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PALAEO-ECOLOGY OF THE STERKFONTEIN HOMINIDS: A REVIEW AND SYNTHESIS

by

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Abstract

Excavations at the Sterkfontein hominid fossil site have yielded a rich and revealing faunal assemblage. Evolutionary transitions are evident in early hominids and associated fauna between the times represented by Members 4 and 5. Member 4 has yielded a large and variable sample of *Australopithecus africanus* as well as evidence of considerable species diversity among the artiodactyls, carnivores and primates. The appearance of early *Homo* along with stone and bone tools in Member 5 coincides with a reduction of species representation in the orders of larger mammals as well as with the occurrence of new derived species and apparent extinctions.

Three hypotheses have been suggested to account for the trends seen in the hominid-bearing members of the Sterkfontein Formation. The 'Climatic Change Hypothesis' accounts for the evolutionary trends by the causal factors of global and local cooling and aridification with evidence of savanna-grasslands supplanting an earlier environment with a denser cover of vegetation. The 'Taphonomic Hypothesis' explains changes in relative species representation at Sterkfontein in terms of the bone-accumulating agents; in Member 4 primary carnivores were largely responsible for the deposition of large mammalian fauna, whereas the scavenging activities of early *Homo* would have accounted for much of the bone and all of the artefacts found in Member 5. A third proposition is the 'Species Interaction Hypothesis', a derivative of the 'Red-Queen Hypothesis'; here the dynamics of species interaction, including competition and commensalism among hominids, carnivores and cercopithecids, propel the evolutionary changes and cause the extinctions.

These hypotheses are not mutually exclusive, but the relative effects of the factors involved must be verified or refuted with better chronological controls and further analyses of the African fossil sites. The Sterkfontein Formation represents a microcosm in which various scenarios of African mammalian evolution can be tested.

INTRODUCTION

Since Robert Broom revealed the first adult specimen of *Australopithecus* in 1936, the Sterkfontein fossil site has been recognized globally as a vital source of information on hominid evolution. Excavations by Broom and J.T. Robinson yielded a wealth of Plio-Pleistocene fauna along with the hominids (Brain 1981). Later work by P.V. Tobias and A.R. Hughes, still in progress today, has significantly multiplied the fossil data base from Sterkfontein (Tobias and Hughes 1969; Tobias 1973; Tobias *et al.* 1990). The time depth and fossil richness of the Sterkfontein Formation thus provide a valuable basis for testing hypotheses concerning the evolution of hominids and other African fauna.

Palaeontological description of the Sterkfontein fossils has focused on hominid morphology, anatomical adaptations and phylogenetic positions. The complete framework of evolution, however, requires a careful analysis of the adaptive milieu in which the early hominids were living. Such ecological analyses are among the stated goals of the current excavation (Tobias & Hughes 1969; Tobias 1973). In this review I address issues of palaeo-ecology from a faunal perspective, updating Brain's (1981) comprehensive analysis with recently published research that has yielded new perspectives on the Plio-Pleistocene environments sampled in the Sterkfontein deposits.

Ecological reconstructions of the ancient Sterkfontein habitats are far from complete. The tasks remain to (1) differentiate climatic from taphonomic effects in fossil representation, (2) identify and assess the total fossil sample within a geological and chronological framework, and (3) apply the data in a holistic manner to hypotheses of current evolutionary theory. Recent work has made significant inroads into these tasks, and here my aim is to review the palaeo-ecological research and construct a framework of testable hypotheses for further analyses.

CONTEXT OF THE STERKFONTEIN HOMINIDS

Contextual information of the Sterkfontein hominids comes from the ancient caves in which they were deposited. The Sterkfontein fossil site formed as one of a number of dolomitic caves in the Blaaubank river valley of the South

African Transvaal. Three other sites in the immediate vicinity have yielded early hominid remains, namely Swartkrans, Kromdraai and Cooper's. The fossils were discovered in cave-fill matrix exposed by lime quarry operations, natural erosion and palaeontological excavation.

In a sedimentological and stratigraphical analysis, Partridge (1978) defined the Sterkfontein Formation as a series of six successive deposits or "members". Of concern here are Members 4 and 5, both of which have yielded hominid remains. Although Member 4 has been further subdivided into Beds A-D, very few of the fossils have been assigned to a specific bed.

Excavations of Sterkfontein Member 4 have produced a large and valuable sample of *Australopithecus africanus* fossils. Within this member it is apparent that the hominid fossils come from different beds of this cone-shaped deposit (Partridge 1978), but the time span represented by this depositional sequence is not yet known. The hominids are so variable that Clarke (1985, 1988a, 1988b) and Kimbel and Rak (1991) have suggested the possibility of two hominid species being represented in different parts of Member 4; this notion requires further substantiation.

Sterkfontein Member 5 is differentiated from Member 4 by the fossils as well as by the artefactual content of Early Acheulian stone tools (Stiles and Partridge 1979; Clarke 1985, 1988b; Mason 1985; but see Leakey 1970) and at least two bone tools (Robinson 1959; Brain 1981) in Member 5. Clarke (1985) was able to discern a distinct, nearly vertical division between the two members along a single transect separating the *Australopithecus* fossils of Member 4 from the artefacts in Member 5. Along with the artefacts were the fossil remains, some of which have been identified as *Homo habilis* (Hughes and Tobias 1977).

Analyses of the stone tool distribution and skeletal remains of Member 5 have led Stiles and Partridge (1979) and Brain (1985) to suggest that it is likely that the entrance to the Sterkfontein cave was occupied by early *Homo*. Thus Member 5 could represent not only a different time period from Member 4, but a distinct part of the cave. In his analysis of the rich microfaunal component of Member 5, Pocock (1987) stated that the fossils were primarily of owl pellet origin, implying accumulation near the outer reaches of the cave (Andrews 1990). Member 4 could have accumulated through a different entrance, consistent with the paucity of microfauna (Brain 1981; Pocock 1987) and the inferred talus-cone shape of the formation.

Differences in the pattern of bone accumulation in Members 4 and 5 are discussed in greater detail in the following sections, but a cautionary note is necessary concerning the possibility of collecting biases toward cranial material among the early fossil collectors. Brain (1981) attributed the paucity of post-cranial material in Member 4 to a loss of the bones before fossilization, implying that the cave was not a death trap for animals (which would result in more complete representation of the body). The continuing excavations have revealed considerably more post-cranial material of all species in Member 4 (Alun Hughes personal communication), including a remarkably complete partial hominid skeleton (Tobias *et al.* 1987). Thus a collecting bias on the part of the earlier investigators may have significantly affected the apparent relative frequencies of skeletal body parts. One cannot exclude the possibility that Member 4 material accumulated in a death trap or place for animals to die, for the total body representation is consistent with such a notion.

Accurate geological dating of the fossil site has proved problematic (Partridge 1982; Jones *et al.* 1986), for the results of the palaeomagnetic assessments have not been definitive. Faunal dating is also somewhat tenuous. Primarily on the basis of the bovid fossils, Vrba (1982, 1985) estimates that Sterkfontein Member 4 was deposited between 2,3 and 2,8 mya. Member 5 is dated to around 1,5 mya (Vrba 1982), but there is a suggestion that a component of Member 5 may be closer to 2 mya (Vrba 1985). Delson's (1984, 1988) cercopithecid chronology places Member 4 just after 2,5 mya; the weak cercopithecid evidence from Member 5 suggests a date between 1,5 and 2,0 mya. Further work is necessary to refine these dates, for an ecological assessment of the hominid adaptive process depends on an accurate chronological correlation of the faunal sites.

Palaeo-ecological studies of the Sterkfontein Formation require an interdisciplinary approach, but have been difficult due to the nature of the cave sites. Palynological data that could reveal the environment surrounding the Sterkfontein caves during periods of deposition have been difficult to find. Although initial pollen analyses by Horowitz (1975) suggested the possibility of an open grassland and drier environment in Member 4 than that present during deposition of Member 5, the presence of *Pinus* pollen revealed that the sample had been contaminated by modern pollen (Scott and Bonnefille 1986). The geological evidence for climatic changes at Sterkfontein, summarized by Partridge (1982), is ambiguous at best. The most revealing clues to the palaeo-environments have come from the fauna preserved in the deposits.

The earlier faunal analyses relate fossils to Robinson's (1962) original stratigraphic sequence or to parts of the excavation site, and some clarification is necessary to correlate the literature. Partridge (1978) equates Member 4 with Robinson's 'lower breccia', encompassing the 'Type Site' in which the *Australopithecus* remains were recovered, and the base of the 'Extension Site' where Robinson worked in 1957 and 1958. Member 5 then corresponds to the 'Middle Breccia', including much of the Extension Site and the uppermost portion of the Type Site. (The 'Upper Breccia' of the Extension Site comprises Member 6.) As will be discussed below, it is important to note that Members 4 and 5 do not necessarily correspond directly to the Type and Extension Sites respectively, thus not all of the fauna of the earlier excavations can be assigned confidently to a specific member or time period.

FAUNAL CHANGES AT STERKFONTEIN AND MAN'S ADAPTIVE ENVIRONMENT

Any environmental changes apparently associated with hominid evolution are revealed in part by the animals that changed, or did not change, within the same local context. Faunal analyses can either corroborate or challenge ecological hypotheses, and provide an important context for the appearance of the genus *Homo* and associated artefacts within a biotic community.

The currently identified fossil species represented among the Sterkfontein large fauna are listed in Table 1. Although an environmental reconstruction can be gleaned from the fossil remains, it must be remembered that the fossil record represents only a portion of the animals living at the time of deposition (Thackeray 1980; Turner 1983b) and that the samples of some taxa are currently too small to be of much value in palaeoecological studies. The taxa discussed below are those that have been assessed in the literature and which have direct relevance to the adaptive environment of early man. The ecological significance of the fauna is subject to varied interpretations.

Bovidae

It is apparent from the list of bovid species in Table 1 that Sterkfontein Members 4 and 5 differ both in number and types of species represented. An extensive analysis of the Sterkfontein fossil bovids is provided in a remarkable series of publications by Elisabeth Vrba stemming from her doctoral thesis work (Vrba 1976). The resulting palaeo-ecological interpretations exemplify the potential as well as the pitfalls of such analyses.

One of the main differences between bovid representations in Members 4 and 5 is the number of *Makapania broomi* and cf. *Hippotragus cookei* (formerly *?Hippotragus*), increasing the Member 4 percentage of buck assumed to be adapted to dense vegetation (Vrba 1976, 1980). Member 4 has the latest representation of these two species (Vrba 1988), suggesting subsequent extinction. A comparison of Sterkfontein Members 4 and 5 also shows a distinct shift in the proportions of bovid types represented. Member 5 contains significantly greater relative frequencies of alcelaphines and antilopines (Vrba 1974, 1975, 1976). Other evolutionary changes among the bovids are indicated by differences in the dental morphology of the dominant species in Member 5 (and Swartkrans Member 1) that suggest a change in the adaptive environment (Vrba 1980, 1988).

Natural habitat preferences of modern bovids provide a model for environmental reconstructions which suggest that changes may have taken place between the times of Members 4 and 5. The basic assumptions of Vrba's palaeo-ecological model are that bovids are adapted to specific environments and thus are sensitive to changes in their habitat (Vrba 1976). Furthermore, this should be reflected in the relative proportions of fossil accumulations at southern African cave sites (Vrba 1980). In particular, abundant representation of the alcelaphini and antilopini tribes are thought to be indicative of open plains and grasslands (Vrba 1975, 1980). Vrba's inference is that the relative frequencies of bovids at Sterkfontein indicate a drier climate with more open grassland in Member 5 times, supplanting the earlier, bush loving forms of Member 4.

Support for the notion of a regional climatic change comes from observations of Kromdraai A and Swartkrans Member 1, close in time to Sterkfontein Member 5, where there are comparably high proportions of alcelaphines and antilopines (Vrba 1976, 1980), consistent with a regional shift to a more grassland environment by 1.5 mya. But an important consideration in the climatic interpretation is that at no site studied in the Blaaubank river valley is the proportion of alcelaphini and antilopini below 51% (Vrba 1975).

Certainly the open grassland area preferred by the alcelaphines and antilopines was at least nearby throughout the depositional sequence. A mosaic of local environments is quite common in southern Africa today, and a predator need not travel far to find a variety of prey in open grassland. Furthermore, Wells (1967) noted that the alcelaphini would have been adapted to a great variety of ecological conditions. He adds: "It is very tempting to interpret these observations in relation to climatic fluctuations. However, it appears wise to be very cautious in this matter." (Wells 1967: 104).

A change in climate is not the only way by which one can account for changes in the relative frequencies of bovid types. Thackeray (1980) noted three factors that could affect ungulate representation in archaeological faunal assemblages: environmental factors including rainfall and temperature, a preservational bias against smaller fauna, and predation by hunters and scavengers.

Under a changing regime of taphonomic agents leading to bovid death and deposition, the frequencies of bovid types would be expected to change. This is suggested by the differences in representation of predators at Sterkfontein, possibly including the genus *Homo*. Member 4 accumulations have been attributed to primary kills of carnivores, whereas the lower percentage of juvenile bovids in Member 5 seems to indicate scavenged remains and indeed could be attributed to the activities of the hominids (Vrba 1975, 1976, 1980). Bovids requiring a mesic or woodland environment could have been in the area, but their representation in the fossil record depends in part on the habits of the predators and scavengers. As Vrba (1980: 258) put it, "As bovids do not live in caves, the vast majority of their remains must have been carried there by other animals".

Some caution is necessary in the interpretation of the bovid assemblages, for Vrba initially did her counts on fossils assigned to the Sterkfontein Type Site and the Sterkfontein Extension Site. Partridge (1978, 1982) warns of the possible mixing during earlier collecting phases of Member 4 and Member 6 fossils into the supposedly Member 5 sample. Vrba (1982) addresses this problem and reassigns some individuals (notably those of

TABLE 1.

List of Large Mammal Species from Sterkfontein Members 4 & 5.

Member 4

Order	Family	Genus	Species
Primates	Hominidae	*Australopithecus*	*africanus*
			sp.?
	Cercopithecidae	*Parapapio*	*jonesi*
			broomi
			whitei
		Papio	*hamadryas robinsoni*
			izodi
		Cercopithecoides	*williamsi*
Carnivora	Felidae	*Panthera*	*pardus*
			leo
		Dinofelis	*barlowi*
		Megantereon	*cultridens*
		Homotherium	*crenatidens*
	Hyaenidae	*Chasmaporthetes*	*silberbergi*
			nitidula
		Crocuta	*crocuta*
		Hyaena	*brunnea*
		Pachycrocuta	*brevirostris*
	Canidae	*Canis*	*mesomelas*
Artiodactyla	Bovidae	*Damaliscus*	sp.1
		or *Parmularius*	sp.
		Connocheates	sp.
		cf. *Megalotragus*	sp.
		Hippotragus	cf. *equinus*
		cf. *Hippotragus*	*cookei*
		Redunca	*darti*
		Antidorcas	cf. *recki*
			cf. *bondi*
		Oreotragus	*major*
		Gazella?	sp.
		Syncerus	sp.
		Tragelaphus	sp. aff. *angasi*
		Makapania	cf. *broomi*
	Suidae	*Metridiochoerus*	sp.
Perissodactyla	Equidae	*Equus*	*capensis*
Proboscidea	Elephantidae	*Elephas*	*recki*

Member 5

Order	Family	*Genus*	Species
Primates	Hominidae	*Homo*	*habilis*
	Cercopithecidae	*Papio*	sp.
Carnivora	Felidae	*Homotherium*	*crenatidens*
		Megantereon	*cultridens*
	Hyaenidae	*Chasmaporthetes*	*silberbergi*
			nitidula
		Crocuta	*crocuta*
		Pachycrocuta	*brevirostris*
	Canidae	*Canis*	cf. *mesomelas*
Artiodactyla	Bovidae	*Damaliscus*	sp. 1
		or *Parmularius*	sp.
		Damaliscus	sp. 2
		cf. *Connochaetes*	sp.
		cf. *Megalotragus*	sp.
		Antidorcas	*recki*
		Oreotragus	*major*
		Taurotragus	cf. *oryx*
	Suidae	gen. indet.	
Perissodactyla	Equidae	*Equus*	*burchelli*
Proboscidea	Elephantidae	*Elephas*	*recki*

Notes: Compiled from Brain (1981), Churcher (1970), Delson (1984), Eisenhart (1974), Turner (1986a, 1987), Vrba (1976, 1982, 1988). Bovids not yet identified to genus are not included. Vrba (1982) questions the presence of *Equus capenis* in Member 4, suggesting that the specimen may have originated from Member 5. For additional information on the mammalian orders not discussed in this paper, see Brain (1981), Churcher (1970), Pocock (1987), Vrba (1982).

Makapania) from Member 5 to Member 4. Although the remaining fossils that could have an incorrect provenance may be insignificant in number, the mixing problem must be acknowledged for it could alter the relative frequencies of species and thus affect the resulting climatic interpretation.

Environmental reconstructions based on the bovid samples are also subject to possible errors due to inherent sample size problems. Vrba's Member 4 sample of bovids is significantly larger than that obtained from Member 5. The continuing excavation at Sterkfontein has uncovered a much larger sample from both deposits and future analysis may reveal a greater number of species present in the deposits.

Differences among the bovids represented in the hominid bearing deposits at Sterkfontein do indicate a change in the adaptive environment. Vrba's model, albeit the most constructive one proposed to date, is limited by problems of deposition, taphonomy, and fossil recovery. Certainly it is clear that local environmental changes occurred between the times represented by Members 4 and 5: there are new derived species and apparent extinctions of other species. To what degree these can be interpreted in terms of the broader contexts of climatic or taphonomic effects remains debatable. Some clues, however, can be found in corroborating evidence from the other faunae represented at Sterkfontein.

Carnivora

Although carnivores appear in low frequencies at Sterkfontein, as is expected of animals at higher trophic levels (Walker 1984), they comprise an important component for ecological analyses. Of the carnivore taxa that have been identified (Table 1), as with the bovids, there are fewer species represented in Member 5 than in Member 4. This complicates notions concerning the environmental implications of the carnivores with considerations of the taphonomy and sampling of the two deposits.

Since Brain (1981) realigned the relationships of hunters to hunted in the minds of palaeontologists, most investigators tend to think of carnivores as the agents of bone deposition in cave deposits. There is only minimal evidence in Sterkfontein Member 4 of carnivore activity as recorded by tooth marks on the bone, but poor preservation possibly obscured further evidence of carnivore damage (Brain 1981). As noted above, the high percentage of juvenile bovids (Vrba 1975, 1976) is suggestive of primary carnivore involvement in Member 4. Brain (1981) also noted an exceptionally high ratio of carnivores to ungulates in the deposit.

Herbivorous animals are almost certainly deposited in the caves by the hunting and scavenging carnivores. One must also consider the forces that led to the deposition of the carnivores themselves. They account for nearly 8,1% of individual animals represented in Member 4 (by the earlier account of Brain (1981)), many of which are primary carnivores. Turner (1984) noted that the small number of scavenging hyaenas and hyaena-damaged bones in southern African cave sites suggested the hyaenas were not using the sites as dens or even consuming much prey near the sites. At least in Member 4 one may envisage a primary carnivore based model of accumulation along the lines of Brain (1981).

It appears that hominids may have been among the accumulating agents in Member 5 as either predators or scavengers. A low ratio of carnivores to ungulates is represented (Brain 1981), and the bovid composition including a greater number of adult specimens suggests scavenged remains (Vrba 1975, 1976, 1980), implying possible hominid scavenging. It is worth noting that some of the bones in Member 5 show signs of having been chewed by carnivores or gnawed by porcupines. These observations indicate at least minimal carnivore involvement in bone accumulation (Brain 1981), but it is also likely that the large carnivores could have been responsible for the carrion scavenged by the hominids.

Fossil carnivore remains give few clues to the prehistoric climatic environment unless considered as a group. Ewer (1967: 120) stated that the diversity of scavenging hyaenids and canids, such as that seen in Sterkfontein Member 4, "presupposes the existence of a rich primary predator fauna: this, in turn, implies an abundance of herbivores as prey". The large number of species represented in Member 4 (Table 1) fit her model well. The apparent pruning of the number of predators and prey represented in Member 5 may suggest some evolutionary changes in the local biotic community that are consistent with Vrba's model of climatic change. On the other hand, the modern carnivore species represented in Member 4 (see below) all prefer drier savanna environments today (Skinner and Smithers 1990). Furthermore, the inclusion of a presumably scavenging form of hominid in Member 5 precludes a confirmation of the climatic model, for it is clear that the hominids probably changed the pattern of bone accumulation in the cave.

There are intriguing clues as to the early relationship between man and the carnivores. Walker (1981) proposed that early hominids were in competition with the guild of carnivores, and not with other hominid species. The evidence is found in the correlations between hominid and carnivore evolution. On the basis of the same evidence, Turner (1986b) opts for an alternative approach, stating that such competition need not be invoked into a model of hominid evolution. He argues for climatic shifts as the agent responsible for coincident speciations in hominids, carnivores and bovids (Turner 1983a).

Inferences drawn from the Sterkfontein carnivore sample do not necessarily support Turner's view. Sterkfontein is especially intriguing for the number of modern carnivore species repersented in Member 4, before the speciation of the hominids. For example, a large *Panthera leo* first appears in the southern African fossil record in this deposit (Turner 1986a). Furthermore, Turner (1984) notes that *Crocuta* fossils from all of the Blaaubank valley sites do not differ from *Crocuta crocuta*

at even a subspecies level. These examples, along with those of *Panthera pardus*, *Hyaena brunnea* and *Canis mesomelas*, demonstrate a distinct lack of speciation 'events' in some key carnivores during a number of hominid 'speciations' in Africa since the time of Member 4 deposition. Whereas some carnivore extinctions may correlate with the evolution of hominids (Ewer 1967; Klein 1977; Walker 1984), it is difficult to account for the carnivore stasis as well as the hominid evolution in a palaeo-ecological model. As discussed below, hominid scavengers may have had a commensal relationship with the surviving primary carnivores.

Cercopithecidae

Numerous taxonomic schemes to categorize the Sterkfontein cercopithecid fossils have been proposed over the years. Ecological assessments of the Sterkfontein cercopithecids have been superseded by years of indecision in systematics, as well as by the lack of analysis of post-cranial material and of Member 5 fossils. The many permutations of species designations for individual fossils from Member 4 cannot be resolved here. Yet the number of cercopithecid species and genera proposed have implications for palaeo-ecological models of the Sterkfontein environment and may bear directly on the competitive forces encountered by early hominids.

The taxonomic assessment of Eisenhart (1974) is adopted here for purposes of this discussion, with the exception that his division of *Parapapio broomi* fossils into two species (small and large) seems to be unjustified. Member 4 then has as many as six approximately coeval species of cercopithecids (Table 1). Any palaeo-ecological model must thus accommodate all of these species as well as *Australopithecus africanus*, all filling an apparently similar niche.

High relative frequencies of cercopithecids are known from Sterkfontein Member 4, with *Parapapio* being the most common found (Brain 1981). *Parapapio* species represent the more primitive form of papionins (Szalay and Delson, 1979; Simons and Delson 1978). The three putative species of *Parapapio* are distinguished largely on the basis of tooth size, as articulated by Freedman (1957). Freedman (1976) and Freedman and Stenhouse (1972) detected a trimodal curve of tooth size, with *P. jonesi*, *P. broomi*, and *P. whitei* in increasing size order. Eisenhart (1974) redesignated some of these individuals to other species on the basis of facial morphology, and saw less distinction among the taxa in tooth size. In particular, *P. broomi* and *P. whitei* are very similar in tooth indices (Maier 1971), with the only significant difference in tooth measurements being in the distal breadth of the M2 (Eisenhart 1974).

Evidence from the stratigraphic relations of the fossils suggests relative contemporaneity of the three species of *Parapapio*. Although Sterkfontein Member 4 could have been deposited over a long period of time, there is no evidence that these three species are separated stratigraphically. Likewise, in Makapansgat Members 2, 3 and 4 there is no evidence of a size change through the deposits in which all three occur (Freedman 1957; Freedman and Stenhouse 1972; Eisenhart 1974; Delson 1984). Thus it is unlikely that the three *Parapapio* species represent chronospecies.

Examination of the morphological data suggests an alternative hypothesis that *Parapapio* fossils could all belong to one highly variable species. In this case it would be no coincidence that the mid-range species (*P. broomi*) is the most common, as would be expected in a normal distribution of size. Furthermore, the mid-range baboons may have been preferred by the collecting agents; there is evidence of carnivore tooth marks on a *P. broomi* mandible (Brain 1981).

Characteristics of the *Parapapio* species suggest that they could have inhabited a range of habitats in the savanna and open woodlands (Eisenhart 1974; Szalay and Delson 1979), with a possibility of greater arboreality than that seen in modern *Papio* (Simons and Delson 1978). Eisenhart (1974) speculates further that *P. jonesi* was adapted to gallery forest and savanna, whereas the elongated muzzle of the smaller specimens of *P. broomi* suggest a terrestrial adaptation. The general implication is that *Parapapio* varieties are most consistent with an interpretation of a local mesic woodland environment during Member 4 deposition.

Other papionin fossils, with a distinctive facial morphology as compared to that of *Parapapio*, fall into two species of *Papio*. *Papio hamadryas robinsoni* (formerly *Papio robinsoni*) is seen as a temporal subspecies of the modern form of baboon found in East Africa (Simons and Delson 1978; Delson 1984). One juvenile specimen of *Papio* is morphologically indistinguishable from *Papio izodi* of Taung (Eisenhart 1974; McKee 1991), but remains the sole representative of this second species of the genus at Sterkfontein.

Living species of *Papio* have a wide range of adaptations, but are primarily terrestrial quadrupeds with a significant degree of arboreal adaptations. Studies of modern baboons have focused on their savanna adaptations (eg. DeVore and Hall 1965), but Rowell (1979) demonstrates the ability of *Papio* to adapt effectively to a forest environment. Jolly (1972) suggested that early *Papio* were forest-fringe dwellers whereas *Theropithecus* species (not found at Sterkfontein) were more common in open savanna. Carbon isotope studies of tooth enamel lend support to this conclusion, showing *Theropithecus* to be more graminivorous, and hold promise for further studies of the cercopithecid diets (Lee-Thorp *et al.* 1989).

Observations on the remaining Member 4 cercopithecoid, *Cercopithecoides williamsi*, suggest that it was a relatively large colobine monkey. The presence of this form may seem to indicate moist forest habitats as with modern African colobines (Tappen 1968), yet the relatively large size of *C. williamsi* suggests that it was probably the most terrestrially adapted colobine ever (Szalay and Delson 1979; Delson 1984). As with *Parapapio* and *Papio*, post-cranial material will be cru-

cial for the determination of their relative reliance on arboreality as opposed to terrestriality.

Generalizations concerning the climatic and environmental implications of the cercopithecid fossils require a consideration of the primates as a group. The net result of this survey is that we have six cercopithecoids as well as the hominid(s) all living in the same local environment. Most would agree that this is a most remarkable situation (Freedman 1976; Eisenhart 1974), for the available niches appear to be somewhat saturated with primate species. All were adapted or adaptable to both savanna and open woodland, and perhaps even forest, making the environmental implications unclear. Tappen (1968) observed that there are strong factors producing speciations among forest monkeys, thus the large number of cercopithecoid species at Makapansgat and Sterkfontein Member 4 could indicate a relatively rich forest environment. This is at least consistent with Vrba's reconstruction of the Member 4 environment, but confirmation of the environmental implications of the cercopithecids can come only with the analysis of the post-cranial material and clarification of the taxonomic problems.

Inevitably one must consider the enigmatic connotations of the negative evidence, but with due caution. Member 4 has yielded none of the very large terrestrial baboons. *Theropithecus* in particular occurs at Makapansgat, before Sterkfontein Member 4 times, and afterwards at Swartkrans. Whereas their absence at Sterkfontein could indicate an environment in which the large graminivores could not adapt or compete, *Theropithecus* existed in association with nearly all of the Sterkfontein types at Makapansgat (where there are as many as seven cercopithecoid species (Eisenhart 1974)).

Cercopithecid remains in Sterkfontein Member 5 are scarce. So far only *Papio* sp. has been identified. Nevertheless, there is a clear lack of *Parapapio* and *Cercopithecoides*. It is tempting to account for this decreased representation with a model of competitive exclusion in an environment saturated with primates, especially in the light of the decreased number of species at other southern African fossil sites through time. Further analyses may verify or refute the inference that Member 5 contains fewer species within the primates as within other orders of mammals. Fortunately, recent work is yielding a larger sample from which various ecological models can be tested further (Tobias *et al.* 1990).

DISCUSSION

Analyses of the Sterkfontein fauna and their context reveal a changing local environment for the evolving hominids. The later deposited Member 5 can be differentiated from Member 4 on the basis of at least four key features: 1) the presence of stone and bone artefacts; 2) fewer number of species represented in mammalian families for which there are adequate samples; 3) the presence of new derived species, including a representative of the genus *Homo*; 4) a change in the proportional representations of species within families. Each of these features may have implications for reconstructions of the early hominid adaptive environment.

Local changes seen in faunal representation between Sterkfontein Members 4 and 5 can be interpreted in a number of ways. From this review it is clear that there are three primary hypotheses to explain the changes in the Sterkfontein fossil record: (1) climatic changes of cooling and aridification in the region caused or propelled evolutionary events among the fauna; (2) changes in the bone accumulating agencies resulted in different proportions of species representation; and (3) interactions of the evolving faunal species caused shifts in the adaptive patterns of members in the biotic community. Although these notions are not mutually exclusive, they are treated individually below.

Climatic Change Hypothesis

Biotic turnover among many African faunal taxa in the Plio-Pleistocene seem to correlate with climatic change. The fossil evidence, and in particular the bovid sample, has led Vrba (1985) and Turner (1983a) to suggest that changes in global climate *caused* the evolution of African mammals in the Plio-Pleistocene. Variations in relative frequencies of bovid species that are thought to be sensitive to the climatic and vegetational environment at Sterkfontein are consistent with such a climatic change hypothesis. Additional supportive evidence comes from the greater species diversity of carnivores and cercopithecids that suggests a richer, wooded local environment during Sterkfontein Member 4 times than the drier, more grassland environment inferred for Member 5.

Analyses of global trends in temperature confirm that the hypothesis is at least tenable. It is evident that sometime between 2.5 and 2.3 mya there occurred considerable cooling and aridification that could have affected southern Africa (Boaz and Burckle 1983; Shackelton *et al.* 1984; Partridge 1986; Van Zinderen Bakker and Mercer 1986; Prentice and Denton 1988). Faunal dates place Sterkfontein Member 4 just before or within this climatic episode, and Member 5 after successive global temperature fluctuations.

Legitimate reasons to question the climatic hypothesis must be raised from the same data used in its support. It is not clear that the inferred climatic changes would have been enough to cause speciation events or even accentuate them. Behrensmeyer and Cooke (1985) remind us that vegetation is under strong local control, and that there would have been a mosaic of local vegetational types. Thus a change in temperature could result in nothing more than local changes in geographic distribution of faunal species as they seek out their preferred habitat.

An alternative model to adaptive evolution in response to climatic change is thus that of species 'distribution drift'. Vrba (1988) acknowledges this possibility, but notes the parsimonious changes among fossil fauna witnessed in both eastern and southern Africa that coincide with changes in African climate. The problem is that her argument for biotic turnover with continental climatic

change is tautologous. The faunal dating of southern African sites is based on eastern African fauna, so it is no coincidence that the continental faunal changes correlate to the same putative event of climatic change.

New fossil evidence has contradicted the notion that the divergence of the 'gracile' and 'robust' hominid lineages corresponded to the putative climatic 'event' at 2.5 mya. The perceived coincidence of biotic turnover with hominid divergence had to be rejected with the discovery of an early hyper-robust form (the 'Black skull') in eastern Africa that predates the 2.5 mya climatic change (Walker *et al.* 1986; Vrba 1988). Vrba (1988: 415) sums up the status of the hypothesis by stating that "the problem of hominid-associated environmental change in South Africa is badly in need of additional approaches".

Conclusions on the tenability of the climatic change hypothesis for mammalian evolution in the African Plio-Pleistocene are not possible at this stage. Further corroborating evidence is needed from analyses of Sterkfontein and other African faunal sites. In addition, accurate dating of the sites is essential before one can correlate faunal changes with the global climatic models.

Taphonomic Agent Hypothesis

Evidence from detailed taphonomic analyses of the Sterkfontein deposits support the notion that changes in the bone accumulating agents contributed to the different proportions of species represented in Members 4 and 5. As discussed above, the scavenging activities of early man may have been a primary source of the bones deposited in Member 5. The appearance of *Homo* along with stone tools, patterns of cut marks on the bones (Brain 1981, 1985), and the lower percentage of juvenile bovids (Vrba 1975, 1976, 1980), all point to the likelihood that early man left his scavenged food remains in the later deposit at Sterkfontein.

An assessment of the negative evidence reveals intriguing but tenuous clues. There is a distinct lack of primates in Member 5; not only cercopithecids but also other hominids are missing. Tobias *et al.* (1987) commented on the expectation that *Australopithecus robustus* would be found in Member 5, but to date no such discovery has been made. This could be interpreted in terms of the local dominance of early *Homo* over his competitors, at least at the cave entrance if not over a larger area, for many of these primate species did exist in Africa at the time. As Huxley (1894: 89) stated in a similar context, "I know of no more striking evidence than these facts afford, of the caution which should be used in drawing the conclusion from the absence of organic remains in a deposit, that animals or plants did not exist at the time it was formed".

Numerical changes in proportions of species between Members 4 and 5 are as consistent with the taphonomic hypothesis as they are with the climatic hypothesis. The evidence for changes in the taphonomic processes between the successive Sterkfontein deposits does not preclude the possibility of climatic change. However, it does inhibit any firm inferences of climatic change based on species representations, for it is not yet possible to differentiate the relative effects of environmental and of taphonomic changes.

Despite the tenability of the taphonomic hypothesis, it deals only with changes in bone accumulation patterns at Sterkfontein. Additional hypotheses must be sought to explain the evolution of derived species that are also apparent at the site.

Species Interaction Hypothesis

The dynamics of species interactions within a changing biotic community may be sufficient to account for the evolutionary changes evident at Sterkfontein and other sites. One thing that is indisputable is that a number of mammalian species evolved in Africa between the times represented by Sterkfontein Members 4 and 5. Apparent extinctions and derived morphological states among numerous taxa are evident at southern African sites and are consistent with evolutionary models of species interactions (Klein 1984), comprising elements of competition, commensalism and mutualism.

Habitats of the australopithecines can be reconstructed most effectively with a consideration of all the roughly coeval species preserved in Sterkfontein Member 4, representing a significant proportion of the local faunal community. There was considerable species diversity in primary carnivores and scavengers, including forms that have remained relatively static in morphology to today. There was also a wide variety of primates, including *Australopithecus*. In line with Vrba's reconstruction, it appears that a rich mesic environment was present at the time allowing for such species diversity.

Environmental constraints on early hominid adaptations were imposed by the coeval species. Because of the number of potential scavengers represented, it is likely that *Australopithecus* fed at low trophic level and remained a non-scavenging omnivore. This ecological consequence is consistent with the dental morphology and clues from the masticatory apparatus suggesting a primary reliance of *Australopithecus* on a vegetarian diet (eg. Robinson 1954; 1963; Grine 1981; McKee 1989). This early hominid was too slow, too small, and ill-equipped to be a scavenger or a predator in competition with the diverse carnivores in the Sterkfontein environment. However, this put *Australopithecus* into potential competition with the other primates filling foraging niches in the same geographic area.

Novel hominid adaptations may have profoundly affected the competitive environment and depositional process by the time of Member 5 deposition. Somewhere in Africa, the early hominid had evolved into a scavenger and was ultimately responsible for accumulating much of the bone and all of the stone tools at Sterkfontein. The development of stone tool technology may have equipped early *Homo* with the competitive edge necessary for entry into a scavenging niche, although perhaps only to a limited extent (Shipman and Walker 1989).

Competitive exclusion models are not sufficient to

explain the fewer number of carnivore species represented in Sterkfontein Member 5; too many forms appear before and after at other nearby sites. Indeed, the primary carnivores were necessary to provide scavenging opportunities for the hominids and other scavenging species. The adaptable hominids persisted; *Homo* and the robust australopithecines had diverged by the time of Member 5 deposition, presumably occupying separate niches. Scavenging opportunities would have been more limited if all the carnivores had survived in this environment with early *Homo*. If one thinks of hunters as impatient scavengers (Colinvaux 1978), then early *Homo* in this environment of reduced opportunity was a prime candidate for an incipient hunter. The diversity of scavengers and large carnivores was eventually reduced due to competition with *Homo* (Klein 1984), except perhaps in the earliest member at Swartkrans.

Local reduction in the number of primates by the time of Member 5 deposition seems to be well substantiated. *Parapapio* species had been excluded from all of the later Transvaal sites, including Sterkfontein Member 5, and *Papio* was reduced in variability. It is entirely plausible that they had been out- competed by a hominid during the *Australopithecus* to *Homo* transition. Some cercopithecids, not represented at Sterkfontein, did persist, as witnessed at Swartkrans and Kromdraai. These were the larger and more graminivorous forms such as *Theropithecus*, that probably were not in direct competition with the omnivorous hominids.

In the above model, the taphonomic hypothesis may be a necessary corollary. The observed reduction in total faunal diversity and altered proportional representation of bovid species at Sterkfontein is not clearly explicable by the species interaction hypothesis alone. But if early *Homo* had indeed become an opportunistic scavenger, then the bone accumulations in Member 5 would have been affected by his scavenging preferences and opportunities.

Mammalian species interactions, including competition among the primates and commensalism of hominids with the primary carnivores, are sufficient to account for the evolutionary and representational processes. Ostensibly, the Red-Queen hypothesis (Van Valen 1973; Foley 1984) of perpetual changes in some species affecting the adaptations of others is indicated. In this model climatic change is not necessary as a driving force.

As with the climatic and taphonomic hypotheses, many aspects remain to be tested and verified. Turner (1983a, 1986b) insists that it is not necessary to propose inter-specific or inter-order competition models, for the coincident changes in species may have been due to climatic shifts. Likewise, Grine (1986) states that it is not necessary to invoke the Red-Queen hypothesis for hominid divergence when climatic changes can account for species differentiation and extinction. But one should not equate correlation of climate and evolution with causality (Boaz and Burckle 1983; Tobias 1985). Even with climatic changes, species interactions must change in order to propel adaptive evolutionary changes. In other words, to adapt to a new vegetational environment caused by putative climatic change, species must compete for altered or diminished food sources at all trophic levels.

CONCLUSIONS

The sequence of fossils represented at Sterkfontein provides a data base for the testing of hypotheses concerning the early hominid role in the biotic community. Man's dual role as a scavenger and forager necessitated interactions with other species in similar niches, with a net result of evolutionary changes in many species. Whether or not one can conclude that this was propelled by climatic changes depends on an accurate assessment of climatic effects on local environments and better chronological controls. Ecological effects on bone deposition and preservation are also inextricably intertwined with taphonomic processes.

Environmental reconstructions of the early hominid habitats must utilize data from the total biotic community; species taken individually reveal very little. Holistic approaches to hominid palaeo-ecology are possible with the abundance of clues exposed at sites such as Sterkfontein. The analyses reviewed here demonstrate the potential value of fossil data, as well as the methodological problems that must be overcome with innovative techniques. It is still true that "there is an urgent need to intensify studies on the comparative fauna" (Tobias and Hughes 1969: 167), for more species from Sterkfontein remain to be identified and analyzed. Alternative hypotheses may then be tested in the fossil 'laboratories' in which the hominid past is preserved.

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