong faunal ties to Makapansgat, Taung, and Sterkfontein, and thus

sees the last appearance of eight time-sensitive species (Table 4). Recently Grine et al. (1993) have suggested a further link between Swartkrans Member 1 and Sterkfontein Member 5 with their identification of similarities in the hominid material, which they tentatively assign to *Homo habilis sensu lato*; Clarke (1985), however, refers the SK 847 cranium from Member 1 to *Homo erectus*. It should be noted as well that Swartkrans Member 1 also picks up five first appearances in the fossil record (or more if Kromdraai A follows it in time), thus clearly separating it from the early *Australopithecus* sites.

Swartkrans Members 2 and 3 then lose most of the fauna from sites of the Sterkfontein Faunal Span. By the time of Member 3, nearly half of the time-sensitive species, and 62% of all the species, are those that are extant today. Member 3 also provides the last glimpse of *A. robustus*.

There is a most remarkable similarity between Members 2 and 3 at Swartkrans, with an FRI for time-sensitive species of 100 and an overall FRI of 96. This may be because of a very close time frame covered by the deposition of the two members, but it is also possible that there has been some inadvertent mixing of specimens from the two members due to the decalcification of Member 3.

Plovers Lake

Plovers Lake, a cave site in the Blaaubank River Valley with Sterkfontein, Swartkrans, and Kromdraai, is the most recent addition to the known faunal assemblages of southern Africa. The fauna from Plovers Lake resembles most closely Kromdraai A and Swartkrans Member 3, and fits most consistently at or near the time of the latter. Plovers Lake presents the last appearance of *Papio robinsoni* (or *Papio hamadryas robinsoni*) and *Procavia transvaalensis*.

Cornelia

Cornelia is the last faunal site before the appearance of archaic *Homo sapiens* in the fossil record of southern Africa. It is especially significant for the last appearance of *Hipparion libycum*, the last time-sensitive species from Makapansgat Member 3. Cor-

nelia has its greatest affinities with the Elandsfontein Main Site. Remarkably, only 33% of all its species are extant. It has yielded many of the species characteristically associated with early *Homo* in southern Africa, but predates the *Homo* sites where extant species appear in greater proportions.

Elandsfontein

The Elandsfontein Main Site ushers in archaic *Homo sapiens* with the "Saldanha" skull. The fossils include the last evidence of some key Plio-Pleistocene boundary species including *Antidorcas recki*, *Theropithecus oswaldi*, and *Metridiochoerus andrewsi*, as well as the last appearance of the genus *Megantereon*, thus attesting to its great age. However, it is the first site to have extant species represented in over half of the time-sensitive fauna.

Cave of Hearths

The Acheulian levels near the bottom of the Cave of Hearths deposits in the Makapansgat valley, yielded a mandible and a radius of a human that have been referred by Tobias (1971) to *Homo sapiens rhodesiensis*. The relative position in time of this Early Stone Age (ESA) site is difficult to ascertain. Cornelia, Elandsfontein, and Cave of Hearths have "Upper Acheulian" (Butzer et al., 1974; Mason, 1988), but the latter site certainly postdates Cornelia and Elandsfontein on the basis of the fauna. The seriation results suggest, as did Cooke (1988), that the faunal assemblage is typical of the Middle Stone Age (MSA) sites. It has very close affinities to the MSA site of Equus Cave and is consequently seriated in variable positions following Elandsfontein. As the site of Equus Cave has apparent fully modern *Homo sapiens* (Grine and Klein, 1985), it fits that Cave of Hearths, with ESA artifacts and archaic *Homo sapiens*, should be older.

Florisbad

Florisbad comes out in the seriation in variable positions following Elandsfontein, with a strong similarity to Equus Cave. As with the other Late Pleistocene MSA sites, the faunal seriation alone can tell us little

about its relative age. However, the MSA deposits of Florisbad has five extinct species (Table 4), and sometimes seriates before the ESA deposits of Cave of Hearths, suggesting that it may be older than some of the other MSA sites. Kuman and Clark (1986) estimate the age of the Florisbad cranium and associated fauna to be in the range of 100,000 to 200,000 years old.

Equus Cave

Faunal remains from Equus Cave show that a somewhat more lush local environment once existed in what is now the desert margin at Taung. The site has yielded only three extinct species: *Antidorcas bondi*, which lasts until at least 38,000 B.P. at Border Cave (Klein, 1977); *Equus capensis*, the large equid which survives to the very end of the Pleistocene; and *Megalotragus priscus*, a giant alcelaphine last seen at 16,000 BP (Klein, 1980). The faunal seriation thus tells us little about the place in time of Equus Cave; the presence of MSA artifacts, however, places it prior to about 40,000 BP (Klein et al., 1991).

Klasies River Mouth

Although Klasies is an important MSA site with some evidence for *Homo sapiens* in a Late Pleistocene context, the faunal analysis of the hominid-associated MSA I and MSA II levels gives few clues as to its relative age. The site bears its strongest resemblance to Equus Cave, but has only one extinct species, *Pelorovis antiquus*, which went extinct between 12,000 and 10,000 BP (Klein, 1980). Attempts have been made to seriate the total faunal assemblage from the cave complex (Binford, 1986), but these studies have been shown to be problematic (Thackeray, 1986, 1987). Despite such uncertainty, there is little question that the lower-most deposits are on the order of 100,000 years, perhaps between 80,000 and 115,000 years old (Deacon and Geleijnse, 1988). Thus Florisbad, Klasies River Mouth, and perhaps Equus Cave, fall within a relatively short time range during which whatever mammalian faunal trends may have

existed could not be picked up by the seriation technique.

SUMMARY AND CONCLUSIONS

The faunal seriation of southern African cave site assemblages has proven to be a useful tool. Although it confirms the general validity of the faunal spans devised in the 1960s by Ewer and Cooke, greater resolution within those spans is now possible. Moreover, as with fossil species, the naming of faunal spans can obscure the evolutionary continuity of many mammals through time, so a sequence of individual sites is preferable.

On the basis of the total analysis, both with the logistical seriation of time-sensitive mammals and subjective scrutiny of the data, the following sequence of sites is most likely: Makapansgat Member 3, Makapansgat Member 4, Taung Dart deposits, Sterkfontein Member 4 and Taung Hrdlička deposits, Sterkfontein Member 5 (in part) and Kromdraai B, Kromdraai A and Swartkrans Member 1, Swartkrans Member 2, Swartkrans Member 3, Plovers Lake, Cornelia, Elandsfontein Main Site, Cave of Hearths Acheulian levels, Florisbad and Equus Cave and Klasies River Mouth.

An important caveat emerges from analysis of the FRI values across the sites. For most of the sites at which there is more than one deposit or "member," the FRI values for each unit are highest for other units of the same site. This is true of Makapansgat, Sterkfontein, Kromdraai, and Swartkrans, and thus seems to be more than coincidental. At each site there are a number of possible explanations including (1) temporal continuity across adjacent members, (2) similar external and internal environments yielding taphonomic consistency, and/or (3) inadvertent mixing of the fossils and breccias from separate deposits. The need to discern among these options highlights the importance of continuing field work and analysis.

The site sequence proposed here may change for some of the closely related sites, as the seriation for those sites is sensitive to the inclusion or exclusion of particular sites and species. The overall picture, however, is consistent for most sites and certainly the

proposed sequence may be used as a working framework for the interpretation of evolutionary patterns among the mammal species and as corroborating evidence for independent geochronological and biochronological techniques. Ongoing research at Sterkfontein, Taung, and Plovers Lake, as well as recently initiated excavations at Gladysvale, Makapansgat, and Kromdraai, undoubtedly will yield evidence that can refine the picture of Neogene mammalian evolution and the place of hominids in it.

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LITERATURE CITED

- Bender PA (1992) A reconsideration of the fossil suid, *Potamochoeroides shawi*, from the Makapansgat Limeworks, Potgeitersrus, Northern Transvaal. *Navors. nas. Mus. (Bloemfontein)* 8:1-67.
- Berger LR (1993) A preliminary estimate of the age of the Gladysvale australopithecine site. *Palaeont. Afr.* 30:51-55.
- Binford LR (1986) Reply to comments by R. Singer and J. Wymer. *Curr. Anthropol.* 27:57-62.
- Brain CK (1981) *The Hunters or the Hunted?* Chicago: University of Chicago Press.
- Brain CK (1985) Cultural and taphonomic comparisons of Hominids from Swartkrans and Sterkfontein. In E. Delson (ed.): *Ancestors: The Hard Evidence*. New York: Alan R. Liss, pp. 72-75.
- Brain CK (1988) New information from the Swartkrans cave of relevance to "robust" australopithecines. In FE Grine (ed.): *Evolutionary History of the "Robust" Australopithecines*. New York: Aldine de Gruyter, pp. 311-316.
- Brain CK (1993) Structure and stratigraphy of the Swartkrans cave in the light of new excavations. In CK Brain (ed.): *Swartkrans: A Cave's Chronical of Early Man*. Pretoria: Transvaal Museum Monograph No. 8, pp. 23-33.
- Brain CK, and Watson V (1992) A guide to the Swartkrans early hominid cave site. *Ann. Trans. Mus.* 35: 343-365.
- Brickhill JAJ (1976) Some small fossil felids from Makapansgat Limeworks. Unpublished B.Sc. Hons. Thesis, University of the Witwatersrand.
- Brink JS (1987) The archaeozoology of Florisbad, Orange Free State. *Mem. nas. Mus. (Bloemfontein)* 24: 1-151.
- Brock A, McFadden PL, and Partridge TC (1977) Preliminary palaeomagnetic results from Makapansgat and Swartkrans. *Nature* 266:249-250.
- Butzer KW (1974) Paleoeology of South African Australopithecines: Taung revisited. *Curr. Anthropol.* 15: 367-426.
- Butzer KW, Clark JD, and Cooke HBS (1974) The geology, archaeology and fossil mammals of the Cornelia Beds, O.F.S. O.F.S. Nat. Mus. (Bloemfontein) Mem. 9.
- Butzer KW, Stuckenrath R, Bruzewica AJ, and Helgren DM (1978) Late Cenozoic paleoclimates of the Gaap Escarpment, Kalahari Margin, South Africa. *Quat. Res.* 10:310-339.
- Churcher CS (1970) The fossil Equidae from the Krugersdorp caves. *Ann. Transvaal Mus.* 26:146-168.
- Clarke RJ (1985) *Australopithecus* and early *Homo* in southern Africa. In E. Delson (ed.): *Ancestors: The Hard Evidence*. New York: Alan R. Liss, pp. 171-177.
- Collings GE (1972) A new species of *Machaerodont* from Makapansgat. *Palaeont. Afr.* 14:87-92.
- Collings GE, Cruikshank ARI, Maguire JM, and Randall RM (1976) Recent faunal studies at Makapansgat Limeworks, Transvaal, South Africa. *Ann. S. Afr. Mus.* 71:153-165.
- Cooke HBS (1949) Fossil mammals of the Vaal River deposits. *Geol. Surv. (S. Afr.) Mem.* 35:1-117.
- Cooke HBS (1967) The Pleistocene sequence in South Africa and problems of correlation. In WW Bishop and JD Clark (eds.): *Background to Evolution in Africa*. Chicago: University of Chicago Press, pp. 175-184.
- Cooke HBS (1978) Suid evolution and correlation of African hominid localities: An alternative taxonomy. *Science* 201:460-463.
- Cooke HBS (1988) The larger mammals from the Cave of Hearths. In RJ Mason (ed.): *Cave of Hearths, Makapansgat, Transvaal*. Archaeological Research Unit (University of the Witwatersrand), Occasional Paper No. 21, pp. 507-534.
- Cooke HBS (1990) Taung fossils in the University of California Collections. In GH Sperber (ed.): *From Apes to Angels*. New York: Wiley-Liss, pp. 119-134.
- Cooke HBS (1991) *Dinofelis barlowi* (Mammalia, Carnivora, Felidae) cranial material from Bolt's Farm, collected by the University of California African Expedition. *Palaeont. Afr.* 28:9-21.
- Cooke HBS (1993a) Undescribed suid remains from Bolt's Farm and other Transvaal cave deposits. *Palaeont. Afr.* 30:7-23.
- Cooke HBS (1993b) Fossil Proboscidean remains from Bolt's Farm and other Transvaal cave deposits. *Palaeont. Afr.* 30:25-34.
- Cooke HBS, and Wells LH (1947) Fossil mammals from the Makapan valley, Potgeitersrus, III Giraffidae. *S. Afr. J. Sci.* XLIII:232-235.
- De Graaff G (1960) A preliminary investigation of the mammalian microfauna in Pleistocene deposits of caves in the Transvaal system. *Palaeont. Afr.* 7:59-118.
- De Graaff G (1988) The smaller mammals of the Cave of Hearths from basal guano underlying the acheulean

- deposits (circa 200,000 BP). In RJ Mason (ed.): Cave of Hearths, Makapansgat, Transvaal. Archaeological Research Unit (University of the Witwatersrand), Occasional Papers No. 21, pp. 535–548.
- De Swardt AMJ (1974) Geomorphological dating of cave openings in South Africa. *Nature* 250:683.
- Deacon HJ, and Geleijnse VB (1988) The stratigraphy and sedimentology of the main site sequence, Klasies River Mouth, South Africa. *S. Afr. Arch. Bull.* 43:5–14.
- Delson E (1984) Cercopithecoid biochronology of the African Plio-Pleistocene: Correlation among eastern and southern hominid-bearing localities. *Cour. Forsch. Inst. Senckenberg* 69:199–218.
- Delson E (1988) Chronology of South African australopithecite site units. In FE Grine (ed.): *Evolutionary History of the "Robust" Australopithecines*. New York: Aldine de Gruyter, pp. 317–324.
- Eisenhart WL (1974) Fossil Cercopithecoids of Makapansgat and Sterkfontein. Unpublished B.A. Thesis, Harvard University.
- Ewer RF, and Cooke HBS (1964) The Pleistocene mammals of Southern Africa. In DHS Davis (ed.): *Ecological Studies in Southern Africa*. The Hague: Dr. W. Junk Publishers, pp. 35–48.
- Freedman L (1957) The fossil Cercopithecoidea of South Africa. *Ann. Transvaal Mus.* 23:122–262.
- Greenwood M (1955) Fossil Hystricoidea from the Makapan Valley, Transvaal. *Palaeont. Afr.* 3:77–85.
- Grine FE, Demes B, Jungers WL, and Cole TM, III (1993) Taxonomic affinity of the early *Homo* cranium from Swartkrans, South Africa. *Am. J. Phys. Anthropol.* 92:411–426.
- Grine FE, and Klein RG (1985) Pleistocene and Holocene human remains from Equus Cave, South Africa. *Anthropology* 8:55–98.
- Grün R (1989) Electron spin resonance (ESR) dating. *Quat. Int.* 1:65–109.
- Grün R, Beaumont PB, and Stringer CB (1990a) ESR dating evidence for early modern humans at Border Cave in South Africa. *Nature* 344:537–539.
- Grün R, Shackleton NJ, and Deacon H (1990b) Electron-spin-resonance dating of tooth enamel from Klasies River Mouth Cave. *Curr. Anthropol.* 31:427–432.
- Grün R, and Stringer CB (1991) Electron spin resonance dating and the evolution of modern humans. *Archaeometry* 33:153–199.
- Harris JM, and White TD (1979) Evolution of the Plio-Pleistocene African Suidae. *Trans. Am. Phil. Soc.* 69:1–128.
- Helgren DM (1979) River of Diamonds: An Alluvial History of the Lower Vaal Basin, South Africa. Chicago: University of Chicago Research Paper no. 185.
- Hendey QB (1974) Faunal dating of the Late Cenozoic of southern Africa, with special reference to the carnivora. *Quat. Res.* 4:149–161.
- Hendey QB (1981) Palaeoecology of the Late Tertiary fossil occurrences in 'E' quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. *Ann. S. Afr. Mus.* 84:1–104.
- Hill A, Ward S, Deino A, Curtis G, and Drake R (1992) Earliest *Homo*. *Nature* 355:719–722.
- Hooijer DA (1958) Fossil Rhinoceroses from the lime-works cave, Makapansgat. *Palaeont. Afr.* 6:1–13.
- Jones DL, Brock A, and McFadden PL (1986) Palaeomagnetic results from the Kromdraai and Sterkfontein hominid sites. *S. Afr. J. Sci.* 82:160–163.
- Klein RG (1976) The mammalian fauna of the Klasies River Mouth site, southern Cape Province, South Africa. *S. Afr. Arch. Bull.* 31:75–98.
- Klein RG (1977) The mammalian fauna from the Middle and Later Stone Age (Later Pleistocene) levels of Border Cave, Natal Province, South Africa. *S. Afr. Archaeol. Bull.* 32:14–27.
- Klein RG (1980) Environmental and ecological implications of large mammals from Upper Pleistocene and Holocene sites in Southern Africa. *Ann. S. Afr. Mus.* 81:223–283.
- Klein RG, and Cruz-Urbe K (1991) The bovids from Elandsfontein, South Africa, and their implications for the age, palaeoenvironment, and origins of the site. *Afr. Archaeol. Rev.* 9:21–79.
- Klein RG, Cruz-Urbe K, and Beaumont PB (1991) Environmental, ecological, and paleoanthropological implications of the Late Pleistocene mammalian fauna from Equus Cave, Northern Cape Province, South Africa. *Quat. Res.* 36:94–119.
- Kuman K (in press) The archaeology of Sterkfontein: Past and present. *J. Hum. Evol.*
- Kuman K, and Clarke RJ (1986) Florisbad—new investigations at a Middle Stone Age hominid site in South Africa. *Geoarchaeology* 1:103–125.
- Maguire JM, Schrenk F, and Stanistreet IG (1985) The lithostratigraphy of the Makapansgat Limeworks australopithecine site: Some matters arising. *Ann. Geol. Surv. S. Afr.* 19:37–51.
- Mason RJ (1988) Cave of Hearths—Makapansgat, Transvaal. Archaeological Research Unit (University of the Witwatersrand), Occasional Paper No. 21.
- McFadden PL (1980) An overview of palaeomagnetic chronology with special reference to the South African hominid sites. *Paleont. Afr.* 23:35–40.
- McFadden PL, Brock A, and Partridge TC (1979) Palaeomagnetism and the age of the Makapansgat hominid site. *Earth Plant. Sci. Lett.* 44:373–382.
- McKee JK (1991) Palaeo-ecology of the Sterkfontein hominids: A review and synthesis. *Palaeont. Afr.* 28:41–51.
- McKee JK (1993a) The faunal age of the Taung hominid deposit. *J. Hum. Evol.* 25:363–376.
- McKee JK (1993b) The formation and geomorphology of caves in calcareous tufas and implications for the study of the Taung fossil deposits. *Trans. Roy. Soc. S. Afr.* 48:307–322.
- McKee JK (1993c) Taxonomic and evolutionary affinities of *Papio izodi* fossils from Taung and Sterkfontein. *Palaeont. Afr.* 30:43–49.
- McKee JK (in press) Faunal turnover patterns in the Pliocene and Pleistocene of southern Africa. *S. Afr. J. Sci.*

- Partridge TC (1973) Geomorphological dating of cave opening at Makapansgat, Sterkfontein, Swartkrans and Taung. *Nature* 246:75–79.
- Partridge TC (1982) The chronological positions of the fossil hominids of Southern Africa. *Proc. Cong. Int. Pal. Humaine, Nice* 2:617–675.
- Partridge TC (1985) Spring flow and tufa accretion at Taung. In PV Tobias (ed.): *Hominid Evolution: Past, Present and Future*. New York: Alan R. Liss, pp. 171–187.
- Pocock TN (1987) Plio-Pleistocene fossil mammalian microfauna of Southern Africa—A preliminary report including description of two new fossil Muroid genera. *Palaeont. Afr.* 26:69–91.
- Randall RM (1981) Fossil Hyaenidae from the Makapansgat Limeworks deposit, South Africa. *Palaeont. Afr.* 24:75–85.
- Schwarz HP, Grün R, and Tobias PV (1993) ESR dating studies of the australopithecine site of Sterkfontein, South Africa. *J. Hum. Evol.* 26:175–181.
- Simpson GG (1960) Notes on the measurement of faunal resemblance. *Am. J. Sci.* 258-A:300–311.
- Skinner JD, and Smithers RHN (1990) *The Mammals of the Southern African Subregion*. Pretoria: University of Pretoria.
- Szalay FS, and Delson E (1979) *Evolutionary History of the Primates*. New York: Academic Press.
- Thackeray JF (1986) Further comment on fauna from Klasies River Mouth, South Africa. *Curr. Anthropol.* 27:511.
- Thackeray JF (1987) Statistical analyses of faunal data from Klasies River Mouth. *Curr. Anthropol.* 29:149–151.
- Tobias PV (1971) Human skeletal remains from the Cave of Hearths, Makapansgat, Northern Transvaal. *Am. J. Phys. Anthropol.* 34:335–367.
- Tobias PV (1973) Implications of the new age estimates of the early South African hominids. *Nature* 246:79–83.
- Tobias PV (1975) New African evidence on the dating and phylogeny of the Plio-Pleistocene Hominidae. In RP Suggate and MM Cresswell (eds.): *Quaternary Studies*. Wellington: Royal Society of New Zealand, pp. 289–296.
- Tobias PV (1978) The South African australopithecines in time and hominid phylogeny, with special reference to the dating and affinities of the Taung skull. In CJ Jolly (ed): *Early Hominids of Africa*. London: Duckworth, pp. 45–84.
- Tobias PV (1991a) Nouvelles hypotheses sur l'apparition de l'homme dans un environnement Africain instable. *L'Anthropologie* 95:379–390.
- Tobias PV (1991b) *Olduvai Gorge, Volume 4: The Skulls, Endocasts and Teeth of Homo habilis*. Cambridge: Cambridge University Press.
- Tobias PV, Vogel JC, Oschadleus HD, Partridge TC, and McKee JK (1993) New isotopic and sedimentological measurements on the Thabaseek deposits and their bearing on the dating of the Taung hominid. *Quat. Res.* 40:360–367.
- Turner A (1983) Biogeography of Miocene-Recent larger carnivores in Africa. In JC Vogel (ed.): *Late Cainozoic: Palaeoclimates of the Southern Hemisphere*. Rotterdam: A. A. Balkema, pp. 499–506.
- Turner A (1986) Miscellaneous carnivore remains from Plio-Pleistocene deposits in the Sterkfontein Valley (Mammalia: Carnivora). *Ann. Transvaal Mus.* 34:203–226.
- Turner A (1987) New fossil carnivore remains from the Sterkfontein hominid site (Mammalia: Carnivora). *Ann. Transvaal Mus.* 34:319–347.
- Turner A (1990) The evolution of the guild of larger terrestrial carnivores during the Plio-Pleistocene in Africa. *Geobios* 23:349–368.
- Turner A, and Wood B (1993) Taxonomic and geographic diversity in robust australopithecines and other African Plio-Pleistocene larger mammals. *J. Hum. Evol.* 24:147–168.
- Vogel JC (1985) Further attempts at dating the Taung tufas. In PV Tobias (ed.): *Hominid Evolution: Past, Present and Future*. New York: Alan R. Liss, pp. 189–194.
- Vogel JC, Partridge TC (1983) Preliminary radiometric ages for the Taung tufas. In JC Vogel (ed.): *Late Cainozoic: Palaeoclimates of the Southern Hemisphere*. Rotterdam: A.A. Balkema, pp. 507–514.
- Vrba ES (1975) Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil Bovidae. *Nature* 254:301–304.
- Vrba ES (1976) The fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai. *Transvaal Mus. Mem.* 21, pp. 1–166.
- Vrba ES (1980) The significance of Bovid remains as indicators of environment and predation patterns. In AK Behrensmeyer and AP Hill (eds.): *Fossils in the Making*. Chicago: University of Chicago Press, pp. 247–271.
- Vrba ES (1981) The Kromdraai Australopithecine site revisited in 1980: Recent investigations and results. *Ann. Transvaal Mus.* 33:17–60.
- Vrba ES (1982) Biostratigraphy & chronology, based particularly on Bovidae, of southern hominid-associated assemblages: Makapansgat, Sterkfontein, Taung, Kromdraai, Swartkrans; also Elandsfontein (Saldanha), Broken Hill (now Kabwe) and Cave of Hearths. In H deLumley and MA deLumley (eds.): *Proc. Congres international de paleontologie humaine, Vol 2*, pp. 707–752. Nice: Union Internationale des Sciences Prehistoriques et Protohistorique.
- Vrba ES (1985a) Environment and evolution: Alternative causes of the temporal distribution of evolutionary events. *S. Afr. J. Sci.* 81:229–236.
- Vrba ES (1985b) Early hominids in Southern Africa: Updated observations on chronological and ecological background. In PV Tobias (ed.): *Hominid Evolution: Past, Present and Future*. New York: Alan R. Liss, pp. 195–200.
- Vrba ES (1987a) New species and a new genus of Hippotragini (Bovidae) from Makapansgat Limeworks. *Palaeont. Afr.* 26:47–58.
- Vrba ES (1987b) A revision of the Bovini (Bovidae) and a preliminary revised checklist of Bovidae from Makapansgat. *Palaeont. Afr.* 26:33–46.

- Vrba ES (1988) Late Pliocene climatic events and hominid evolution. In FE Grine (ed.): *Evolutionary History of the "Robust" Australopithecines*. New York: Aldine de Gruyter, pp. 405–426.
- Vrba ES (1992) Mammals as a key to evolutionary theory. *J. Mamm.* 73:1–28.
- Watson V (1993) Composition of the Swartkrans bone accumulations, in terms of skeletal parts and animals represented. In CK Brain (ed.): *Swartkrans: A Cave's Chronicle of Early Man*. Pretoria: Transvaal Museum Monograph No. 8, pp. 35–73.
- Wolpoff MH (1974) CA* comments on Butzer. *Curr. Anthropol.* 15:412–413.