

FURTHER CHRONOLOGICAL SERIATIONS OF SOUTHERN AFRICAN PLIOCENE AND PLEISTOCENE MAMMALIAN FAUNAL ASSEMBLAGES

by

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ABSTRACT

Mammalian fossil assemblages from Pliocene and Pleistocene sites of southern Africa have recently been seriated in order to establish a relative chronology (McKee *et al.* 1994). Although an order was inferred for 17 site assemblages of fossil mammals, only ten sites could be seriated at a time. The logistical seriation method has now been modified to handle a greater number of sites at once. Seriations were run on a matrix of Faunal Resemblance Index values for an updated list of time-sensitive mammals of 18 fossil site assemblages. In addition, each assemblage was systematically excluded from analysis in successive seriations to test the robusticity of the method against the influence of individual assemblages. The seriations gave largely consistent results, with the exception of the terminal Pleistocene sites. The most likely chronological sequence inferred from the logistical seriations alone, with corrections for stratigraphic considerations, is: Makapansgat Member 3, Makapansgat Member 4, Taung Hrdlička deposits, Sterkfontein Member 4, Kromdraai B, Sterkfontein Member 5 (in part), Kromdraai A, Swartkrans Member 1, Swartkrans Member 2, Swartkrans Member 3, Gondolin, Plovers Lake, Cornelia, Elandsfontein Main Site, Florisbad/Equus Cave, Cave of Hearths and Klasies River Mouth.

INTRODUCTION

Temporal context is critical for assessing the possible evolutionary roles and associations of fossil mammals. Southern African fossil sites representing the Pliocene and Pleistocene have been problematic in that the nature of most sites has inhibited successful dating by available geochronological techniques (see reviews in Partridge 1986; McKee 1993; McKee *et al.* 1995). Thus our current conception of the temporal framework for these sites is largely reliant on biochronological assessments of the fossil fauna.

Previous approaches to faunal chronologies of southern Africa sites have relied on establishing faunal spans (e.g. Ewer & Cooke 1964; Cooke 1964), or relied on sequences within taxonomic families (Hendey 1974; Vrba 1975, 1982, 1985; Harris & White 1979; Delson 1984; Turner 1990). In order to update the earlier approaches, and use all identified fossil mammals to test the within-family chronologies, a data base of identified mammal species from southern African Neogene sites was compiled and an initial attempt was made to seriate the fossil assemblages (McKee *et al.* 1995). Although a chronological sequence was established for 17 fossil sites, the logistical seriation technique was limited to dealing with only ten sites at a time. The final site sequencing was then compiled from multiple seriations. It was also found that the inclusion or exclusion of particular site assemblages could affect the results of the seriations. In order to overcome these difficulties, the seriation technique has been modified and the new results are reported herein. Additionally, the data base has been updated to accommodate recent developments in Plio-Pleistocene palaeontology.

MATERIALS AND METHODS

A data base of identified mammals from southern African fossil sites (SAFAUNA) was updated from that reported in McKee *et al.* (1995). The updates included the addition of a faunal list from Gondolin (Watson 1993), a modified faunal list for Makapansgat Members 3 and 4 based on the recent assessment by Reed (1995), and the synonymy of *Oreotragus major* with *Oreotragus oreotragus* (Watson & Plug, 1994). The fossil site assemblages used in this analysis are listed in Table 1.

TABLE 1

Fossil site faunal assemblages and codes used in Tables 2-3.

Makapansgat Member 3	MAK3
Makapansgat Member 4	MAK4
Taung Hrdlička deposits	TAUH
Sterkfontein Member 4	STS4
Sterkfontein Member 5	STS5
Kromdraai A	KROA
Kromdraai B	KROB
Swartkrans Member 1	SWT1
Swartkrans Member 2	SWT2
Swartkrans Member 3	SWT3
Gondolin	GOND
Plovers Lake	PLOV
Cornelia	CORN
Elandsfontein Main Site	EFTM
Cave of Hearths (Acheulian levels)	COHA
Florisbad springs	FLOS
Equus Cave (MSA levels)	EQUU
Klasies River Mouth (MSA I & II levels)	KLAS
Extant species in southern Africa	EXTA

	M A K 3	M A K 4	T A U H	S T S 4	K R O B	S T S 5	K R O A	S W T 1	S W T 2	S W T 3	G O N D	P L O V	C O R N	E F T M	E Q U U	F L O S	C O H A	K L A S	E X T A
CARNIVORA																			
<i>Lycaon pictus</i>														*	*	*			*
<i>Vulpes pulcher</i>							*	*											
<i>Dinofelis barlowi</i>	*			*				*											
<i>Homotherium crenatidens</i>				*		*	*												
<i>Megantereon cultridens</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>Gigantohyrax maguirei</i>	*	*																	
<i>Procavia transvaalensis</i>		*					*	*	*	*	*	*							

Logistical seriation of the assemblages was based on Simpson's (1960) Faunal Resemblance Index (FRI), a robust measure of the degree of similarity between assemblages of time-sensitive fauna. 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 $FRI = C/N_1 \times 100$. This standardizes site comparisons, and limits the effect of differential sampling of mammal species from the fossil assemblages. These values were calculated for every pair of sites, resulting in the matrix displayed in Table 3.

Optimally seriated matrices should have successively greater FRI values running toward the diagonal (where each assemblage, compared with itself, has an FRI value of 100). In other words, adjacent sites in the sequence should have assemblages that are more similar to each other than to more chronologically distant sites. Although the choice of time-sensitive species and the calculation of FRI values is meant to minimize the effects of non-temporal factors, a perfect logistical seriation is highly improbable given the incomplete nature of the fossil record (see McKee 1995). The seriation technique must minimize deviations from a

series of values increasing toward the diagonal; these deviations are called "backward steps". A "score" is calculated for each ordering of the matrix by summing the absolute value of differences between adjacent sites in a row showing "backward steps". The matrix with the site sequence yielding the lowest score, or the fewest deviations from an ideal matrix, is deemed to represent the optimal seriation.

Computerized logistical seriation techniques used previously were able to seriate only ten assemblages at a time. This is because the number of total orderings of a matrix of ten sites is a factorial ten, or 3,628,000 possibilities, taking about 1.5 hours on a personal computer. Larger matrices would continue to multiply the time needed to try every possible site sequence. However, once a preliminary sequence is established it is not necessary to try every possible order. For example, it is not logical to bother scoring a matrix in which a Pliocene site such as Taung is placed between two Late Pleistocene sites such as Florisbad and Equus Cave. Yet there is value in seriating the entire matrix of 18 sites at once, so that the influence of all the documented sites can be used to determine the optimal order.

A matrix of all 18 sites was seriated with an iterative method by testing permutations of orderings for ten assemblages of the matrix at a time. Thus, while a score was calculated on the basis of all sites, all possible sequences were attempted by reordering sites 9 through 18. Once an optimal seriation was found (as measured by a minimal score), all possible sequences of sites 1 through 10 were tested (holding the remaining sites in a constant order). This process continued iteratively until no improvements in the score were found for either sets (1-10 or 9-18). In this way all reasonable sequences were tested, and the remaining possible site sequences were assumed to be less than optimal.

The final aspect to be considered was that the inclusion or exclusion of a site assemblage could affect the seriation. Thus after the entire matrix of 18 sites was seriated, the process was repeated 18 times on matrices of 17 assemblages, each time excluding a different site assemblage. This systematically tested the robusticity of the seriation against the influence of individual assemblages.

RESULTS

In Table 3 the optimal sequence of 18 site assemblages of time-sensitive mammals is listed along with the matrix of FRI values. Out of the subsequent 18 seriations of 17 sites, each with one successive site assemblage eliminated, 12 yielded the same optimal sequence. Variant sequences of the remaining six seriations included a reversal of the positions of Florisbad and Equus Cave (five seriations), one reversal of Cave of Hearths and Florisbad, and one reversal to correct stratigraphic order of Swartkrans Members 2 and 3.

Out of all the logistical seriations, Makapansgat 3 and 4 were consistently in the incorrect stratigraphic order. Likewise, Swartkrans Members 2 and 3 were reversed in all but one of the seriations. However, when

the seriation was rerun with these sites forced into their correct stratigraphic order, there was no effect on the relative positions of any other sites.

DISCUSSION

New developments of the logistical seriation technique, in which all of the 18 sites could be seriated in a single matrix, resulted in a chronology that is largely consistent with that reported by McKee *et al.* (1995). Moreover, the relative consistency of results achieved with the sequential exclusion of individual site assemblages attests to the robusticity of the seriations against the influence of particular sites. However, whereas most of the earlier conclusions regarding the inferred chronology of fossil site assemblages still hold, there are a few noteworthy changes in the sequence.

The relative position of Kromdraai B consistently fell before Sterkfontein Member 5, whereas previously the reverse order was more common. This discrepancy points to the problem noted earlier that the fauna from Sterkfontein Member 5 may represent an extended time period, as confirmed by the archaeological analysis of Kuman (1994). The most reasonable conclusion would be that part of the Sterkfontein Member 5 deposit is penecontemporaneous with Kromdraai B.

It should be cautioned as well that the seriation technique does not have the statistical power to differentiate between the positions of any of the penecontemporaneous sites. This is because sites that lie within 100,000 years or so of each other would probably not sample a distinctly different faunal community, given the slow rates of speciation and extinction (McKee 1995). This is illustrated by the reversals of stratigraphic order seen in the seriations of Makapansgat and Swartkrans. Thus, although the Taung Hrdlička deposits consistently seriate before Sterkfontein Member 4, this alone does not provide sufficient evidence that the sites differ significantly in time. Likewise, the relative positions of the Middle Stone Age (MSA) sites of Equus Cave, Florisbad and Klasies River Mouth do not necessarily reflect a clear chronology.

Mammalian fossils from the Cave of Hearths still present an interpretive problem. Despite the presence of Acheulian artefacts in the deposit, the faunal assemblage consistently seriates among MSA sites. Cooke (1988) also noticed that the fauna were typical of the MSA. Although it is tempting to propose ecological or cultural explanations for this anomaly, it would perhaps be more wise to reassess the Cave of Hearths fauna in light of more recent advances in mammalian taxonomy.

CONCLUSION

Evaluation of the logistical seriations of time-sensitive mammals from 18 faunal assemblages, correcting for known stratigraphic order, suggests the following optimal chronological sequence: Makapansgat Member 3, Makapansgat Member 4, Taung Hrdlička deposits, Sterkfontein Member 4, Kromdraai B, Sterkfontein Member 5, Kromdraai A, Swartkrans Member 1, Swartkrans Member 2, Swartkrans Member 3, Gondolin,

Table 3

List of shared species at southern African faunal assemblages, in optimal seriated order. A) Absolute frequencies of shared species. B) Faunal Resemblance Index (FRI). (Site codes are listed in Table 1).

		A																	
		MAK4	MAK3	TAUH	STS4	KROB	STS5	KROA	SWT1	SWT3	SWT2	GOND	PLOV	CORN	EFTM	EQUU	FLOS	COHA	KLAS
MAK4		12	12	10	4	1	3	3	0	0	0	0	0	0	0	0	0	0	0
MAK3		12	19	5	15	5	2	7	7	1	1	2	0	1	0	0	0	0	0
TAUH		4	5	7	5	4	1	3	4	1	1	1	1	0	0	0	0	0	0
STS4		10	15	5	24	8	8	10	11	4	3	1	1	1	2	2	1	1	1
KROB		4	5	4	8	12	4	9	9	5	4	1	2	2	1	1	1	1	0
STS5		1	2	1	8	4	11	8	6	6	4	2	1	3	2	2	2	2	0
KROA		3	7	3	10	9	8	23	15	12	8	8	7	6	6	7	4	6	5
SWT1		3	7	4	11	9	6	15	26	16	13	7	5	5	8	8	3	4	6
SWT3		0	1	1	4	5	6	12	16	20	16	8	7	5	9	10	5	4	5
SWT2		0	1	1	3	4	4	8	13	16	16	7	5	5	8	7	4	2	3
GOND		0	2	1	1	1	2	8	7	8	7	11	5	5	6	5	4	4	3
PLOV		0	0	1	1	2	1	7	5	7	5	5	10	3	6	6	4	5	3
CORN		0	1	0	1	2	3	6	5	5	5	5	3	11	9	4	6	5	3
EFTM		0	0	0	2	1	2	6	8	9	8	6	6	9	21	12	9	8	10
EQUU		0	0	0	2	1	2	7	8	10	7	5	6	4	12	24	13	11	14
FLOS		0	0	0	1	1	2	4	3	5	4	4	4	6	9	13	15	8	6
COHA		0	0	0	1	1	2	6	4	4	2	4	5	5	8	11	8	13	9
KLAS		0	0	0	1	0	0	5	6	5	3	3	3	3	10	14	6	9	17
		B																	
		MAK4	MAK3	TAUH	STS4	KROB	STS5	KROA	SWT1	SWT3	SWT2	GOND	PLOV	CORN	EFTM	EQUU	FLOS	COHA	KLAS
MAK4		100	100	57	83	33	9	25	25	0	0	0	0	0	0	0	0	0	0
MAK3		100	100	71	79	42	18	37	37	5	6	18	0	9	0	0	0	0	0
TAUH		57	71	100	71	57	14	43	57	14	14	14	14	0	0	0	0	0	0
STS4		83	79	71	100	67	73	43	46	20	19	9	10	9	10	8	7	6	6
KROB		33	42	57	67	100	36	75	75	42	33	9	20	18	8	8	8	0	0
STS5		9	18	14	73	36	100	73	55	55	36	18	10	27	18	18	18	0	0
KROA		25	37	43	43	75	73	100	65	60	50	73	70	55	29	30	27	29	29
SWT1		25	37	57	46	75	55	65	100	80	81	64	50	45	38	33	20	35	35
SWT3		0	5	14	20	42	55	60	80	100	100	73	70	45	45	50	33	31	29
SWT2		0	6	14	19	33	36	50	81	100	100	64	50	45	50	44	27	15	19
GOND		0	18	14	9	9	18	73	64	73	64	100	50	45	55	45	36	36	27
PLOV		0	0	14	10	20	10	70	50	70	50	50	100	30	60	60	40	50	30
CORN		0	9	0	9	18	27	55	45	45	45	45	30	100	82	36	55	45	27
EFTM		0	0	0	10	8	18	29	38	45	50	55	60	82	100	57	60	62	59
EQUU		0	0	0	8	8	18	30	33	50	44	45	60	36	57	100	87	85	82
FLOS		0	0	0	7	8	18	27	20	33	27	36	40	55	60	87	100	62	40
COHA		0	0	0	8	8	18	46	31	31	15	36	50	45	62	85	62	100	69
KLAS		0	0	0	6	0	0	29	35	29	19	27	30	27	59	82	40	69	100

Plovers Lake, Cornelia, Elandsfontein Main Site, Florisbad/Equus Cave, Cave of Hearths, and Klasies River Mouth. The true chronology may vary slightly, for the seriations cannot effectively differentiate between penecontemporaneous sites. Nevertheless, the robusticity of the method suggests that the seriated sequence can provide a generally sound chronological framework for interpreting the southern African fossil record.

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