The Plio-Pleistocene Paleoecology of Makapansgat: A Site Overview and Review of Paleoecological Reconstructions from the Time of Australopithecus africanus

GILLIAN SLOGETT

ABSTRACT

The ‘Makapansgat Formation’ of the Makapansgat Valley, Limpopo Province, South Africa, has yielded 29 *Australopithecus africanus* specimens representing at least 10 individuals that date to as early as 3.33 Ma. This remarkable hominin component has garnered considerable interdisciplinary attention, and has motivated extensive palaeontological and paleoecological research. In an attempt to synthesize the myriad arguments that contribute to this discourse, this paper presents a comprehensive review of the organic and inorganic features of the site as well as of previous paleoecological interpretations, with focus on the potential habitat of *A. africanus*. Following an overview of the geology and lithostratigraphy of the Makapansgat Formation, issues with dating are discussed. Subsequently, a review of organic and inorganic materials recovered from the site is provided, followed by a discussion of relevant taphonomic considerations. Further, previous paleoecological reconstructions are critiqued in an attempt to ascertain the most probable paleoecological scenario. The implications for *A. africanus*, and hominid evolution are discussed. This paper concludes that during the Plio-Pleistocene, Makapansgat was a relatively moist environment with a flexible mosaic bush, woodland, and forest ecosystem, with limited areas of grassland that increased in relative abundance during the Pleistocene. This mosaic of habitats supported a wide array of fauna including *A. africanus*, and may have encouraged the diversification of its dietary strategy and by extension, bipedal tendencies.
Introduction

The Makapansgat Valley of Limpopo Province, South Africa has yielded a more thorough record of the “human adventure” than any other site in the world (Rayner et al. 1993:219). Permeated by fossil-bearing caves, Makapansgat’s Plio-Pleistocene sediments have produced an abundance of vertebrate remains, dominated by mammalian taxa such as bovids (Wells and Cook 1957), cercopithecoids (Delson 1984), felids (Brain 1981), hyenas (Maguire et al. 1980), and rodents. Of greatest import to the anthropological community has been the discovery of 29 *Australopithecus africanus* specimens representing at least 10 individuals that date to as early as 3.33 Ma (Partridge et al. 2000), making Makapansgat the earliest hominid bearing locality in southern Africa (McKee 1995; Vrba 1995 2000). This remarkable hominid component has garnered considerable interdisciplinary attention, and has motivated extensive paleontological and paleoecological research.

Attention was first drawn to Makapansgat in 1925, when a schoolteacher observed fossil material in the dumps of a mining operation at Limeworks Cave. In the process of mining travertine for use in the cement industry, miners had unknowingly extracted the bulk of an enormous Plio-Pleistocene fossil deposit (Rayner et al. 1993). Material was sent to Raymond Dart, an anatomist and anthropologist who, in 1947, began a systematic study of what has come to be known as the ‘Makapansgat Formation’ (Partridge 1979). Within the first field season, Dart was rewarded with the discovery of a nearly complete *A. africanus* skull, encased in pink breccia (Dart 1948).

Extensive research at Limeworks Cave followed this discovery, and has produced hundreds of thousands of prepared faunal specimens, as well as extensive pollen and sediment samples (Rayner et al. 1993). While a collection of this magnitude would typically be considered a paleoecological gold mine, the vast majority was extracted *ex-situ* from mine dumps, and is therefore unprovenanced. Efforts at stratigraphic reconstruction of the original deposit have been impeded not only by the puzzle-piece nature of the mine-dump breccias, but also by the lack of vertical and lateral continuity in the remaining *in-situ* portions of the deposit (Maguire 1985). This is complicated by the irregular nature of the cave floor that, during deposit formation, shaped sediments into a fragmented patchwork of laterally discontinuous sequences. Though modern techniques such as paleomagnetic dating have been employed to make sense of this complex structure, the dating of fossils has been difficult. Considerable debate, therefore, surrounds the age of ‘Member 3,’ the densest faunal deposit in the formation and that from which most of the *A. africanus* remains were extracted (Partridge 1989).

This issue has had important implications for identifying, reconstructing and sequencing the different paleoecological stages at Makapansgat. Early on,
paleoecological studies focused on biostratigraphy (e.g. Well, 1962) and sedimentology (e.g. Brain 1958; Cooke 1964). More recently, stable isotope and trace element analysis have been used to infer ecosystem structure and moisture content, as well as to reconstruct the dietary ecology of bovids, cercopithecoids, and other genera (e.g., Delson 1984; Hopley et al. 2007; Sponheimer et al. 1999). Similarly, paleodietary analyses of dental microwear and mesowear have been used to infer the diets of fossil taxa (e.g. Schubert et al. 2006). Further, palynological studies have attempted to quantify flora abundance and distribution over time (e.g., Cadman and Rayner 1989; Zavada and Cadman 1993). Other studies have based ecological reconstructions on geomorphological and climatological reconstructions (e.g., Rayner et al. 1993). Unfortunately, despite the respective strengths of these approaches, the paleoecology of Makapansgat remains relatively unresolved. Considerable disagreement has risen between studies that indicate a dry, savanna environment during the Plio-Pleistocene, and those that indicate a humid, forested environment (Rayner et al. 1993).

Therefore, the study of the Plio-Pleistocene environment at Makapansgat has been characterized by debates over the chronology and ecological context of A. africanus. In an attempt to synthesize the myriad arguments that contribute to this discourse, this paper presents a comprehensive review of the organic and inorganic features of the site as well as of previous paleoecological interpretations, with a focus on the potential habitat of A. africanus. Following an overview of the geology and lithostratigraphy of the Makapansgat Formation, the issue of dating will be discussed. Subsequently, a review of organic and inorganic materials recovered from the site will be provided, followed by a discussion of relevant taphonomic considerations. Further, previous paleoecological reconstructions will be critiqued in an attempt to ascertain the most probable paleoecological scenario. The implications for A. africanus and hominid evolution will be discussed. This paper concludes that during the Plio-Pleistocene, Makapansgat was a relatively moist environment with a flexible mosaic bush, woodland, and forest ecosystem, with limited areas of grassland that increased in relative abundance during the Pleistocene. This mosaic of habitats supported a wide array of fauna including A. africanus, and may have encouraged the diversification of its dietary strategy and by extension, bipedal tendencies.

Geology and Lithostratigraphy

Since Mesozoic times, uplift of the southern African subcontinent has occurred episodically, with long intervening phases of stasis. Prior to the Post-African 1 period of Late Pliocene uplift, successive phases of uplift and associated inland erosion shaped the major features of South Africa’s topography (Partridge and Maud 1987).
The Makapansgat Valley was formed within the Precambrian Metamorphic Black Reef Quartzite sequence, which was later covered by Malmani Dolomite, a sedimentary carbonate rock that formed the surface of the valley during the Plio-Pleistocene (Rayner et al. 1993). The Malmani sequence has an outcrop area of approximately 15,000 km², and encompasses nearly all of the early hominid sites in South Africa (Partridge 2000). Due to the soluble nature of dolomite, it is highly susceptible to the formation of karst features along bedding plane faults or fracture zones (Calitz 2001). As such, the Malmani sequence of the Makapansgat Valley was once permeated with caves, the remainders of which have become critical for paleoecological reconstruction (Partridge 1979). Remaining caves of Plio-Pleistocene origin include the Cold Air Cave, Buffalo Cave, Limeworks Cave and the Cave of Hearths (Figure 1). While most of the Plio-Pleistocene valley floor and overlying ecological material has since eroded, these caves have served to preserve abundant organic and inorganic material from the past several million years (Partridge 2000).

Figure 1: Map of the Makapansgat Valley, Limpopo Province, South Africa (based on Hopely et al. 2007: Fig 1)

For the purposes of paleoenvironmental reconstruction, the most important surviving cave in the valley is Limeworks Cave. Limeworks contains the Makapansgat Formation, which is the major fossil unit in the valley and comprises the largest hominid bearing cave deposit in southern Africa (Partridge 2000). The mining of travertine through peripheral quarries and tunnels (Figure 2) exposed the
inner clastic filling of the original cave, the structure and stratigraphy of which have yielded important information about the development and depositional sequences of the Makapansgat Formation.

Figure 2: Locality plan of the Makapansgat Limeworks (based on Partridge 2000: Figure 7-3)

During the cave’s development, travertine deposits of relatively pure calcium carbonate formed on the floor, walls and roof of the cavern, exceeding 10 m in thickness in some places (Wells and Cooke 1957). The structure of the basal travertine is such that floor of the cave forms four major depositional basins, separated by floor highs. As an opening to the surface developed and enlarged, external material accumulated within the cave. The center of the resulting deposit is composed of a partially eroded calcified debris cone, which has an average thickness of 20 m. Much of the cave ceiling and deposit has been abraded by the erosion of the valley side, and Partridge (2000) estimates (based on a study of analogous caves) that the original apex of the debris cone was up to 50 m above the contemporary land surface. Its size may be attributed to the extensive contribution of material from within the cave, as is suggested by enormous roof-fall blocks (measuring up to 20 m across) that litter the floor (Brain 1958; Partridge 1979).
Initial stratigraphic schemes proposed by Wells and Cooke (1957) and Brain (1958), attempted to make sense of the relationships between depositional units in the Makapansgat Formation. These schemes were re-evaluated by Partridge (1979), who defined the Makapansgat Formation in terms of a five-fold stratigraphic subdivision. Partridge identified five distinct members (M1 through M5). The earliest, M1, is equated with the cave’s travertine floor and an overlying layer of re-crystallized calcite and silty loam. Concentrations of bone, including several articulated skeletons, are present in distal areas. The second member, M2, is characterized by contemporaneous deposition of sediments in at least two depositional basins, separated by an elevated area of the cave floor. Component material includes silty loam, broken speleothems, rolled calcite pebbles, collophane lenses, and local concentrations of bone. Partridge (2000) suggested that this member was deposited beneath the fluctuating surface of the water table. This appears to have occurred gradually under low energy conditions. Next, M3 contains sandy to silty loam, calcite intergrowths, broken speleothems, pebbles, carrion fly pupae, several coprolites, lenses of collophane, and an abundance of faunal material. This member demonstrates horizontally and finely bedded sediments, with limited evidence of unconformities. This suggests that deposition occurred gradually under standing water. M4 comprises two beds, A and B. Though it contains far fewer bones, bed A is composed of similar materials as M3, with the addition of oolitic concretions, re-crystallized calcite lenticles. Sedimentation appears to have occurred in shallow, localized pools. Bed B contains similar materials, as well as an abundance of chert and dolomite fragments. This bed appears to be composed of gravelly colluvium from roof-collapse debris, and some aeolian material. Finally, M5 consists of beds A to E. Though the content of beds A, B, and D vary, they are essentially gravelly, and contain preserved carrion fly pupae. Bed C is less gravelly, and its contents appear to have undergone less friction than those in the surrounding beds. Bed E has a substantially lower coarse content, and is characterized primarily by silty loam. Viewed as a sequence, M5 sediments appear to have been deposited by rapid episodic flushing of unconsolidated, gravelly soil from the hillside into impermanent pools within the cave (Partridge 1979).

Though potentially useful for establishing the provenance of fossils contained within the mined breccias through matrix comparison (Maguire 1985), there are several major flaws with Partridge’s (1979) model. First, it grossly oversimplified the lithostratigraphy of the Makapansgat Formation. The vertical and lateral continuity of deposition that the five-member scheme suggests is in fact, artificial; in no section of the Makapansgat Formation do all five strata occur together in this sequence (Partridge 2000). The principle of superposition cannot be applied to the Makapansgat Formation, as sedimentary units occur in a patchwork throughout the four depositional basins, rather than in the superimposed and cave-wide sequences as the model suggested (Herries et al. 2009). Further, the five-member model does
not afford the possibility that different sedimentary units may represent contemporaneous facies, despite final deposition in different basins. As all sedimentary units in the Makapansgat Formation contain organic materials that may be used to identify different environment types and their changes over time, this has clear implications for paleoecological interpretation (Herries et al. 2009; Partridge 2000). Lastly, the inability of the five-member scheme to adequately distinguish and chronologically order the sediment units within the Makapansgat Formation creates significant difficulties in sampling the units for the purposes of paleomagnetic dating.

**Dating**

Within the debate over the nature of Makapansgat’s Plio-Pleistocene ecology, is a secondary debate over the provenance and age of organic and inorganic remains. Numerous dating schemes for the Limeworks Cave sediments have been developed based on biostratigraphic (e.g. Delson 1984; Wells 1962), paleomagnetic (e.g. Brock et al. 1977; Partridge 1979, 2000), and combined (e.g. Herries et al. 2009) analyses. The primary positional and temporal foci of these analyses have been (1) the initial opening of Limeworks Cave, which represents the maximum age for externally-sourced cave deposits, and (2) the fossil-rich, hominid-bearing breccias of M3 (as defined by Partridge (1979).

The initial development of an opening in the walls of Limeworks Cave is indicated by the appearance of lenses of externally-sourced reddish sediment, small amounts of bone, pollen, and collophane in the upper portion of M1 (Partridge 2000). Core drilling has revealed that the central debris cone lies directly over the travertine floor of the cave, suggesting that a debris mound began to form shortly after an opening was formed. In 1977, Brock et al. conducted a paleomagnetic analysis and concluded that M1 dated to 3.7-3.32 Ma, suggesting that an opening to the cave was formed 3.7 Ma. This date went uncontested until 2003, when a second paleomagnetic study produced a date of 4.19 Ma for the upper levels of M1 (Herries, 2003). As both studies followed Partridge’s (1979) five-member model, they must be examined with caution. The model presumed lateral and vertical continuity within sediment-units, and did not account for changing rates of deposition over time. Therefore, the basin and depth from which samples were selected may significantly skew the results of paleomagnetic analysis (Maguire 1985). In light of this, it may be argued that the maximum age for externally-sourced cave deposits is estimated to range between 4.19 and 3.7 Ma, but is not yet conclusively determined.

Unfortunately, uncertainty also surrounds the dating of M3 breccias. Faunal analyses have resulted in relatively vague conclusions, such as Wells’ (1962) assertion that differences between the Sterkfontein and Makapansgat (M3) faunal
deposits suggest those from Makapansgat are older. As faunal age estimates for the Sterkfontein deposit range from 2-3 Ma, this conclusion is not very precise. In a similar vein, Vrba (1995) used bovid evidence from M3 to suggest a date range of 2.5-3 Ma for the Makapansgat faunal assemblage.

Attempts at accurate paleomagnetic and combined analyses of M3 have fared little better. To a great extent, this is because the poor mechanical properties of M3 at accessible locales have prevented testing of the member itself. As such, studies have assumed an intermediate physical and temporal position for M3 between Members 2 and 4, with the dates produced for these two members taken as indicative of the date span of M3 (Brock et al. 1977; Partridge 1979 2000). Following this approach, Brock et al. (1977) determined that the M2 deposit dates to 2.8-3.33 Ma, which places the onset of M3 at less than 2.8 Ma. Based on the same data set, Partridge (1979) argued that the onset of M4 can be dated to 2.9 Ma, and suggested that M3 must have predated this time. In 2000, Partridge et al. re-evaluated these conclusions. They argued that Members 1 and 2 likely spanned from just before the Gilbert-Gauss boundary to the Mammoth Event, from which they inferred that Members 1 and 2 must be older than 3.58 -3.33 Ma. Based on this reasoning, they consider M3 to have begun to form between 3.33-3.11 Ma. Further, Herries (2003) used paleomagnetic analysis to determine a range of 3.03-2.58 Ma as the period of M3 formation, but refined it to 2.85-2.58 Ma based upon depositional rates and faunal analysis. This conclusion has been supported by both Hopely et al. (2007) and Warr and Latham (2007), among others.

In summary, the proposed ages for the onset and conclusion of M3 range from 3.33-2.85 Ma, and 2.9-2.58 Ma respectively, indicating that the period of extensive organic deposition within Limeworks Cave occurred in the second half of the Pliocene. The range of dates indicates that this period of deposition lasted between 50,000 and 750,000 years. The clarification of these dates is of primary importance for paleontologists involved in the ongoing controversy over the phylogenetic placement of *A. africanus*, as even a fraction of a million years may be significant to identifying its phylogenetic relationships to *A. afarensis*, *Paranthropus*, and *Homo* (Maguire 1985). Additionally, these dates are of critical importance to paleoecological reconstructions of Makapansgat, as they contribute to our understanding of many factors including local species abundance, ecological relationships, and the potential impacts of shifts in regional and global climate (Partridge 2000).

**Organic, Inorganic Materials and Taphonomic Considerations**

Before paleoecological reconstructions are addressed, it is important to review the organic and inorganic material preserved within the Makapansgat Formation, its
practical applications for paleoecological studies, and the role of taphonomic processes in its accumulation. Concentrated in the distal sections of M3, an unusually large and well-preserved faunal assemblage spans Members 3 and 4 of the Makapansgat Formation. Bone preservation is exceptional due to standing water and extensive calcification within the interstitial spaces of bone assemblages (Maguire et al. 1980; Partridge 1979). Makapansgat’s bone-filled breccias contain a large vertebrate assemblage consisting of hominids, cercopithecoids, bovids, felids, rodents, giraffes, horses, elephants, hyraxes, rhinos, hippos, pigs, chalicothere, hyenas, bats, insectivores, and arthropods (Cooke 1978; Ewer and Cooke 1964; Maguire et al. 1980). According to McKee (1995), over two-thirds of the mammalian species recorded within the formation are now extinct, and a greater proportion of extant species is found in the overlying M4. The four most abundant species across members are all bovids: Redunca darti, Phenacotragus vanhoepeni, Makapania broomi, and Connochaetes taurinus (Wells and Cooke 1957). The relative abundance of bovids is confirmed by Reed (1997), who reports that they represent the majority (at least 60%) of the craniodental material recovered at Makapansgat. This may suggest their relative abundance in the corresponding ecosystem, or reflect predation bias.

Though no other floral material has been preserved, pollen is found in abundance throughout the Makapansgat Formation. Cadman and Rayner (1989) have subdivided the pollen assemblage into ecologically related groups based on the general type of plants represented. The groups include forest and forest margin taxa, bushveld trees of rocky and relatively moist habitats, bushveld trees with relatively wide ranges of habitat, plains bushveld trees of relatively dry habitats, small shrubs and herbs, herbs of dry habitats, sedges, grasses, and known contaminants. Analysis of the changing relative abundance of pollen in an assemblage can reveal important information about the floral structure of local paleoenvironments, as well as information about changing climatic conditions.

In addition to the organic material that has been discussed thus far, speleothems and other forms of flowstone are important sources of paleoecological data (Hopely et al. 2007). They are abundant in southern African paleocaves, and formed throughout the Plio-Pleistocene in the Makapansgat Valley caves. Variations in the chemical and isotopic compositions of speleothems can be studied to infer paleoclimatic variables such as mean annual temperature, amount and type of precipitation, and both type and richness of external vegetation (McDermott, 2004). They can be dated using magnetostratigraphic techniques, and are therefore a veritable archive of changing climatic and ecological conditions at prehistoric cave sites.

The influence of taphonomic bias on their contemporary character is as important as the presence of the aforementioned materials. A ubiquitous taphonomic
consideration for material from the Makapansgat Formation is that the vast majority was removed from its in situ deposits due to mining activities (Partridge 1979). As has been previously stated, this material is both unprovenanced and incomplete; as lime workers mined preferentially for travertine (Wells and Cooke 1957), the remaining material is not fully representative of the Plio-Pleistocene deposit.

Aside from the remains of bats, rodents, and other small animals that may have inhabited Limeworks Cave during the formation of Members 3 and 4, the animals represented in the bone-breccias form a taphocoenoses (death assemblage) rather than a biocoenoses (life assemblage) (Vrba 1980). Given the morphology of the cave at the time deposition, it is highly unlikely that larger animals – including hominids - entered alive, let alone whole (Brain 1981; Maguire et al. 1980). In his seminal report on the “Makapangat proto-human,” Dart (1948) suggested that A. africanus was a big-game hunter responsible for the slaughter, accumulation, and concentration of large mammals in the distal recesses of Limeworks Cave. Today, this hypothesis is widely rejected (e.g. Brain 1981; Maguire et al. 1980). Detailed analysis of the crush and gnaw patterns on M3 mammal bones has led to a general consensus that the primary bone accumulating agents at Limeworks Cave were hyenas, and that the concentrating mechanisms were gravity and water flow, assisted by the irregular slope of the cave floor (Brain 1981; Latham et al. 1999; Rayner et al. 1993; Reed 1996). This conclusion implies that the faunal assemblage in the Makapansgat Formation may represent a strong predation bias, particularly against arboreal and aquatic species (Reed 1997). However, the possibility of preservation bias is limited by the sub-aqueous conditions of deposition, which has resulted in excellent overall preservation (Partridge 1979).

In contrast, there is almost certainly a preservation bias in the floral remains (Zavada and Cadman 1993). As pollen is the only surviving plant component in the deposit, it may be inferred that other plant detritus decomposed prior to or during deposition. This is likely due to the slow rate of deposition in what Partridge’s (1979) stratigraphy tells us was a relatively moist cave setting. Additionally, there is likely a strong selection bias, as the pollen assemblage may be assumed to have derived primarily from within the vicinity of the cave’s entrance (Cadman and Rayner 1989). Therefore, the pollen assemblage may not be representative of the valley at large, but rather of habitats local to the Limeworks Cave catch basin (Partridge 2000).

**Previous Paleoecological Reconstructions**

Using various elements of the geological, temporal, material, and taphonomic information that has been discussed thus far, numerous attempts have been made to reconstruct Makapansgat’s Plio-Pleistocene paleoecology. Not long after Dart’s (1925) preliminary report on A. africanus was published, a debate emerged within
the literature between studies that indicate a primarily dry, savanna and/or bush dominated environment at Makapansgat during the Plio-Pleistocene, and those that indicate a primarily humid, woodland or forested environment. This debate has been discussed in detail by Rayner et al. (1993), and will be summarized here.

Supporting Dart’s (1948:1) claim that the “big game” remains in the faunal assemblage had lived in an open savanna environment, early studies by Bosazza et al. (1946), Oakley (1954) and others suggested arid environmental conditions that were influenced by the fluctuating expansion of the Kalahari Desert. Arid conditions were also proposed by Brain (1958) and Cooke (1964), among others (Rayner et al. 1993). Notably, Brain (1958) conducted a comparative analysis of the Limeworks cave sediments and modern dolomitic soils. Brain concluded that the Limeworks Cave sediments exhibit a trend from arid towards semi-arid over the period of deposition (Rayner et al. 1993). It is significant that the majority of studies suggesting arid conditions were based on sedimentological analyses. It may be relevant that, aside from Brain’s study, the aforementioned analyses were conducted without a developed stratigraphic scheme.

In contrast to the arid-savanna hypotheses, Meester (1955), Cooke (1957), Butzer (1980) and other early studies concluded that a relatively moist woodland and/or forested environment characterized the Plio-Pleistocene paleoenvironment of Makapansgat. Though his later sedimentary studies (Cooke 1964) concur with the dry-savanna hypotheses, Cooke (1957) first argued that the Makapansgat sediments we laid down in a wet period associated with glacio-pluvial processes affecting eastern Africa. Further, a lack of soil detritus within the Makapansgat Formation was taken by Butzer (1980) to suggest that the environment surrounding Limeworks Cave boasted an effective vegetative cover and, therefore, adequate moisture. Though these particular examples include inorganic studies, it is worth noting that the majority of early studies that support these conclusions were based on organic remains. In addition, Butzer and other post-Brain (1958) authors were able to follow the structure of his stratigraphic scheme.

Falling towards the middle of the spectrum, several early studies took the position that Plio-Pleistocene conditions were consistent with current conditions. Today, the Makapansgat Valley is semi-arid and supports a mosaic of grassveld, bushveld, and woodland vegetation. Based on this analogue, in 1951, King (p. 148) argued that conditions have “probably never varied very much from a semi-arid mean.” This argument was echoed by Ewer (1958), Klein (1977), Partridge (1982), and others. Further, though Rayner et al. (1993) cited their results as ‘inconclusive,’ both Wells and Cooke (1957) and Ewer and Cooke (1964) argued for mosaic environments that were neither singularly arid-savanna type, nor moist-forest type. Evidently, disagreement between widely differentiated ecosystem models characterized paleoecological research at Makapansgat from the 1950’s to 1970’s.
By the mid 1980’s, enhanced by an arsenal of new technologies and techniques (e.g. paleomagnetic dating, stable isotope analysis), paleoecological reconstructions of Makapansgat have taken on a new form. While there is still considerable debate about the exact floral composition during the Plio-Pleistocene, the spectrum of proposed paleoecosystems has narrowed considerably. Overall, there has been a shift away from the dry, savanna-grassland hypothesis, towards models that suggest the presence of mosaic ecosystems with a definite arboreal component. The following section will review some of the most prominent paleoecological studies of the last several decades. They have been divided based upon their use of faunal, floral, or inorganic data.

**Faunal**

In her attempt to reconstruct the habitat of *A. africanus* at Makapansgat, Reed (1997) examined Plio-Pleistocene mammalian fossil assemblages from hominin-bearing sites across eastern and southern Africa, as well as extant mammalian communities from eight distinct habitat types. Using ecological diversity methods to analyze the mammalian fossils from Members 3, 4 and 5 of the Makapansgat Formation, she found that the 30,000 specimens recovered from M3 represent 55 species, of which 14.95% are frugivorous and 5.45% are arboreal. From these statistics, he inferred the presence of bushland and medium density woodlands. Further, 3.44% of species are known fresh grass grazers, and the 1.84% are aquatic mammals. Reed concluded that a mosaic of habitats characterized the M3 environment, including riparian woodland, bushland, and edaphic grassland elements.

M4 contained 257 mammalian specimens representing 31 species. Of these, 20% of species are frugivorous and 7% are arboreal. Compared to M3, this increase may not be significant, given that 80% of the collection is made up of cercopithecoids, and there are very few bovid remains. Reed (1996) suggested that this is a reflection of predation bias, as the primary bone accumulators in M4 were not hyenas, but rather birds of prey and leopards. The potential role of both birds and leopards as bone accumulators has been acknowledged elsewhere (Brain 1981; Maguire et al. 1980). Hence, while M4 statistics indicate a more wooded habitat, this may not have been the case (Reed 1997). Though there have been no primates recovered from M5, it is analyzed to reveal potential trends in ecosystem structure over time. Reed articulated that of the 13 mammalian species in this member, 0% are frugivorous and 0% are arboreal. However, 15.4% of these are aquatic and 15.4% are fresh grass grazers. This trend indicates the presence of edaphic grasslands and water, in what may have been a more open environment.

A trend of relatively static, moist bush and woodland environments emerges when one considers the other *A. africanus* bearing fossil assemblages in Reed’s
The Plio-Pleistocene Paleoecology of Makapansgat: A Site Overview and Review of Paleoecological Reconstructions from the Time of Australopithecus africanus

vis-à-vis: Explorations in Anthropology

study. As the mammalian assemblages suggest more open environments, Reed concluded that over time, hominids disappear from the fossil record. She speculated that a gradual change to more arid and open habitats may have been accompanied by a more pronounced dry season. When combined, these paleoecological changes may have resulted in the extinction of Australophecines in southern Africa around 2.8-2.5Ma.

This bush and woodland hypothesis is, in fact, supported by several faunal studies that focused on bovid dentition. Bovids are frequently used in paleoenvironmental reconstructions because they are easily separated into general dietary categories that reflect habitat preferences, and because bovid craniodental material is often abundant in Plio–Pleistocene fossil assemblages. Three main dietary categories reflect the relative percentages of monocots and dicots that a species consumes: browsers (consume mostly dicots and inhabit densely vegetated habitats), grazers (consume mostly monocots and inhabit more open habitats), and mixed feeders (flexible consumption patterns that are often seasonal in nature) (Vrba 1980). Dietary (and hence habitat) preference may be recorded in the stable isotope content and wear patterns of bovid teeth (Schubert et al. 2006; Sponheimer and Thorpe 2003; Vrba 1980). Therefore, Schubert et al. (2006) conducted dental microwear analysis on seven species of bovids found in M3.

After accurately establishing a baseline for dental microwear among extant bovids with known diets, Schubert et al. (2006) analyzed the shearing facets of the upper and lower second molars in their sample using a NanoSurf II Pro white light scanning confocal microscope. Multivariate ANOVA was then used to analyze microwear feature dimensions. In brief, this microwear analysis succeeded in separating extinct taxa into two groups, with the same degree of separation as extant browsers and grazers. Their results were compared against a study by Sponheimer et al. (1999), which had previously determined dietary categorizations within the M3 bovid assemblage using taxonomic uniformitarianism, stable carbon isotope analysis, ecomorphology and dental mesowear analysis. When tallied, the results of Schubert et al.’s (2006) microwear analysis concurred with that of Sponheimer et al.’s multivariate analysis, and indicate that browsers are dominant in the Makapansgat bovid fossil assemblage. As browsers typically inhabit densely vegetated habitats, both studies conclude that M3 fauna lived in a mosaic bush and woodland habitat.

Unfortunately, the sample sizes used by Schubert et al. (2006) were quite small in the case of all seven bovid species studied, ranging from N=12 to N=2. This was not helped by the sample sizes employed by Sponheimer et al. , which ranged from N=9 to N=1 for the same seven species. As these species included Redunca darti, Phenacotragus (Gazella) vanhoepni and Makapania broomi, three of the most abundant species in faunal assemblage (Wells and Cooke 1957), the use of such small sample sizes is unfortunate. Though the results of different analyses (e.g. stable
carbon isotope, dental microwear) are consistent, small sample sizes may limit the significance of their results.

Further, tooth enamel from Makapansgat’s *A. africanus* specimens has been subject to stable carbon isotope ($\delta^{13}C$) analysis. Challenging the assumption that *A. africanus* had a primarily frugivorous diet (Ungar and Grine 1991), several studies have shown that this species was actually consuming a considerable amount of C$_4$ vegetation (Sponheimer and Lee-Thorp 1999 2007; van der Merwe et al. 2003). Sponheimer and Lee-Thorp (1999) studied the enamel of four teeth from M3 of Makapansgat, and found them to have $\delta^{13}C$ levels of -5.6, -7.7, -8.1, and -11.3. These levels are consistent with those calculated for seven *A. africanus* samples from Sterkfontein (van der Merwe et al. 2003). To illustrate the practical significance of these numbers, Sponheimer and Lee-Thorp (2007) compared them against a mean $\delta^{13}C$ of C$_3$ and C$_4$ consuming herbivores (indicative of pure C$_3$ and C$_4$ diets), and determined that on average, between 35 and 40% of *A. africanus*’ diet consisted of C$_4$ vegetation. Further, there appeared to be no significant trend in $\delta^{13}C$ enrichment with time, and at any given time, $\delta^{13}C$ appears to be highly variable.

Sponheimer and Lee-Thorp took these results to suggest that *A. africanus* were more eurytopic than previously believed. They attempted to determine what sort of C$_4$ foods were being consumed, and made a case for grasses, sedges, and animal protein. Dental microwear revealed that *A. africanus* had heavily pitted molars, and was likely not consuming grass as a main food source. It might be that they were consuming grass roots, but this cannot be determined conclusively. Similarly, while sedges might have been consumed, there is currently no concrete evidence for this in dentition. The authors raised the possibility that the underground storage organs of sedges and rootstocks might have been an important resource for which there was little to no competition; though these organs were inaccessible to most mammals, hominids might have employed crude digging sticks to access them. They also suggested that the consumption of C$_4$-consuming animal foods (including, perhaps, small vertebrates, arthropods, birds eggs, etc.) could have contributed to high C$_4$ levels observed in *A. africanus*. Though all three of these food sources might indeed be viable, Sponheimer and Lee-Thorp concluded that more research is required to determine what foods account for the $\delta^{13}C$ enrichment of *A. africanus*. What this study made evident, however, was that the diet of *A. africanus* at Makapansgat was likely highly flexible, and may have included both arboreal and non-arboreal plant components. This conclusion seemed to support the hypothesis that M3 fauna lived in a mosaic habitat, which included elements of grassland, woodland, and forest.
Floral

In 1989, Cadman and Rayner published new palynological evidence derived from the ‘Classic Section,’ a vertically exposed conformable section of the Makapansgat formation that includes Members 1 through 3, as well as two undefined units above M3. As the sediments in M2 and subsequent strata were externally derived, the pollen they contain reflects the external environment of Limeworks Cave. Cadman and Rayner were particularly interested in the changing ratio of arboreal vs. non arboreal taxa, as the presence and abundance of trees can provide climatic information. So, from lithologically distinct layers in the Classic Section, they collected 16 500 g in situ samples. These were macerated and analyzed for pollen content.

The results of their analysis indicate that tree cover at Makapansgat had fluctuated dramatically over time. Samples G1 and G2, taken from the base of the Classic Section, contain a limited arboreal component and are dominated by grasses and shrubs. The dominant taxa represented are bushveld plants with relatively wide ranges of habitats, particularly euphorbias. Moving up into G3, G4 and G5, however, Cadman and Rayner observed a sudden increase in arboreal pollen to nearly 100% of the pollen assemblage. There was a change in dominant taxa, indicating a shift to forest and forest margin trees, with some moist bushveld taxa. Following this spike, the relative abundance of arboreal pollen decreased gradually across G6 through G11, and returned to the previous low in G12. Cadman and Rayner detected a shift towards more mesic vegetation, with a considerable grassland component. However, in S25 and M3 (correlated with M3 of Partridge’s (1979) scheme), a second spike in arboreal taxa was observed. Percentages reached over 80% in S25, and over 50% in M3. Though at first the dominant taxa were dry bushveld trees, by the time of M3 deposition, the dominance of wet forest types was observed, indicating a dramatic vegetation shift. Following this sequence, there was a return to lower levels of arboreal pollen, and a shift in dominant taxa occurred. The majority of the pollen represented Chenopodiaceae/Amaranthaceae type plants, which are considered to indicate colder and dryer conditions.

In an attempt to understand the relationship between this data and regional climatic shifts, Cadman and Rayner turned to a study by Brain (1981) which indicated that the time period represented by the Classic Section deposits coincided with a global temperature decline, as suggested by the simultaneous formation of Arctic and Antarctic ice sheets in the late Neogene. Though this puts forward the macroclimatic regime within which these depositions occur, it did not account for the relatively rapid fluctuations in pollen types observed, which appeared to have occurred over hundreds or thousands of years. Therefore, Cadman and Rayner posited that the two arboreal spikes indicate different moisture regimes. They suggested that the first spike resulted from a gradual decrease in temperature, which
led to decreased evapotranspiration, and thus an increase in moisture. The second spike is attributed to a rapid rise in absolute moisture due to a rise in temperature. The authors argued that this variable vegetation hypothesis does not contradict studies that indicate mosaic ecosystems, as shifts in vegetation likely occurred over space and time at Makapansgat. Their data clearly indicated the presence of forest habitats in the valley during Australopithecine times (equated with M3). As such, they concluded that the preferred habitat of *A. africanus* was relatively closed forest or forest margin.

While Cadman and Rayner were very careful to limit, identify and exclude contaminants in their study, the significance of their results may be limited by well-known problems associated with pollen production, dispersal, and preservation in the fossil (Scott and Bonnefille 1986). Zavada and Cadman’s (1993) research provided a secondary analysis of pollen from M3 and M4. Their work discussed the results of palynological studies of M3 deposits from four distinct depositional areas in Limeworks Cave. As pollen from the Classic Section had already been studied (Cadman and Rayner 1989), they analyzed pollen excavated *in situ* from three other areas: Cone B, Cone C and Rodent Corner. These four areas are associated with different areas of the four depositional areas in the cave floor. It should be noted that the time period sampled in this study is considerably shorter than in the previous study, and spans a depositional period from mid-M3 through M4.

For each of the four areas in Limeworks Cave, Zavada and Cadman identified differences in relative abundance of arboreal and non-arboreal pollen as well as species composition and diversity. Cone C and Rodent Corner contained high levels of non-arboreal pollen throughout the section, though they exhibited notable differences in species composition. The arboreal component of Cone C was composed mainly of taxa that indicate moist or riparian habitats, as well as bushveld taxa indicative of drier habitats. Further, arboreal taxa found in the Rodent Corner deposits were dominated by taxa that inhabit a wide range of habitats. Contrarily, Cone B contained a very high percentage of arboreal pollen, which fluctuated between 60 and 100% of the pollen assemblage across most of the samples. The dominant taxa throughout this period were bushveld trees of wide ranging habitats. Palynological differences in floras, abundance, composition, and diversity indicated that deposition in each area occurred asynchronously, and that there might have been variation in sediment source area for each deposit. As the pollen in each of the four areas of the cave came primarily from the local drainage basin, fluctuations in the palynological record might have reflected changes in moisture abundance or distribution in the basin.

In conclusion, Zavada and Cadman suggested that variations in the pollen assemblage of each area reflected fluctuations in the composition of local vegetation, but not changes in the abundance of pant resources. The variable presence of arboreal and non-arboreal pollen appeared to reflect fluctuations in ecology centered on
relatively riparian and/or bushveld-like floral compositions, rather than grand ecological shifts. Their findings support the mosaic ecosystem hypothesis that has been proposed thus far.

**Inorganic**

The inorganic features of the Makapansgat Formation have provided ample data for use in paleoecological reconstructions. In a seminal study, Hopely et al. (2007) conducted carbon and oxygen isotope studies on two flowstone speleothems from the Makapansgat Valley in order to model monsoon rainfall intensity and the relative presence of \( \text{C}_3 \) and \( \text{C}_4 \) plants in the late Neogene. The role of orbital cycles (in particular, precession cycles) in climatically forced macroevolution was also considered. The two flowstones were taken from Limeworks Cave (and is referred to as ‘Collapsed Cone’ throughout the article) and Buffalo Cave (a cave contemporaneous with Limeworks that formed ~1.5 km up the valley), and date to 4-5 Ma and 2-1.5 Ma, respectively.

Oxygen isotopes indicate that during insolation maxima, Makapansgat Valley experienced increased humidity, whereas during insolation minima, the environment was dryer. Unfortunately, the restructuring of local ecosystems evident in the fossil record is not clearly reflected in the \( \delta^{18}\text{O} \) record. In contrast, stable carbon isotope ratios used as a proxy for \( \text{C}_4 \) grasses indicate two clear shifts towards increased savanna grasslands in the Makapansgat Valley: the first approximately 4 Ma, and the second approximately 1.7 Ma. The data suggested that at the time of early hominin occupation in Makapansgat Valley, the percentage of \( \text{C}_4 \) plants in the local environment was increasing. Hopely et al. (2007) found the data to suggest a transition from mid-Miocene forested habitats to mosaic savanna and woodland habitats in the Plio-Pleistocene. Given the wet and dry phases controlled by precessional cycles, it is likely that pollen assemblages accumulated under more than one climatic state, and that variations in ecomorphology reflect inter-annual and long-term climate fluctuations around a changing mean.

Rayner et al. (1993) identified the shortcomings of previous reconstructions and highlighted the major problems facing the development of an accurate one: the unknown provenance of disturbed fossil remains, the difficulty of reconstructing the habitats of extinct species, and taphonomic bias. Stepping away from methods involving organic material, therefore, the authors attempted a reconstruction of Makapansgat based primarily on tectonics, climatology, and geomorphology. On the basis of detailed reconstruction in these three areas, Rayner et al. proposed that at the time of Australopithecine occupation, the Makapansgat Valley was less deep than today, had a higher water table, and was overlain by thick, fertile alkaline paleosols.
Though they made several grand generalizations and unsupported assumptions about climatic variables, their geological analysis corroborated Partridge and Maud’s (1987) study of geologic shifts of the southern African subcontinent since the Plio-Pleistocene.

Though the latter study focuses primarily on inorganic data, Rayner et al. called on Cadman and Rayner (1989) to supplement their data. The authors found that the ecosystem structure suggested by pollen analysis is consistent with the climatic scenario implied by the form and moisture levels of the Makapansgat Valley in Plio-Pleistocene times. As their climatic analysis likely overestimated the amount of precipitation, however, Rayner et al. argued for a more wet forest environment at the onset of Australopithecine occupation than is suggested by Cadman and Rayner. They concluded that the likelihood of year-round access to fruits and insects in a forested environment, along with evidence of both arboreal and bipedal tendencies among *A. afarensis* at Hadar, suggested that *A. africanus* at Makapansgat were omnivorous, non-predatory, arboreal bipeds living in a sub-tropical forest environment. Though the use of *A. afarensis* as an analogue and the over-estimation of temperature and humidity might be misguided, the elements of Rayner et al.’s reconstruction that involved tectonics, geomorphology, water table estimation, and paleosols structure do support the possibility of a forested environment at Makapansgat during the Plio-Pleistocene.

**Discussion and Conclusion**

It appears that during the Plio-Pleistocene, both the faunal and floral assemblages at this critical *A. africanus* site were characteristic of a heterogeneous ecosystem that itself varied with fluctuating moisture regimes. Though the tendency in paleoenvironmental reconstructions is to identify a single, dominant environment type, homogenous environments rarely occur in nature. It is probable that the Plio-Pleistocene environment in the area surrounding Limeworks Cave would have supported a mosaic of habitat types, including bush, woodland, forest, and C₄ grassland. Though the changing relative abundance of the former three habitat types is not irrefutably determined at this stage, there appears to have been a shift towards more abundant C₄ plants over the course of the Plio-Pleistocene. The findings of Reed (1997), Cadman and Rayner (1998) and Zavada and Cadman (1993), suggest that this may have been a part of a regional ecological shift away from abundant forest and woodland, and towards a more open landscape.

Therefore, at least during the period represented by M3 (between 3.33-2.85 Ma, and 2.9-2.58 Ma), *A. africanus* at Makapansgat lived in a heterogeneous environment that experienced ecosystem shifts rather than major turnovers. As potential omnivores with a highly flexible dietary strategy that included C₃ and C₄
food sources, local *A. africanus* benefited from access to dense, forested habitats, as well as more open landscapes for foraging. The effective exploitation of such diverse floral resource zones would have required both adaptations for upright locomotion and the retention of traits related to arboreal locomotion, which is consistent with the findings of morphological studies (i.e. van der Merwe et al. 2003; Green et al. 2007). Ground-based gathering and scavenging likely increased over time as forested areas thinned out and areas of continuous canopy with abundant fruit became increasingly restricted. The gradually changing ecosystem structure is likely to have contributed to the diversification of *A. africanus* dietary strategies and the further development of bipedal tendencies. In this manner, the Plio-Pleistocene paleoenvironment at Makapansgat both sustained and influenced the evolution of *A. africanus*, and may therefore have played an important role in the direction of hominid anatomical and ethological evolution.

Future research will have to contend with the bias implied by animal-accumulated bone deposits and the local derivation of pollen, as well as the jumbled nature of datable materials. However, high-resolution research involving larger and more representative sample sizes will undoubtedly continue to shed light on the composition of Makapansgat’s prehistoric ecosystems. Additionally, more critical comparative studies of other *A. africanus* sites such as Sterkfontein would help to define both the chronology and nature of *A. africanus*’ occupation at Makapansgat. While taphonomic factors alone may not account for the distribution of known sites, the systematic identification of paleoecological commonalities across sites could contribute significantly to our understanding of preference and choice in the habitat selection of *A. africanus* and its descendants.

**References**

Bosazza, V.L., Adie, R.J. And Brenner, S.

Brain, Charles K.

Brain, Charles K.

Brock, A., Mcfadden, P.L. And Partridge T.C.
1977 Preliminary Palaeomagnetic Results from Makapansgat and Swartkrans. Nature
vis-à-vis: Explorations in Anthropology • Volume 13, Number 1, August 2016

226(5599):249-250.

Butzer, Karl W.

Cadman, Ann and Rayner, Richard J.

Calitz, Frederik

Cooke, H. Basil S.


Dart, Raymond A.


Delson, Eric

Ewer, R.F.

Ewer, R.F. and Cooke, H. Basil S.
The Plio-PleistocenePaleoecology of Makapansgat: A Site Overview and Review of Paleoeological Reconstructions from the Time of Australopithecus africanus

• vis-à-vis: Explorations in Anthropology

Green, David J., Gordon, Adam D. and Richmond, Brian G.

Herries, Andy I.R.

Herries, Andy I.R., Curnoe, Darren and Adams, Justin W.


King, Lester C.

Klein, Richard G.

Latham, Alf G., Herries, Andy I.R., Quinney, Patrick, Sinclair, Anthony and Kuykendall, Kevin L.

Maguire J.M.

Maguire J.M., Pemberton, D. and Collect, M.H.

Medermott, Frank

McKee, J.K.

Meester, J.
Oakley, Kenneth P.  

Partridge T.C.  


Partridge T.C., Latham, A.G., Shaw, J. And Heslop, D.  

Partridge T.C. And Maud, R.R.  

Rayner, Richard J., Moon, Bernard P. and Masters, Judith C.  

Reed, Kaye  

Schubert, Blaine W., Ungar, Peter S., Sponheimer, Matt and Reed Kaye E.  

Scott, Louis and Bonnefille, Raymond  

Sponheimer, Matt and Lee-Thorp, Julia A.  


The Plio-Pleistocene Paleoecology of Makapansgat: A Site Overview and Review of Paleoecological Reconstructions from the Time of Australopithecus africanus

• vis-à-vis: Explorations in Anthropology

Sponheimer, Matt, Reed, Kaye E. and Lee-Thorp, Julia A.

Ungar, Peter and Grine, Frederick

Van Der Merwe, Nikolaas J., Thackeray, J. Francis, Lee-Thorp, Julia A. and Luyt, Julie

Vrba, Elisabeth S.


Warr, Ginette L. and Latham, Alf G.

Wells, L.H.

Wells, L.H. and Cooke, H. Basil S.

Zavada, Michael S. And Cadman, Ann.

76