




Insights into the Middle Pleistocene fauna of South Africa: Zooarchaeology, stable isotopes and dating of Pniel 6

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ABSTRACT: The Florisian Land Mammal Age (FLMA; 773–12 ka) is characterised by specialist, often extinct, grazing as well as wetland species, many of which are no longer present in the southern African interior. Middle Pleistocene FLMA faunal assemblages are rare, particularly those associated with artefacts, limiting reconstruction of environmental conditions and hominin subsistence strategies. One exception is the faunal assemblages of Pniel 6 on the Vaal River, which are associated with Fauresmith lithics. Here, we present a comprehensive faunal analysis including stable isotope measurements and intracrystalline protein diagenesis (IcPD) analysis from several excavations since the 1980s. Twenty-one animal species were identified, with size class III bovinds and typical FLMA species dominating. The results suggest a rich grassland environment supported by considerable water components. While most of the assemblage exhibits signs of a natural death assemblage, a few taphonomic modifications may indicate a human factor. Two distinct IcPD data clusters provide relative age estimates, suggesting that the teeth do not represent a single short depositional event. All results support the interpretation of Pniel 6 as a series of distinctive archaeological accumulations of human origin during the Middle Pleistocene, with a minor component of younger material mixed up close to the modern surface.

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Introduction

The Middle Pleistocene (773–129 ka) was a highly dynamic period in hominin evolution, encompassing both the origin of modern humans as well as the emergence of prepared point technologies typical of the Middle Stone Age (MSA). These developments were set against a long-term trend of increasing aridity, punctuated by dry and substantial wet phases in Africa (Brink, 2016; Lukich and Ecker, 2022). In South Africa's central interior, the latter half of the Middle Pleistocene (~470–129 ka) provides evidence for both *Homo sapiens* biological evolution (i.e., the Florisbad cranium) as well as the transition from Early Stone Age (ESA) to MSA lithic technocomplexes, represented by the Fauresmith technocomplex (Lombard et al., 2022). This period coincides with the Florisian Land Mammal Age (FLMA; 773–12 ka), which encompassed most of the southern African interior regions, with the exception of the coastal vegetation belts (Hendey, 1974; Brink, 2016; Van Couvering and Delson, 2020). The FLMA is charac-

terised by extinct specialist grazing species such as the giant alcelaphine (*Megalotragus priscus*), the Cape zebra (*Equus capensis*), the extinct blesbok (*Damaliscus niro*), and Bond's springbok (*Antidorcas bondi*), the last one endemic to the southern African interior. Compared to the preceding Cornelian Land Mammal Age, which was dominated by mixed feeding species, analysis of carbon and oxygen stable isotopes of enamel has shown the beginnings of the modern strong grazer-browser divide in almost all large mammal herbivores by the FLMA (Codron et al., 2008; 2023; Ecker et al., 2018). Another key characteristic of the FLMA is the presence of wetland species no longer found in the region, such as the lechwe antelope (*Kobus leche*), the hippopotamus (*Hippopotamus amphibius*) and the waterbuck (*Kobus ellipsiprymnus*) (Hendey, 1974; Klein, 1984; Brink and Lee-Thorp, 1992; Lacruz et al., 2002; Brink, 2016; Van Couvering and Delson, 2020). However, despite the enormous geographical range of the FLMA, faunal assemblages from the late Middle Pleistocene are rare, particularly those associated with *in situ* human-made artefacts (Smith et al., 2019; Toffolo, 2024). This scarcity presents a challenge in reconstructing the environmental conditions and human subsistence strategies during this time period.

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Beyond the eponymous site of Florisbad, FLMA faunal assemblages are particularly numerous in the Grassland Biome, which covers mostly the Free State Province (Mucina and Rutherford, 2006), including Late Pleistocene assemblages at Erfkroon (Lyons et al., 2014; Brink et al., 2016; Bousman et al., 2023), Lovedale (Richard et al., 2022; 2023; Wroth et al., 2022), the undated Vlakkraal site and collections along the Free State rivers and pans (review in Toffolo, 2024). In the adjacent Northern Cape Province, FLMA assemblages tend to be older and are often associated with Fauresmith (Kathu Pan 1; Mohale et al., 2022) or early MSA lithic assemblages (Wonderwerk Cave; Chazan et al., 2020; Bundu Farm; Kiberd, 2006). Pniel 6, located on the southern bank of the Vaal River, is a key site due to its location at the boundary between the Savanna, Grassland and Nama-Karoo Biomes (Fig. 1) and its several collections of faunal remains associated with lithics. These include surface collections along the river edge and from mining dumps, which produced an FLMA faunal assemblage and mainly ESA lithic types (Beaumont, 1990; Hutson, 2012). There were also several excavations in the 1980s (Beaumont, 1990), in 2000 (Underhill, 2012) and in the late 2010s (Ecker et al., 2021), which produced mainly Fauresmith/early MSA lithic types. While the fauna from the surface collections has been analysed and published (Hutson, 2018), the fauna from the excavations has not yet been thoroughly examined.

In this study, we present a comprehensive faunal analysis and stable isotope measurements of the fauna from the Beaumont (Beaumont 1990) and Ecker and Morris (MINERVA Project, Ecker et al., 2021) excavations at Pniel 6. Furthermore, we undertook amino acid geochronology on enamel from some of the same specimens, providing relative age estimates. This constitutes the first successful chronometric dating technique applied at Pniel 6 since a single optically stimulated luminescence (OSL) date by Beaumont (Beaumont, 1999), which lacks supporting data and an exact location. By comparing Pniel 6 to well-dated reference sites in both the Savanna (Wonderwerk Cave, Kathu Pan 1) and Grassland Biomes (Florisbad), we discuss the human behaviour at Pniel 6 and how the site fits into the emerging picture of the past environment of interior South Africa.

Background

Pniel 6

Pniel 6 is located on the southern shore of a large bend in the Vaal River, c. 30 km from Kimberley and c. 8 km from Barkly West in the Northern Cape Province of South Africa (Fig. 1). Beginning in 1870, diamond prospecting along the Vaal River, as well as fluvial erosional processes, has unearthed ESA and MSA stone tools together with faunal remains at a number of sites along the river at Pniel (Power, 1955; Beaumont, 1990). At Pniel 6, Peter Beaumont collected ESA stone tools and faunal remains in the 1980s from abandoned mid-river diamond diggers' debris dumps (Beaumont, 1990). In addition to collecting, Beaumont removed some of the Holocene overbank silts at Pniel 6 and systematically excavated the underlying assemblage, which consisted of lithics and faunal remains. John McNabb led a small excavation at Pniel 6 together with Beaumont in 2000, extending the previous excavation grid (McNabb, pers. comm. 2016). In 2017, an excavation project was started at Pniel 6 by some of the authors, which included three field seasons (MINERVA project excavations 2017–2019) (Ecker et al., 2021).

Beaumont divided the deposits into four strata (Beaumont, 1990), trying to match these divisions with the broader

sequence of Vaal River terraces described by Butzer et al. (1973). Stratum 1 is Holocene, and Stratum 2 (labelled 'Silt') is silts of potentially late Pleistocene age that contained very few isolated finds. Both Stratum 1 and 2 were removed by Beaumont with a mechanical digger before excavation. Stratum 3 (which we assume are the boxes labelled 'Rubble' based on the work of some of us with Beaumont) and Stratum 4 (which we assume are the boxes labelled 'Gravel') contain Acheulean, Fauresmith and/or early MSA lithics (Beaumont, 1990, 1999). However, the distinction between Stratum 3 and 4 is not well documented and potentially does not hold up after full analysis of the contents (McNabb, personal communication 2016). The 2017–2019 excavations at Pniel 6 have corroborated Beaumont's observation of artefacts and faunal remains together with andesite clasts and foreign pebbles in distinct pockets along the Vaal southern river bank. In the new project, four areas were excavated, none of which directly connected to the previous excavations by Beaumont or McNabb (Fig. 1, Ecker et al., 2021). Areas 2, 3 and 4 of these newly excavated areas each showed a unique sequence of sand and clay layers. However, the descriptions of sediment, the lithic forms and species composition of the faunal remains suggest the same or a very similar horizon between the MINERVA excavations in Area 3 and the Beaumont excavation.

Radiometric dating at Pniel 6 poses significant challenges due to the complex nature of the site's depositional processes. Beaumont reported an OSL sample taken from the base of their Stratum 2, which yielded a date of c. 120 ka (Beaumont, 1999). However, the specific details of the methodology and the exact location were not published, leaving some uncertainty about this interpretation. Beaumont attempted to correlate Stratum 3 with the marine oxygen isotope stage (MIS) record based on similarities to other sites, particularly the Florisbad 'Old Collection'. He initially suggested that Stratum 3, the main find Stratum, may have accumulated during MIS 6 (~130–190 ka) (Beaumont, 1990), but later considered the possibility that it could date back to MIS 8 (~243–300 ka) (Beaumont, 1999). During the 2017–2019 excavation, five sediment samples from Area 3 were dated using infra-red radiofluorescence optically stimulated luminescence dating (IR-RF OSL) on K-feldspar grains, which gave Holocene ages (Birin 2019). This unexpectedly young age is probably due to partial bleaching of grains during flooding events, and is compounded by their location close to the modern surface (Ecker et al., 2021).

The lithic assemblage from Beaumont's excavation was never completely published. It is sometimes described as early MSA and sometimes as Fauresmith (Underhill, 2012). The assemblage includes blades, scrapers, convergent points and laterally retouched points struck from a range of raw materials including hornfels and andesite (Beaumont, 1990). A rough estimate of the material, housed in the McGregor Museum in Kimberley, suggests there are over 3000 lithics from the Beaumont excavation. The most recent excavations produced over 500 lithic artefacts in the much smaller Area 3. The published description of the Area 3 lithics (Ecker et al., 2021) suggests a homogenous assemblage, characterised by a high percentage of hornfels as the main raw material, similar stages of weathering across the artefacts, and a near absence of rolled artefacts. The assemblage is dominated by prepared core flake and blade production and shows technological similarities to other local Fauresmith assemblages. However, with one exception of a very rolled handaxe near the surface, there are no large cutting tools in the Area 3 assemblage (Ecker et al., 2021). The association of fossils together with stone tools in the same deposits was recognised as unique among the Vaal River sites early on (Power, 1955), and this remains true to this day. Moreover, Pniel's location between the Nama Karoo Biome to the south,

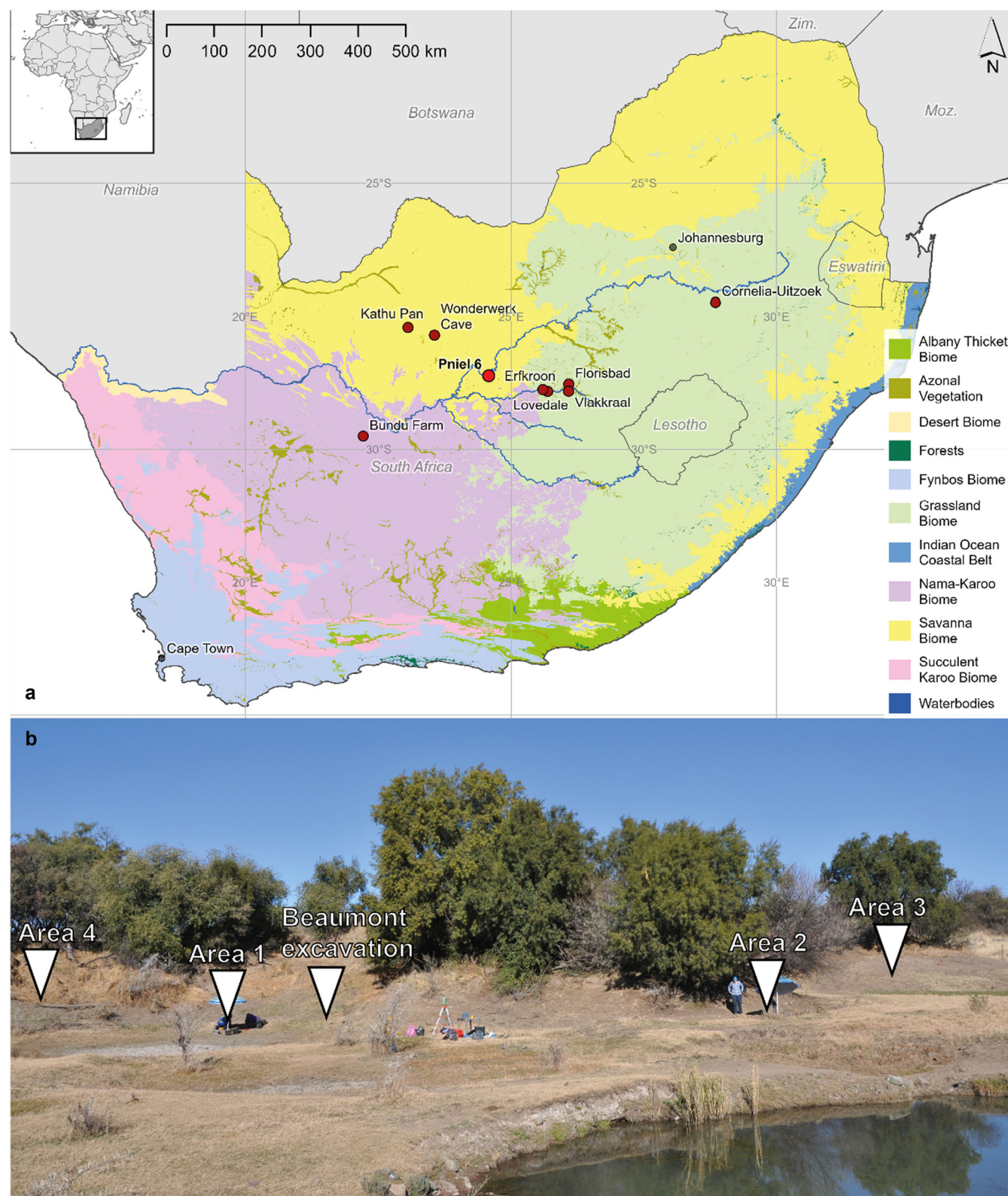


Figure 1. Pniel 6. (a) Location of Pniel 6 within modern biomes of South Africa (after Mucina and Rutherford 2006), and other sites mentioned in the text. (b) Photograph of Pniel 6 in 2017 with Beaumont and MINERVA excavations marked. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jqs.70002)] See the Terms and Conditions (<https://onlinelibrary.wiley.com/terms-and-conditions>) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

the Savanna Biome to the north and the Grassland Biome to the east allows for studies of biome shifts in the past.

Previous faunal work at Pniel 6

The faunal remains from Beaumont's surface collections from 1984 onwards have been analysed in previous studies (partly by James Brink in 1986 (see Beaumont, 1990) and by Jarod M.

Hutson in 2012 (see Hutson, 2012; 2018)), but no research was carried out on the faunal assemblage from Beaumont's excavation nor from the 2000 excavation by McNabb and Beaumont, the latter because of the poor state of conservation of the faunal material (Hutson, 2012). According to Beaumont (1990), Brink analysed some large mammal remains that Beaumont had retrieved from a riverbank dump. The faunal composition of Brink's sample was considered to be very

similar to the Florisbad 'Old Collection' and dominated by large grazing ungulates typical for open environments and wetlands, especially the *Kobus* and the *Hippopotamus* specimens (Beaumont, 1990). Some extinct species have been recognised, including *E. capensis*, *Megalotragus* sp., *D. niro* and *A. bondi*. Brink also reports two specimens belonging to an unidentified proboscidean, and identified suid bones as desert warthog (*Phacochoerus aethiopicus*). He identified the plains zebra (*Equus burchelli* (nowadays *quagga*)) and the blesbok *Damaliscus dorcas* (nowadays a subspecies of *Damaliscus pygargus*) specimens.

Hutson (2012) analysed 972 identifiable specimens from Beaumont's collection at Pniel 6 (accession number 6755 in the McGregor Museum), potentially the same from which Brink took his sample, but now almost entirely derived from what was assumed to relate to Stratum 3, with just a few pieces assumed to relate to the upper part of Stratum 4. Hutson found the same taxa as Brink and could specify some of them further, attributing the indeterminate *Megalotragus* specimens to *M. priscus*, the *Connochaetes* sp. to the black wildebeest (*Connochaetes gnou*) and the *Antidorcas* sp. to *A. bondi* by the hyper-hypsodont tooth crowns. Hutson also assumes the indeterminate medium-sized alcelaphine to be an *Alcelaphus* sp., probably the hartebeest (*Alcelaphus buselaphus*). He suggests that there are two *Damaliscus* species in the assemblage, most likely *D. dorcas* (*D. pygargus*) and *D. niro*. He was not able to clarify the proboscidean specimens formerly identified by Brink, but he speculates that they are possibly of the extant African bush elephant (*Loxodonta africana*) and not from Reck's elephant (*Elephas recki*). Hutson attributes the warthog specimens to the warthog (*Phacochoerus africanus*), unlike Brink, who had identified *P. aethiopicus*. While Hutson could not identify any lechwe specimen, he was able to add the African buffalo (*Syncerus caffer*), a hyenid species, a crocodile (*Crocodylus niloticus*) and an indeterminate large bird, potentially a vulture, to the list (Hutson, 2012). Both studies assign the identified fauna to the FLMA.

The FLMA in the southern African interior was characterised by wetlands and highly productive grasslands with a fauna including waterbuck (*K. ellipsiprymnus*), lechwe (*K. leche*) and hippopotamus (*H. amphibius*). This faunal evidence, suggestive of a wetter climate, is supported by stable isotope analyses of fauna from interior sites such as Cornelia-Uitzoek (Codron et al., 2008), Wonderwerk Cave (Ecker et al., 2018, Chazan et al., 2020), the Florisbad Spring site (Codron et al., 2008), Equus Cave (Lee-Thorp and Beaumont, 1995; Johnson et al., 1997) and Kathu Pan 1 (Mohale et al., 2022), which led to the conclusion that in the Early and Middle Pleistocene mixed C₃/C₄ landscapes dominated in the central interior and later shifted to more open C₄ landscapes in the later part of the Pleistocene. The carbon isotope values of animals, which are known as primary grazers today, indicate that C₄ and C₃ grasses have been available during the Middle Pleistocene, suggesting a cooler climate than today (Ecker et al., 2018; Mohale et al., 2022). The evidence of specialised grazing ungulates and wetland species, the isotope evidence, and additionally pan sediment proxies from dried up paleolakes (Brink, 2016) together suggest a Pleistocene environment defined by open grassland vegetation within a system of active lakes, springs and rivers (Lukich and Ecker, 2022). In contrast, the modern environment at Pniel 6 is heavily overgrazed and dominated by woody plants such as thorn bushes. The mean annual rainfall currently is 300–400 mm per year and highly seasonal, occurring mainly in the austral summer months (Ward et al., 2014). Reeds grow directly at the riverbank in patches, and some larger trees grow along the river course. The Vaal

River flows year-round, and the water table fluctuates depending on the rainfall amount and modern dams further upstream.

Reconstructing environments with stable isotopes

Enamel contains the highest mineral content in the animal body, often making it the best preserved tissue in animals (Hillson, 2005). In large mammals, enamel usually forms during the first few months to years of an animal's life, varying between species. The isotope ratios in enamel represent this formative period and are resistant to change over time (Passey and Cerling, 2002). However, some alterations in the carbonate fraction can appear (Sponheimer and Lee-Thorp, 1999). Stable carbon isotope analysis is used to investigate animal diets, as the carbon isotope values of organic tissues of herbivores reflect the plants they consume. By measuring the ratio of the stable carbon isotopes ¹³C and ¹²C, the ingestion of C₃- and C₄-plants can be reconstructed (Quade et al., 1992; Cerling et al., 1993; Sharp, 2017). One important factor in interpreting these results is the photosynthetic pathway of the consumed plants (Cerling et al., 1993). All C₄ plants are tropical grasses and sedges, but C₃ plants consist of temperate grasses, trees, shrubs, and herbs. Thus, the δ¹³C values differ between herbivores with C₃, C₄ and mixed diets (Sponheimer et al., 2003). The average δ¹³C value of C₃ plants is −27‰, ranging from −12.4‰ to −37‰ (Marshall et al., 2007). Plants using the C₄ photosynthetic pathway have higher values around −14‰ (Koch, 2007). Moreover, δ¹³C values are influenced by the CO₂ sources of plants, for example, atmospheric CO₂ and CO₂ from organic-bound CO₂. They can also differ between various plant tissues and leaf positions (Medina et al., 1986). The isotope enrichment between the consumed plants and tooth enamel of mammals is about 14‰ for large bovids (Passey et al., 2005). δ¹³C values of −8‰ or lower are interpreted as representing predominantly C₃ diets. δ¹³C values between −1‰ and −8‰ are interpreted as a mixed diet of C₃ and C₄ plants and δ¹³C values of more than −1‰, are interpreted as predominantly C₄ diets (Negash and Barr, 2023).

Stable oxygen isotope analysis of enamel is used to reconstruct the humidity and climate of past environments (Fricke et al., 1995). For this, the ratio of the stable isotopes ¹⁸O and ¹⁶O is measured against a standard. In terrestrial water sources, precipitation is the original water source, which is influenced by the progressive rainout of ¹⁸O-enriched meteoric water, depending on continentality, seasonality and altitude (Dansgaard, 1964; Rozanski et al., 1993). With the phase transitions of the water, fractionation occurs, resulting in an enrichment of the liquid phase (Dansgaard, 1964; Rundel et al., 1989). Oxygen in animal body water originates from food and drinking water as well as inhaled oxygen and is isotopically preserved in enamel (Bryant and Froehlich, 1995). Water source, diet, drinking behaviour, and physiology influence body water δ¹⁸O composition. There is a consistent but species-related relationship of the δ¹⁸O in the bioapatite with the body water. For example, the size and metabolic rates of mammals influence the δ¹⁸O values of bioapatite (Fricke et al., 1995; Bryant and Froehlich, 1995; Kohn, 1996). After accounting for these factors, the isotopes from bioapatite within tooth enamel can, therefore, be used as a proxy for the reconstruction of the climatic conditions of past environments (Fricke et al., 1995).

Amino acid geochronology

Amino acid geochronology is a technique that leverages the time-dependent decomposition of proteins in biominerals to estimate the age of fossil materials. A key parameter for this age estimation is racemisation, which involves the gradual inter-conversion of

L-amino acids to an equilibrium with their D-amino acid counterparts. Historically, amino acid geochronology in Africa has predominantly focused on ostrich eggshell (e.g., Brooks et al., 1990; Miller et al., 1992; Murray-Wallace et al., 2015), but recent studies have extended its application to *Achatina* shell (Baldreki et al., 2024a) and mammalian enamel (Baldreki et al., 2024b).

Intracrystalline protein decomposition (IcPD) analysis, which targets amino acids encapsulated within the crystal matrix of biominerals, has been shown to improve the reliability of amino acid geochronological data because it removes environmental effects other than temperature (Penkman et al., 2008; 2011; Dickinson et al., 2019). This approach has proven valuable for age estimation across Quaternary timescales in a variety of biominerals, including those based on calcium carbonate (e.g., Hendy et al., 2012; Penkman et al., 2013) and, more recently, calcium phosphate (Baleka et al., 2021; Bhat et al., 2024; Dickinson et al., 2024).

Given that amino acid geochronology is temperature-dependent, enamel—especially in warm regions like southern Africa—may offer the potential to provide age estimates that extend further back in time than those derived from other biominerals (Dickinson et al., 2019). Additionally, by dating the enamel in tandem with other biomolecular techniques, such as isotopic analysis, we are able to provide chronostratigraphical context to the paleoenvironmental data. This makes enamel a promising material for refining chronological frameworks in these regions.

Materials and Methods

Included in this study were the faunal remains from Beaumont's excavations (no accession number in the McGregor Museum, stored by Brink at the Florisbad Quaternary Research station until this study) and the MINERVA project excavations (accession number 7519 in the McGregor Museum) (Ecker et al., 2021). The Florisbad Quaternary Research Station comparison collection (National Museum Bloemfontein), which contains modern animals as well as extinct ones, was used for comparison. The fauna of the Beaumont excavation has been stored in four large boxes, two of which were labelled 'Rubble', one was labelled 'Gravel' and one 'Silt'. These labels most likely correspond to the Strata 3 ('Rubble'), 4 ('Gravel') and 2 ('Silt') described by Beaumont (1990). The material from Beaumont's excavation was in its original packaging and had not been opened before. The MINERVA material was derived from Area 4 (all Layer DA but three from Layer LP), Area 3 (all from Layer LH with one exception from Layer T) and one specimen from Area 2 (Layer G). All specimens were sorted first into unidentifiable and possibly identifiable specimens. All possibly identifiable specimens were provided with a new ID number and photographed.

Zooarchaeology

Faunal specimens recovered from all layers at Pniel 6 exhibit different stages of preservation, with the majority of specimens highly fragmented and bearing few morphological features diagnostic of family, genus, or species-level identification. Where possible, class of vertebrates, mammal size class, bovid size class (after Brain, 1974 and Klein, 1976 with minor changes and additions as described further below), taxon, and species were recorded (following Faith (2014) for extinct species, Groves (2014) for bovids and Groves and Grub (2011) for other taxa) (Tables S1 and S2). Following Hutson (2012), *M. priscus* was added to bovid size class IV, *A. bondi* to bovid size

class II and *D. niro* and *D. pygargus* to bovid size class III, to enable comparisons with the Pniel 6 assemblage studied by Hutson (2012). For each specimen, skeletal part, skeletal element symmetry, and, if possible, ageing data (i.e., state of epiphyseal fusion and tooth wear) were recorded (Table S1). Potential human-made modification of bone specimens (including breakage, percussion marks, burning or any other) was also recorded after Fernández-Jalvo and Andrews (2016).

Taxonomic abundance was quantified by the number of identified specimens (NISP) (Grayson, 1979) and the minimum number of individuals (MNI) based on White's (1953, as cited in Lambacher et al., 2016) MNI method. This was partly because the taphonomically altered bones from Pniel 6 rarely presented diagnostic morphological landmarks such as articular surfaces or visible foramina, and therefore, more elaborate methods such as the zonation system described by Knüsel and Outram (2004) or the landmark system of Mack et al. (2015) were not feasible. During the identification process, long bone fragments were recorded as proximal end, distal end, shaft fragment or complete bones. For MNI estimation, first the minimum number of elements (MNE) was estimated from the present element parts following the third method of Bunn et al. (1986; as described by Lyman (1994)) to determine the minimum number of complete elements represented by shaft specimens as well as specimens with one or two articular ends preserved. When MNE was estimated for a specific species, obvious size differences were taken into account between adult and juvenile bones. The teeth were described as either complete, half, one-third or fragments of indeterminate size and if buccal, labial, mesial, distal or lingual side or crown was preserved.

Only a very limited time was available to conduct a very preliminary taphonomic study of bone specimens, which is based on Fernández-Jalvo and Andrews (2016). However, a selection of 20 specimens was examined under a stereo microscope with a 10x magnification and an objective with a maximum magnification of 40x. The specimens were selected based on visually detectable linear marks, impact marks and notches, or atypical shape. Colour changes and structures are included in the documentation. Weathering stages have been described following Behrensmeyer (1978). For bone breakage, the criteria developed by Villa and Mahieu (1991) have been used.

Stable isotope analysis

182 teeth were identifiable, of which 177 originated from Beaumont's excavations and six from the MINERVA excavation. Of these, 65 were chosen for stable isotope analysis, all of them from the Beaumont excavations. The aim was to analyse the teeth of every species represented in the material to provide an overview of the complete palaeoecology. The criteria for choosing teeth were the outer appearance and the hardness of the enamel. Teeth with traces of burning and deciduous teeth were excluded. Moreover, the spit and square of individuals of the same species did not overlap to prevent sampling the same individual repeatedly. Teeth from the 'Silt Stratum' were excluded because it is likely that the fauna of Strata 2 dates younger. The outer tooth surface was cleaned with a Proxxon drill using a diamond tip. Bulk enamel powder samples were then taken over the whole tooth crown length. The enamel powder was collected on folded weighing paper and put into 1.5 mL plastic microcentrifuge tubes (Eppendorf). If the enamel was breaking, enamel splinters were collected in 1.5 mL plastic microcentrifuge tubes (Eppendorf) instead and homogenised in an agate mortar and pestle. Long splinters were preferred to cover the tooth crown length. For pretreatment, samples were soaked in 1.8 mL of 0.1 M acetic acid (CH₃COOH) for 10 min. Included in the

10 min were 3–5 min of centrifugation at maximum until the samples were clearly separated from the liquid. The supernatant liquid was removed with a new pipette for each sample, and the samples were rinsed with distilled water three times. After all water was removed, the tubes were closed with parafilm, and the samples were freeze-dried overnight. Stable isotope measurements were performed at the Leibniz Laboratory for Radiometric Dating and Stable Isotope Research at Kiel University with a Thermo Scientific MAT 253 mass spectrometer paired with a Thermo Scientific Kiel IV carbonate preparation unit. The analytical precision was $<\pm 0.08\text{‰}$ for $\delta^{18}\text{O}$ and $<0.05\text{‰}$ for $\delta^{13}\text{C}$. On 59 samples, duplicate measurements (subsamples of the same powdered enamel material) were performed to check the quality of sample material (Table S2). In five cases (ID numbers 12421/269, 12423/246, 12434/419, 12435/220, 12437/380), this was not possible due to the small sample size. In one case (ID number 12441/418), a technical issue prevented repeat measurement. The results are expressed as per mil (‰) in the delta notation (δ) versus the international VPDB standard.

Intracrystalline protein decomposition analysis

For this study, 21 of the teeth analysed for isotopic analysis were also analysed for IcPD (Table 1, Table S3), to better understand the temporal context of the material. This included five zebra (*E. capensis* and *E. quagga*) teeth, five hippopotamus (*H. amphibius*) teeth, four springbok (*Antidorcas marsupialis* and *A. bondi*) teeth, one African buffalo (*S. caffer*) tooth and six teeth belonging to the Alcelaphini tribe (one *Megalotragus* sp., one *A. buselaphus* and four teeth that could only be identified to tribe level).

11 samples for IcPD analysis were analysed from the powders generated for isotopic analysis, and 10 were sampled directly from teeth. For the direct sampling of teeth, an enamel sample was removed from each tooth with a precision drill (Dremel) using a diamond coated abrasive cutting disc, and the outer layer was removed with a diamond coated abrasive bit burr, usually a 2 mm ball or flame shaped bit. Care was taken to remove any visible dark discolouration that was present (Dickinson et al., 2024). To prevent contamination of enamel samples with the powders of other dental components,

chips were washed twice in HPLC-grade water and then once in ethanol (analytical-grade), and air-dried before being finely powdered using an agate pestle and mortar.

Preparation and analysis for the IcPD followed the methods developed in Dickinson et al. (2019). 15–30 mg of powdered enamel was weighed accurately into a 2 mL plastic microcentrifuge tube (Sarstedt), and NaOCl (12%, Fisher Scientific, analytical grade, $50\text{ }\mu\text{L mg}^{-1}$ of enamel) was added. Samples were exposed to NaOCl for 72 h whilst being continuously agitated to ensure complete penetration. The NaOCl was removed, and the powdered enamel was washed five times with HPLC-grade water. To remove any remaining NaOCl, powders were washed with methanol (HPLC-grade) before the sample was left to air dry overnight.

Subsamples were analysed from each bleached portion of enamel: one subsample was directly demineralised, and the 'free' amino acids (FAA) analysed, and the second was treated to release the peptide-bound amino acids, thus yielding the 'total hydrolysable' amino acid fraction (THAA). FAA samples were demineralised in HCl (1 M, $25\text{ }\mu\text{L mg}^{-1}$) in a sterile 0.5 mL plastic microcentrifuge tube (Eppendorf); if all visible signs of undissolved material had not disappeared, samples were sonicated for up to 3 min to aid in dissolution. THAA samples were placed in sterile 2 mL glass vials and dissolved in HCl (7 M, $20\text{ }\mu\text{L mg}^{-1}$). The vials were purged with N_2 to prevent oxidation, sealed, and heated at 110°C for 24 h. The acid was removed by centrifugal evaporation. THAA samples were redissolved in HCl (1 M, $20\text{ }\mu\text{L mg}^{-1}$) and transferred into a sterile 0.5 mL plastic microcentrifuge tube (Eppendorf). For both the FAA and THAA samples, the pH of the solution was raised with KOH and then centrifuged for 5 min at 13 000 rpm, whereupon a biphasic solution formed (Dickinson et al., 2019). The supernatant was extracted and dried via centrifugal evaporation.

Samples were rehydrated with a solution containing an internal standard (L-homo-arginine; 0.01 mM), sodium azide (1.5 mM) and HCl (0.01 M), to enable quantification of the amino acids. Separation of chiral amino acid pairs was achieved using an Agilent 1100 Series HPLC fitted with a HyperSil C18 base deactivated silica column ($5\text{ }\mu\text{m}$, $250\times 3\text{ mm}$) and fluorescence detector, using a modified method outlined by Kaufman and Manley (1998) (modifications in Penkman, 2005).

Table 1. List of specimens analysed for IcPD analysis and type of sampling procedure used.

Accession number	Taxon	Directly from tooth	Powder from isotope analysis
9254/11	<i>Equus capensis</i>	X	
9245/97	<i>Equus quagga</i>	X	
9266/385	<i>Equus capensis</i>	X	
9251/60	<i>Equus capensis</i>	X	
9260/215	<i>Equus quagga</i>	X	
9258/393	Alcelaphinae	X	
9263/359	Alcelaphinae	X	
9247/360	Alcelaphinae	X	
9265/225	<i>Megalotragus priscus</i>	X	
9253/399	<i>Alcelaphus buselaphus</i>	X	
9231/262	Alcelaphinae	X	
12426/309	<i>Hippopotamus amphibius</i>		X
12429/323	<i>Hippopotamus amphibius</i>		X
12436/391	<i>Hippopotamus amphibius</i>		X
12442/375	<i>Hippopotamus amphibius</i>		X
12444/386	<i>Hippopotamus amphibius</i>		X
12439/431	<i>Syncerus caffer</i>		X
12433/177	<i>Antidorcas marsupialis</i>		X
12422/15	<i>Antidorcas marsupialis</i>		X
12423/246	<i>Antidorcas marsupialis</i>		X
12448/434	<i>Antidorcas bondi</i>		X

Accession number shows Archaeological Stable Isotope Laboratory (ASIL) number/specimen ID number.

The column temperature was controlled at 25°C, and a tertiary system containing sodium buffer (23 mM sodium acetate trihydrate, sodium azide, 1.3 µM EDTA, adjusted to pH 6.00 ± 0.01 with 10% acetic acid and sodium hydroxide), acetonitrile and methanol was used as the mobile phase. During the preparation of samples, asparagine and glutamine undergo a rapid, irreversible deamination to aspartic acid and glutamic acid, respectively (Hill, 1965). Therefore, it is not possible to distinguish between these amino acids and their derivatives, and they are reported together as Asx and Glx. Both FAA and THAA samples were prepared in duplicate from bleached powders, with standards and blanks prepared and analysed alongside samples.

Results

Zooarchaeology results

Of a total of 5560 fragments (22.394 kg) of bones and teeth, 504 specimens from the Beaumont excavation and 13 specimens

from the MINERVA excavation were determined as partly or fully identifiable and were subsequently analysed more closely (Table S1). In the end, we identified 87 bones or bone fragments and 182 teeth (across both excavations, for example, see Figs. 2, S7–S13 and S16–S22) to the tribe or higher level, which is 4.8% of the combined faunal assemblage. Of these, 30 bones and bone fragments and 128 teeth were identified to species level. One additional specimen could be identified as an ostrich eggshell (ID 519). The number of identified specimens of the MINERVA excavations is very low—only one identified bone specimen (ID 477, an *A. buselaphus* calcaneus) and six identified teeth. For this reason, the specimens of the MINERVA excavations are included together with the Beaumont specimens in the analysis (Table 2). Bovidae dominate (MNI = 26), followed by Equidae (MNI = 7).

The bovid size classes II, III and IV are present in the material, and most specimens belong to size class III ($n = 111$) (Fig. S1). A classification into the broad juvenile and adult categories shows that most bones are from adults, as either the epiphysis was fused or the proportions were comparable to those of adult specimens from the comparative collection. Six

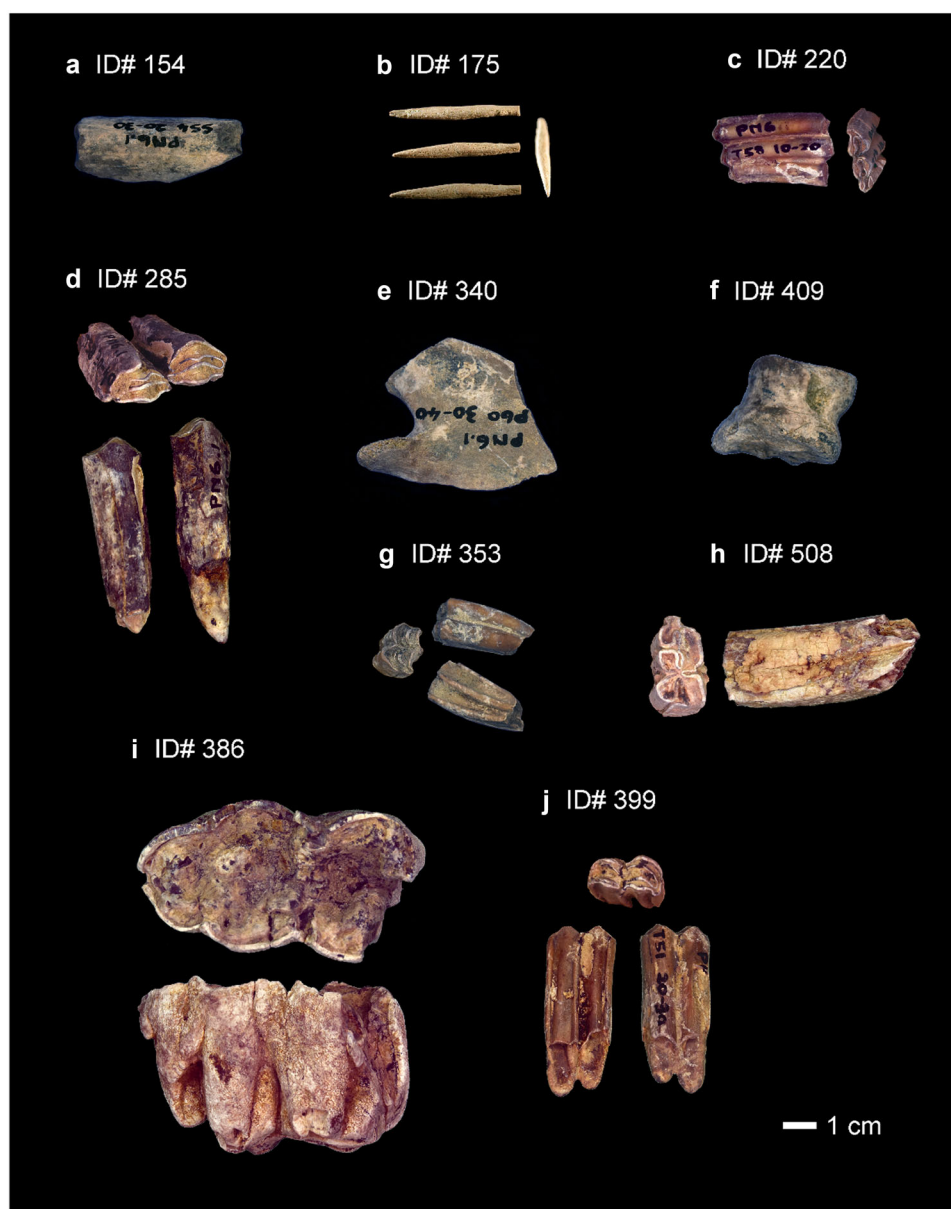


Figure 2. Examples of faunal remains from Priel 6. (a) Bovid bone fragment with possible impact fracture; (b) Shaped bone fragment; (c) *Antidorcas bondi* M₃; (d) *Megalotragus pricus* lower molar; (e) *Connochaetus taurinus* cf. mandible fragment; (f) *Kobus leche* cf. astragalus; (g) *Kobus leche* M₃; (h) *Equus quagga* tooth; (i) *Hippopotamus amphibius* M₃; (j) *Alcelaphus buselaphus* M₂. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

Table 2. Animal representation for the Beaumont and MINERVA excavations in identified bones and teeth numbers of identified specimens (NISP) and minimum number of individuals (MNI).

Taxon	NISP (Beaumont)	MNI (Beaumont)	NISP (MINERVA)	MNI (MINERVA)
Indet. large mammal	24	0	0	0
Indet. bovid size class	3	1	0	0
<i>Syncerus caffer</i>	1	1	0	0
<i>Taurotragus oryx</i>	3	1	0	0
Indet. Alcelaphinae	35	0	0	0
<i>Alcelaphus buselaphus</i>	11	2	3	1
<i>Connochaetes</i> sp.	5	1	0	0
<i>Connochaetes gnou</i>	6	1	0	0
<i>Connochaetes taurinus</i>	3	2	0	0
<i>Damaliscus</i> sp.	10	2	0	0
<i>Damaliscus pygargus</i>	7	1	0	0
<i>Megalotragus priscus</i>	13	1	0	0
<i>Kobus</i> sp.	4	1	0	0
<i>Kobus ellipsiprymnus</i>	4	1	0	0
<i>Kobus leche</i>	8	3	0	0
<i>Antidorcas</i> sp.	5	2	0	0
<i>Antidorcas bondi</i>	6	2	0	0
<i>Antidorcas marsupialis</i>	7	2	0	0
<i>Pelea capreolus</i>	1	1	0	0
<i>Equus</i> sp.	7	2	2	1
<i>Equus capensis</i>	5	1	0	0
<i>Equus quagga</i>	17	1	1	1
Equidae	0	0	2	1
<i>Ceratotherium simum</i>	1	1	0	0
<i>Hippopotamus amphibius</i>	17	1	1	1
Suidae	3	2	0	0
<i>Phacochoerus africanus</i>	10	3	0	0
<i>Lepus capensis</i>	2	1	0	0
<i>Struthio camelus</i>	1	1	0	0

bones were classified as possibly juvenile or juvenile by either state of epiphyseal fusion or proportions (Table S1).

Identifiable skeletal elements are listed in Table 3. Teeth (NISP = 323) dominate, with metapodials (NISP = 15) being the next most abundant skeletal part (Table 3). Limb long bones make up 57% of the identified elements if teeth are excluded. If the actual MNE values of the individual element types are compared to the expected MNE based on the calculated MNIs of each taxonomic family, expressed as a percentage (i.e., % survivorship), a slightly different picture emerges. Here, rib survivorship compared to its expected values is low, with only 0.2% survivorship in bovids and 2.6% survivorship in suids. Teeth of bovids and suids (between 8.1% survivorship in bovids and 9.8% survivorship in suids) and mandibles of bovids (6.3% survivorship) as well as long bones of bovids and leporids (6.3% survivorship in bovids and 50% survivorship in leporids) are represented much better in the archaeological record, even though % survivorship values are low in all elements. This suggests that of the original death assemblage, only a small number of bones survived to be excavated and identified, with the relative majority of the identified elements being teeth, mandibles and long bones.

Taphonomic results

The bones and teeth from Pniel 6 are in different stages of weathering, and most are highly fragmented. Specimens recovered as part of the MINERVA excavations are even more fragmented than the Beaumont material. Of all the bones, just four pieces have been found complete in the Beaumont material and none in the MINERVA specimens. In the Beaumont excavation, 48 specimens of the analysed specimens have fractures indicative of green bone breakage. A further 13 bones have smooth fracture edges, but with transversal breakage

Table 3. List of elements for Pniel 6 (all excavations) with number of identified specimens (NISP).

Element	Sum of NISP of elements
Teeth	323
Rib	9
Humerus	6
Metapodial	5
Radius	5
Tibia	5
Metacarpal	5
Metatarsal	5
Mandible	4
Vertebra	3
Astragalus	2
Femur	2
Calcaneum	1
Ulnar carpal bone	1
Ulna	1
Scapula	1
Proximal phalanx	1
Skull	1
Intermediate phalanx	1
Sum of all NISP elements	381

outlines and a perpendicular angle, indicative of fossil bone breakage. 14 bones were identified as potential predepositional dry breaks. The overall appearance in the analysed bones of the breakages is that there are nearly twice as many spiral fractures (green bone breakage) as dry or fossil bone breaks. The MINERVA bones reveal mostly old breakages with smoothed edges. The different fracture patterns were not recorded for the unanalysed bones; it was assumed that the analysed bones were representative of the same pattern. In both excavation

assemblages, most bones are discoloured, with many specimens darkened or stained with black spots and patches indicative of manganese staining in temporarily wet conditions. Other bones are bleached, patinated or encrusted with chalky crust or patination. Several pieces have reddish-stained spots. Most bones ($n=55$) fall in Behrensmeyer's weathering stages 1–2, and 43 are unweathered. The bones from the MINERVA excavation have weathering stages from 0 to 2 and a single piece that is weathered more heavily (Table S1).

There were traces of burning in the form of calcinations, charring and typical cracking, distinctly different from manganese staining on two unidentifiable specimens of the Beaumont excavations (Fig. S14). Some potential signs of rodent gnawing, clear carnivore bite marks or chewing by bovids were found on the identified bones (some examples are shown in Figs. S2–S3 and S15) but need to be evaluated under a microscope for a full assessment.

Overall, the Beaumont and MINERVA assemblages reveal similar patterns of low weathering and some discolouration of the bones through manganese staining, indicating wet conditions. While the distribution of breakage pattern is slightly different, with a higher number of dry breaks in the MINERVA assemblage, many rounded edges show that many fractures are old and have been smoothed either by abrasion in soil or during water transport.

Nine bone fragments from the Beaumont excavation were noted for their symmetrical shape as well as features that resemble possible impact fractures on their tips, percussion marks, or longitudinal striae (e.g., Figs. 2(a) and S4–S6). Of these, the most striking is ID175 (Fig. 2(b)), a 5 cm long, compact bone that is completely rounded and is thinning towards a tip. This suggests the possibility that a small percentage of Pniel 6 bones has been modified by humans. However, further microscopic studies on these bones are needed to test this hypothesis.

Stable isotope results

Of the 65 enamel samples that were measured for carbon and oxygen stable isotope ratios, 31 samples had to be excluded from further analysis due to large differences ($>1\text{‰}$ difference) in duplicate measurements (performed on different days) in at least one isotope ratio of the same sample (carbon or oxygen isotope ratio, or both; Table S2). The reason for these differences is not clear, as they appear across all species, sampling methods (drill vs. mortar), tooth types, excavation squares and depths. We expect that the difference is due to bad mineral preservation, leading to

isotopic alteration, as these samples show high internal errors during isotope measurement, which suggests contaminated CO_2 from those samples. Mineral diagenesis in some of the samples was also indicated by the IcPD analysis, with two of the 21 teeth showing open-system behaviour consistent with diagenetic alteration. Therefore, only the 34 samples with duplicate measurements of $<1\text{‰}$ difference were included in the discussion below. For three species (*A. marsupialis*, *C. gnou*, and *T. oryx*) there are no duplicate measurement isotope data, but we included them in the discussion (Table S2). For *C. simum*, the only duplicate measurement shows a difference of -2.8‰ in $\delta^{18}\text{O}$, so this species had to be excluded completely from the interpretation. For the calculation of the species means, all samples with only one available measurement were included. For all other measurements, the arithmetic mean of both duplicate measurements was taken and is presented in Table 4.

Across species means, *A. buselaphus* yielded the highest $\delta^{13}\text{C}$ mean value with 0.9‰ , and *T. oryx* the lowest $\delta^{13}\text{C}$ mean value with -10.7‰ . Thus, there is a range of 11.6‰ in the $\delta^{13}\text{C}$ mean values between all species. Comparing the individual measurements, one *A. bondi* individual yielded the highest $\delta^{13}\text{C}$ value of $+2.5\text{‰}$, and a *T. oryx* individual had the lowest $\delta^{13}\text{C}$ value of -10.9‰ , leading to an even larger range of 13.5‰ . The grazing species show a $\delta^{13}\text{C}$ range between 0.9‰ (*A. buselaphus*) and -5.7‰ (*H. amphibius*). *K. leche* has the highest standard deviation, caused by one extremely low individual value (-10.0‰). For the species $\delta^{18}\text{O}$ mean values, the species yielding the highest value is *E. quagga* with a $\delta^{18}\text{O}$ value of 4.4‰ , while the lowest $\delta^{18}\text{O}$ value of -2.3‰ is from *H. amphibius*, so the range was 6.7‰ . For single measurements, the highest $\delta^{18}\text{O}$ value with 7.8‰ is also from an *E. quagga* individual, while the lowest single measurement $\delta^{18}\text{O}$ value of -2.3‰ is from the only *H. amphibius* individual; therefore, the $\delta^{18}\text{O}$ in individual measurements spans 10.1‰ . The highest standard deviation is among the large Alcelaphini, in which different species are potentially represented. There were no obvious differences or trends between the Rubble and Gravel stratum stable isotope values.

Enamel IcPD results

Two of the samples subjected to IcPD analysis—one from *S. caffer* (Sample 431) and one from *A. marsupialis* (Sample 246)—did not align with the expected trends for closed-system amino acids (Fig. 3(a)). These samples were analysed for IcPD from leftover powders from the isotopic analysis. This divergence could result

Table 4. $\delta^{13}\text{C}_{\text{VPDB}}$ and $\delta^{18}\text{O}_{\text{VPDB}}$ measurement results from Pniel 6: number of individuals, mean values, minima, maxima and standard deviation (SD) by species.

Species	<i>n</i>	Mean $\delta^{13}\text{C}$	Min $\delta^{13}\text{C}$	Max $\delta^{13}\text{C}$	SD	Mean $\delta^{18}\text{O}$	Min $\delta^{18}\text{O}$	Max $\delta^{18}\text{O}$	SD
<i>Antidorcas bondi</i>	3	0.0	-2.5	2.5	2.0	3.1	2.5	5.4	1.6
<i>Alcelaphus buselaphus</i>	4	0.9	1.1	1.3	0.5	0.5	-1.3	2.4	1.4
<i>Antidorcas marsupialis</i>	1	-5.0	n/a	n/a	n/a	1.3	n/a	n/a	n/a
<i>Connochaetes gnou</i>	1	-2.1	n/a	n/a	n/a	1.9	n/a	n/a	n/a
<i>Connochaetes taurinus</i>	1	-1.4	n/a	n/a	n/a	3.9	n/a	n/a	n/a
<i>Damaliscus</i> sp.	2	0.2	-0.1	-1.6	0.3	0.0	-1.6	1.6	1.6
<i>Equus capensis</i>	2	-2.7	-3.7	-1.7	1	2.8	0.8	4.8	2.0
<i>Equus quagga</i>	3	-2.1	-4.6	0.4	2.1	4.4	1.5	7.8	2.6
<i>Hippopotamus amphibius</i>	1	-5.7	n/a	n/a	n/a	-2.3	n/a	n/a	n/a
<i>Kobus ellipsiprymnus</i>	3	-1.2	-3.0	0.2	1.3	2.5	1.3	3.7	1.0
<i>Kobus leche</i>	3	-3.9	-10.0	-0.5	4.4	2.0	1.0	3.5	1.1
<i>Megalotragus priscus</i>	2	-1.6	-1.8	-1.3	0.3	2.9	2.6	3.3	0.4
<i>Phacochoerus africanus</i>	4	-0.8	-1.0	-0.4	0.2	-0.4	-0.9	0.8	0.7
<i>Syncerus caffer</i>	1	-2.7	n/a	n/a	n/a	-0.5	n/a	n/a	n/a
<i>Taurotragus oryx</i>	2	-10.7	-10.9	-10.6	0.2	4.0	2.0	6.0	2.0
Large Alcelaphine	2	-1.0	-1.6	-0.3	0.7	3.8	1.7	6.0	2.2

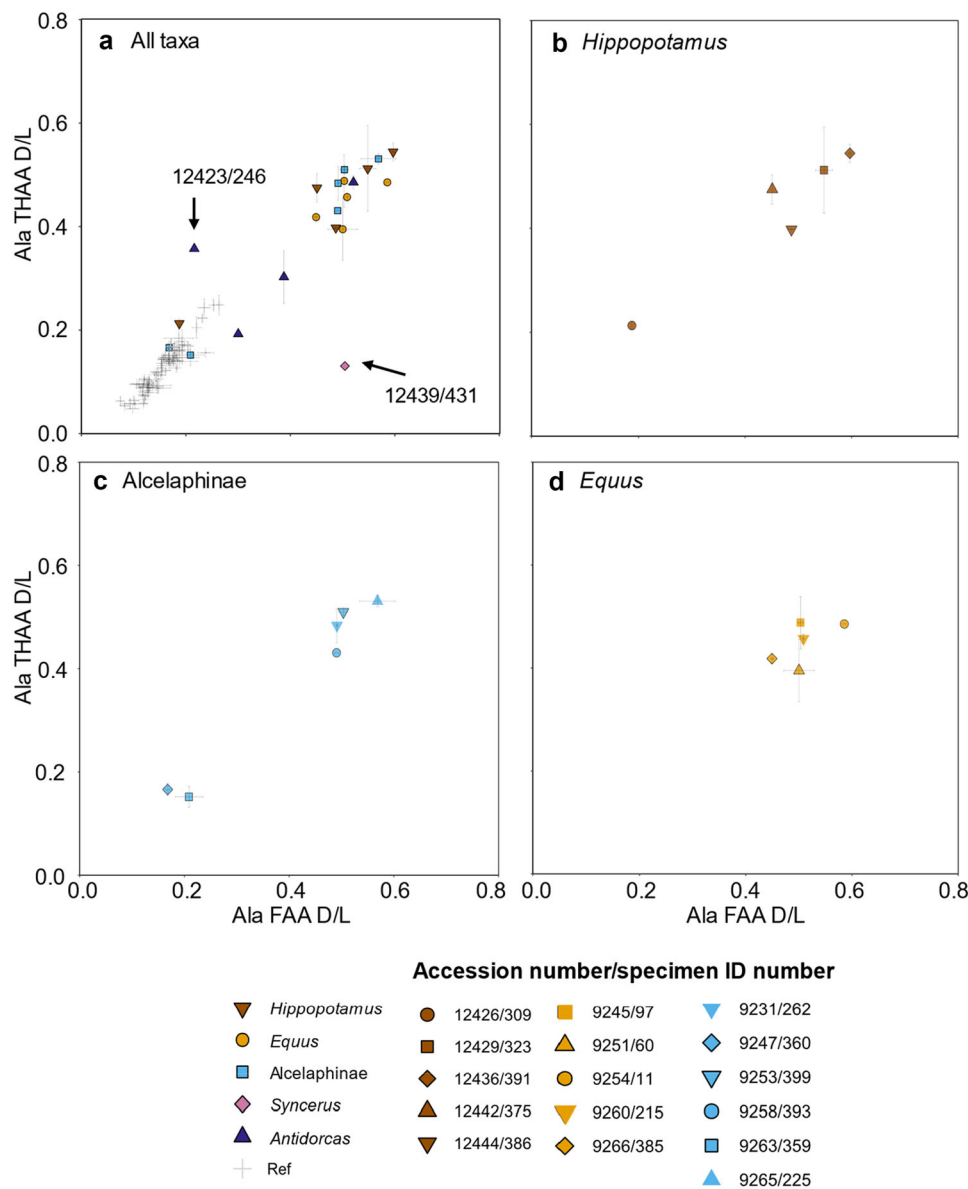


Figure 3. (a) Comparison of 'free' amino acids (FAA) versus 'total hydrolysable' amino acid fraction (THAA) intracrystalline racemisation for alanine (Ala) in mammalian enamel from Pniel 6, including a reference dataset (greyed out data points) of other elephantid, *E. ferus* and *B. priscus* teeth (Dickinson et al., 2024) to illustrate the expected trend between FAA and THAA values for closed system enamel. The samples 12439/431 (*Syncerus caffer*) and 12423/246 (*Antidorcas marsupialis*) do not fall on the same trend as the rest of the material analysed, and were therefore not used for age estimation. Comparison of FAA versus THAA intracrystalline racemisation for alanine (Ala) in (b) *Hippopotamus amphibius*, (c) Alcelaphinae, and (d) *Equus* enamel from Pniel 6. The error bars depict one standard deviation about the mean based on replicate subsamples. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

from diagenetic alteration of the enamel (Dickinson et al., 2024), or that the procedures used for sampling for isotopic analysis have the potential to introduce contamination of enamel powders that can impact IcpD analysis.

For the samples that did conform to expected IcpD trends, two distinct data clusters were observed for the *H. amphibius* and Alcelaphine (Fig. 3(b),(c)) while all *Equus* data plotted in a similar region (Figs. 3(c), 4). Four samples—two from Alcelaphini, one from *H. amphibius*, and one from *Antidorcas*—exhibited lower IcpD levels than the others, implying that they likely originated from a more recent period. This, therefore, suggests that rather than being a single aged deposit, the teeth were deposited during at least two separate time periods.

Due to the small number of samples analysed by IcpD, the faunal remains may reflect continuous accumulation at the site over an extended period, rather than distinct episodes of deposition. This interpretation aligns with the site's location along the Vaal River, where ongoing sedimentary processes could have

contributed to the high fragmentation and rounded edges observed in the assemblage. The broader spread of *H. amphibius* in Asx and Glx THAA D/L values (Fig. 4) supports the possibility of prolonged accumulation within the older cluster. Additionally, while some *Antidorcas* specimens fall between the two clusters (Fig. 3(a)) in Ala D/L (Fig. 3(a)), this is not observed in the THAA D/L values of Asx or Glx. Lack of comparative *Antidorcas* data precludes further interpretation. Either way, recognition of this deposit representing a larger span of time than had been anticipated is critical for accurate interpretation of the isotopic proxies.

Discussion

Environmental reconstruction

Large grazing species dominated the animal community, including very large species such as *M. priscus*. Typically categorised as grazing species are *A. buselaphus* (Cerling et al., 2003), *C. gnou*,

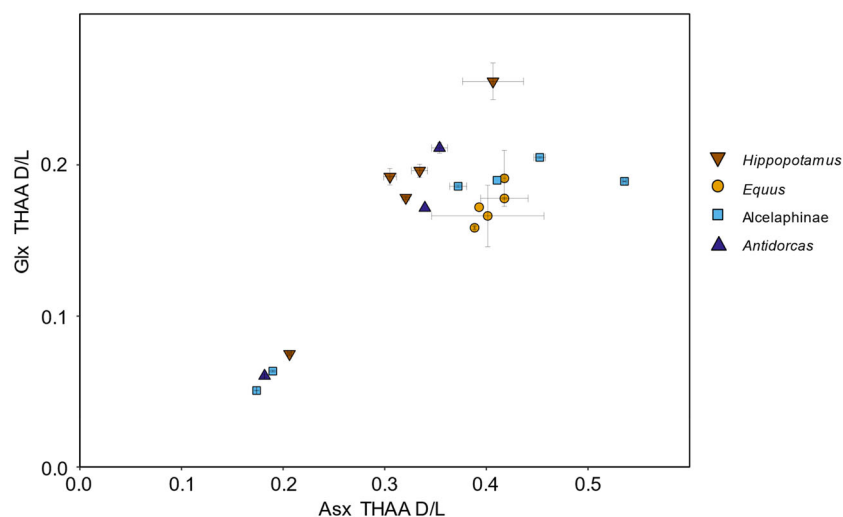


Figure 4. Comparison of 'total hydrolysable' amino acid fraction (THAA) aspartic acid/asparagine (Asx) versus THAA glutamic acid/glutamine (Glx) intracrystalline racemisation in mammalian enamel from Pniel 6, showing that the samples analysed are not of the same age. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jqs.70002)]

C. taurinus (Cerling et al., 2003), *D. pygargus* (Skinner and Chimimba, 2005), *M. priscus* (Brink and Lee-Thorp, 1992), *K. leche* (Jeffery and Nefdt, 2013), *E. capensis* (Lee-Thorp and Beaumont, 1995), *E. quagga* (Apps 2012), *C. simum* (Apps, 2012), *H. amphibius*, *A. bondi* (Brink and Lee-Thorp, 1992; Ecker and Lee-Thorp, 2018) and *P. africanus* (Cumming, 2013). *Syncerus caffer* is an occasionally browsing species which mostly feeds on grass, similar to *K. ellipsiprymnus* (Apps, 2012). Most of these species yield carbon isotope values expected for the ingestion of C_4 plants (Figs. 5 and 6). The Equidae and *S. caffer* have the lowest $\delta^{13}C$ values of the grazing species. *Antidorcas marsupialis* is a mixed feeder in the literature (Apps, 2012; Skinner, 2013) as well as in our stable isotope measurements. *Kobus leche* $\delta^{13}C$ values in this analysis also indicate a mixed diet, in contrast to the literature on modern lechwe (Gagnon and Chew 2000). *Taurotragus oryx* is a browser with small amounts of grass intake, which can vary in the populations (Apps, 2012), and indicates a pure C_3 diet in our study, with $\delta^{13}C$ values below -10‰ .

The high abundance of mixed feeders and pure C_4 feeders indicates a dominating presence of C_4 grasses. The overall results suggest an open grassland environment at Pniel 6 with some trees or shrubs and herbs. Considering the research of Negash and Barr (2023) and Norwood et al. (2025), a dominance of grazers does not necessarily imply the presence of grassland. Still, most species at Pniel 6 depend on open areas, such as *C. gnou* (Brink, 2016), which makes high abundances of trees unlikely. Most of the species represented at Pniel 6 are typical grazers today, but overall their $\delta^{13}C$ values are often somewhat lower than would be expected in modern specimens. This could be an indicator that some part of the C_3 plants does consist of grasses, such as has been suggested for other Middle Pleistocene sites in the region (Codron et al., 2008; Ecker et al., 2018; Mohale et al., 2022). Thus, the C_3 plants at Pniel 6 might be diverse: when combining the carbon isotope data with the species diets, it is plausible that some amount of C_3 plants consisted of C_3 grasses, with herbs, shrubs and trees also present.

Another important result of the species composition at Pniel 6 is the presence of water-dependent species such as *K. leche*, *K. ellipsiprymnus* and *H. amphibius*, that do not exist in this area today. Interpretation of $\delta^{18}O$ values (Figs. 5–7) is complex, and different explanations were considered. Lüdecke et al. (2022) reported a $\delta^{18}O$ difference between ruminants and nonruminants. For Pniel 6, this could not be observed (Fig. 6). One possible influence is different diets, which are partly reflected in the values (Makarewicz and Pederzani 2017). *Taurotragus oryx*, the only browser, has the second highest $\delta^{18}O$ species value, but this may be skewed by the one

T. oryx individual which has much higher values than most of the other species. Considering the water dependence of all the species, which correlates with the diet, most are obligate drinkers. While *A. marsupialis* and *T. oryx* are nonobligate drinkers, they drink when they have the opportunity. The $\delta^{18}O$ values for *A. marsupialis* are not particularly high, but in the medium range of all species. The most water-dependent species is *H. amphibius*, which has the lowest $\delta^{18}O$ values, as expected in comparison to terrestrial herbivores (Bocherens et al., 1996). Thus, there are slight differences in the $\delta^{18}O$ values based on the water-dependence of the species, but they are not visible in every case. *Phacochoerus africanus* was expected to have among the lowest values of all grazing taxa (Sponheimer and Lee-Thorp, 2001), which is true for Pniel 6. *Kobus leche* and *Kobus ellipsiprymnus* are two other water-dependent species, but their values (mean $\delta^{18}O$ value 2.5‰ , three individuals) are not as low as expected, for example, compared to Sponheimer and Lee-Thorp (2001). The species classification and the stable isotope analysis both suggest a rich grassland environment with open water components such as the Vaal River for Pniel 6, which certainly would have provided many resources for *H. sapiens*.

There are three extinct species in the assemblage: *A. bondi*, *E. capensis* and *M. priscus*, all of which went extinct in the late Pleistocene. It is unlikely that they went extinct due to human impact, and an environmental change is the most probable explanation (Brink, 2016). Being part of a unique grazing succession (Brink and Lee-Thorp, 1992), it has been suggested that these species were dependent on each other. If changes in the vegetation structure caused a loss in highly productive grassland, the basic food resource for all three species would have been missing (Brink and Lee-Thorp, 1992). Six of our species (*D. pygargus*, *K. leche*, *K. ellipsiprymnus*, *C. simum*, *H. amphibius*, *P. africanus*) are not present in this region anymore (Apps, 2012), in addition to the three extinct species.

Accumulation agents

The recovery of the faunal remains, completely mixed up in the stone tools, with no clustering visible, but all in the same distinct layer, suggests that the faunal remains and lithics were deposited together. There are no clear trends visible between the 'Rubble' and 'Gravel' strata specimens regarding the stable isotope values or the species and skeletal element representation. Furthermore, the difference between these two strata has not been sufficiently documented by Beaumont to ascertain why he made a distinction. No difference appears between the two excavations or within excavation areas (horizontally or

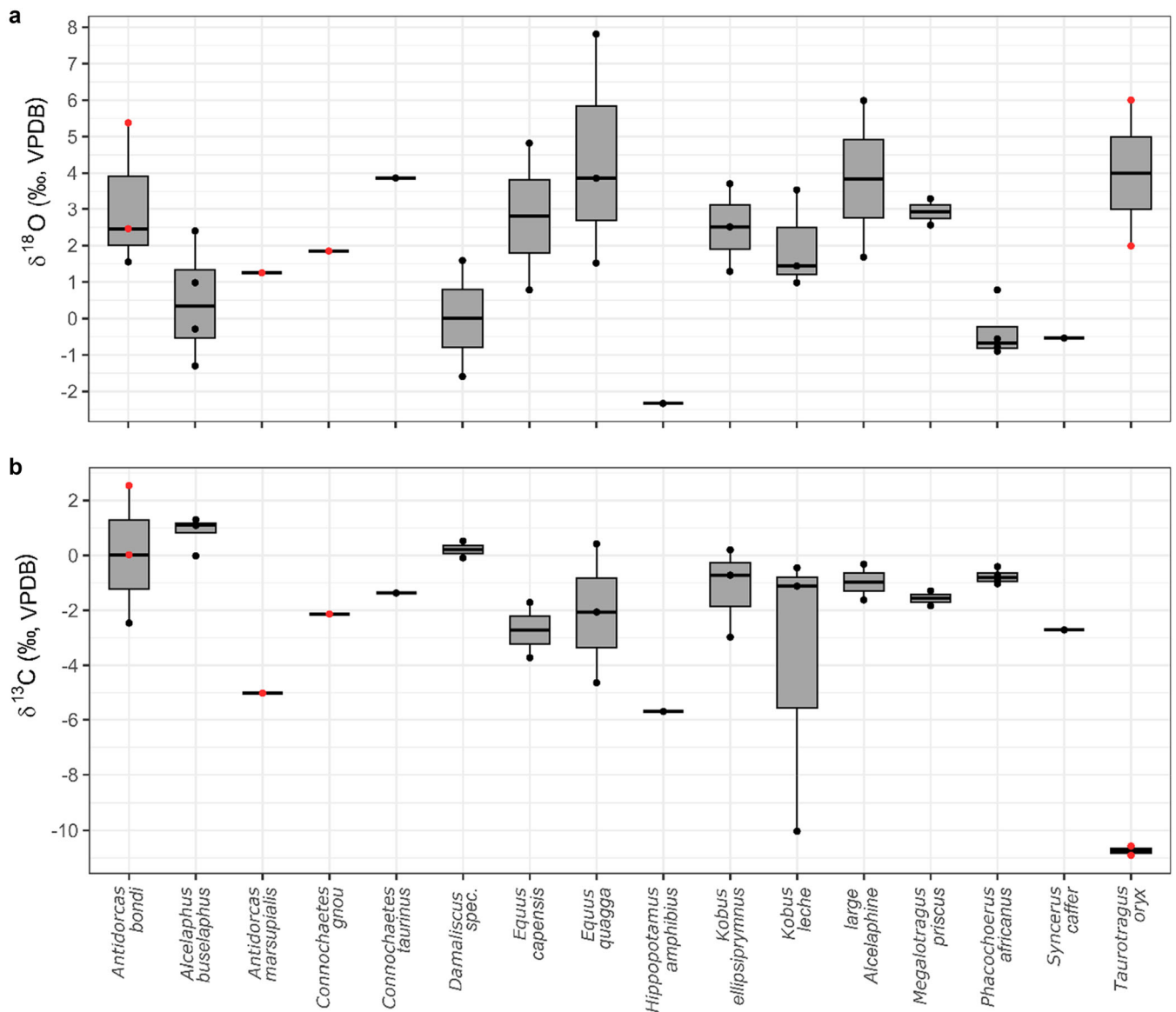


Figure 5. Boxplot of stable isotope results. Individual measurements are presented as dots, including single measurements in red (the rest is confirmed by duplicate measurements). (a) $\delta^{18}\text{O}$ values (‰, VPDB); (b) $\delta^{13}\text{C}$ values (‰, VPDB). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

vertically). This suggests that the assemblage might be considered one single deposition, deposited by colluvial and/or fluvial action in pockets along the Vaal River southern bank. It supports the interpretation of a late Middle Pleistocene faunal assemblage associated with early MSA or Fauresmith technocomplex lithics, with no significant older ESA component underneath. It cannot be excluded that a small number of specimens in both assemblages are intrusive from younger deposits, particularly in the first 20 cm below the surface (see discussion 5.3 below). This could be because of bioturbation or during repeated flooding in the last hundred thousand years. While the assemblage could be a natural death assemblage deposited by fluvial transport, a small human factor cannot be excluded.

Compared to other FLMA faunal assemblages in the wider area (Table 6), some differences could be due to different accumulation agents responsible for the formation of the assemblages. Two assemblages from Florisbad, the 'Old Collection' and the 'MSA Assemblage', which are dated to the Middle Pleistocene as indicated by their species representation (Brink, 1987), can be compared with our study. The 'Old Collection' of Florisbad consisted of ungulates of all size classes representing 95.69% of the occurring species, as well as carnivore species (Brink, 1987)

which are absent at Pniel 6. The assemblage was interpreted as a natural death assemblage with carnivores being the primary agents of accumulation. This was supported by the presence of hyena chewing on bones, the absence of cut marks, relatively complete bones with a minor component of unidentifiable fragments and representation of the complete range of body parts (Brink, 1987). In contrast, the Florisbad 'MSA Assemblage' contained mostly smaller ungulates. Brink (1987) argues that the lack of large grazers in the 'MSA Assemblage' could be due to the fact that humans without technologically sophisticated hunting weapons would rather hunt animals in their own size class (Brink, 1987). No evidence of carnivore damage by bite or chewing marks has been found on the 'MSA Assemblage' specimens. On the contrary, several specimens show chop marks, scraping marks, cutmarks or slice marks (Brink, 1987). On several bones, hammerstone marks (lunate fraction scars) and their counterparts (crescent-shaped bone flakes) have been observed (Brink, 1987). The Pniel 6 assemblage differs in many respects from the 'Old Collection' and is more similar to the 'MSA Assemblage', having no presence of carnivores in the excavation assemblages, a heavily fragmented bone appearance with most bones being unidentifiable, a rather randomly body part representation and diverse taphonomic

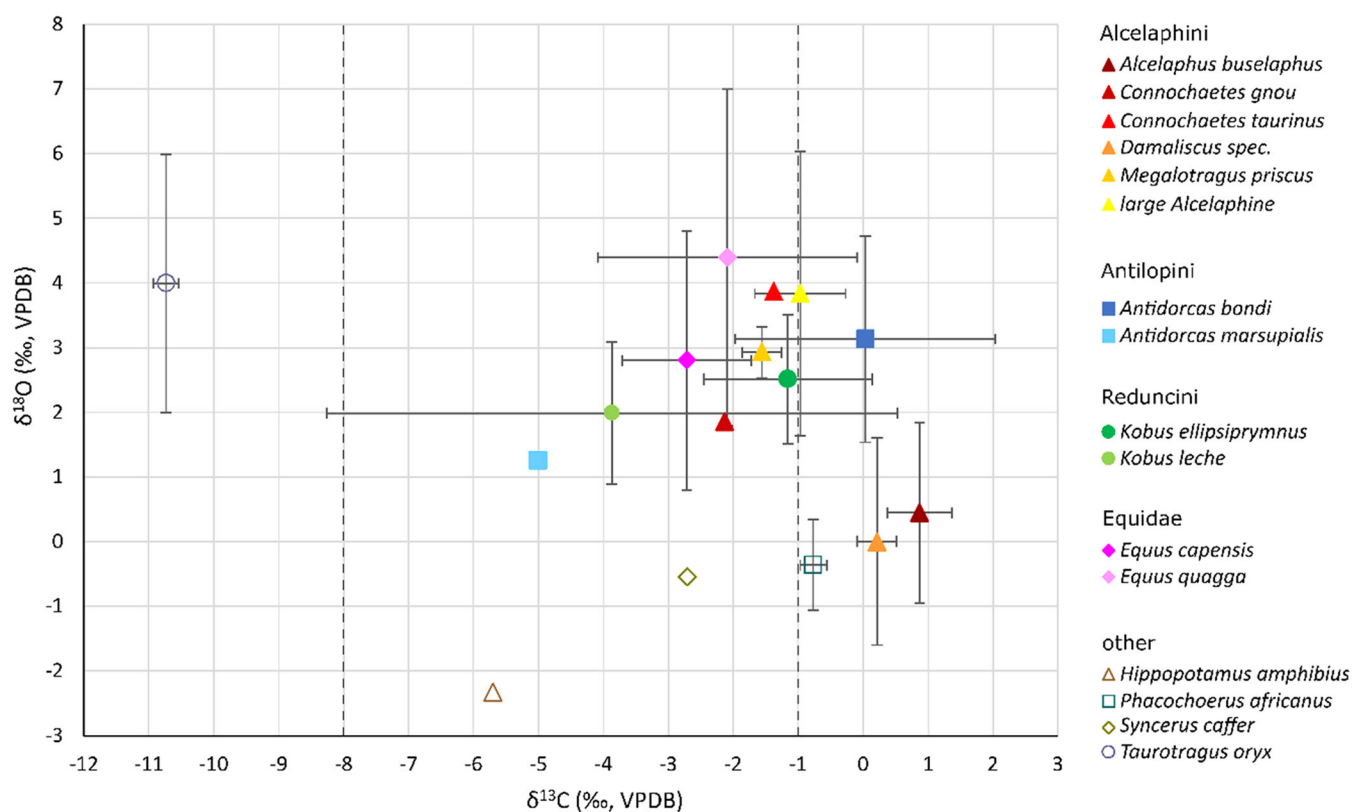


Figure 6. Carbon and oxygen stable isotope results for species means with standard deviation, including single measurements. Dotted lines implicate the borders between a predominant C_3 (values lower than -8.0‰), C_3/C_4 (values between -8.0‰ and -1.0‰) and C_4 plant diet (values higher than -1‰). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jqs.70002)]

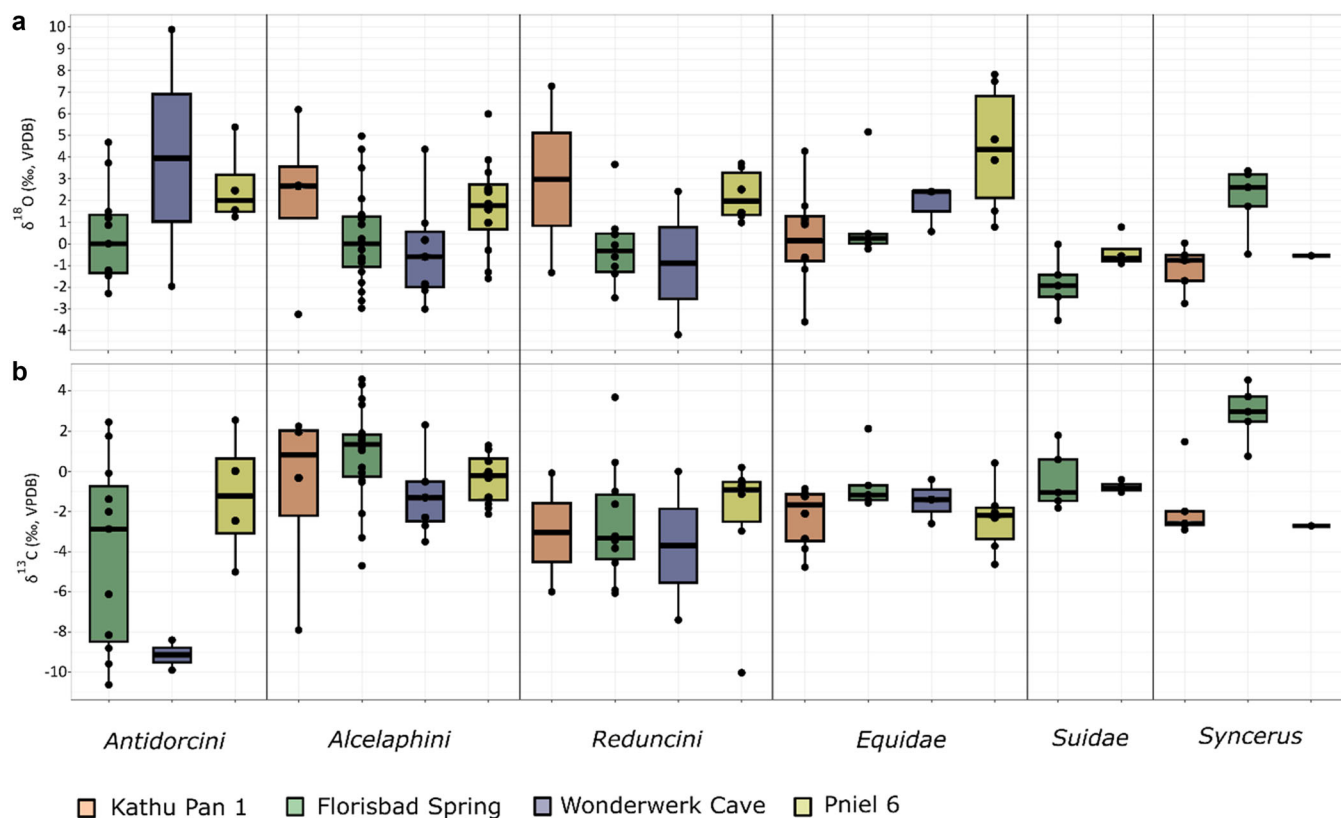


Figure 7. Comparison of Antidorcini, Alcelaphini, Reduncini, Equidae, Suidae and *Syncerus* at Kathu Pan 1 (red), Florisbad Spring (green), Wonderwerk Cave (blue) and Pniel 6 (yellow). The last *Syncerus* belongs to Pniel 6. (a) $\delta^{18}\text{O}$ values (‰, VPDB) (b) $\delta^{13}\text{C}$ values (‰, VPDB). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jqs.70002)]

indicators including possible human processing of the bones (such as linear marks, burning and percussion marks which have to be further examined by an explicit study). This may indicate that the agent of accumulation might have a human element in parts. However, the high fragmentation rate at Pniel 6 could also be due to river transport, which might also be indicated by rounded edges and manganese staining of the bones.

The age of the Pniel 6 assemblages

The IcPD data reveal two distinct clusters, indicating the faunal assemblage from Pniel 6 is derived from at least two different time periods. The cluster with higher D/L ratios is consistent with a Middle Pleistocene age, while the cluster with lower D/L ratios suggests a younger date, likely a late Middle Pleistocene or Late Pleistocene age. Although we anticipate some taxonomic effects, which limit direct comparisons between species, it is noteworthy that the same clustering is observed in two different taxa. All of the *Equus* material analysed, including both *E. capensis* and *E. quagga*, consistently plot within the older cluster, indicating these species were contemporaneous during the Middle Pleistocene. Similarly, the *M. priscus* and *A. buselaphus* samples analysed also fall within this older cluster. However, two Alcelaphini samples, which lack specific taxonomic identification, plot with the younger cluster.

Only a limited comparative dataset is available, but *Equus* material from Pniel 6 has been compared to that from Zambia: Mumbwa Caves (>172 ka), and Twin Rivers (Middle Stone Age) (Baldeki et al., 2024b). Differences in temperature between Zambia and South Africa limit direct comparison, as the warmer climate in Zambia would accelerate IcPD rates. The D/L values from Pniel 6 *Equus* are higher than those from Twin Rivers and overlap with the lower range of those from Mumbwa Caves. The extent of racemisation would be consistent with the cluster of higher D/L values being Middle Stone Age.

Three of the *H. amphibius* samples predominantly group within the older cluster, though one sample is from a later time, indicating hippo was present at Pniel 6 during at least two time periods. The *Antidorcas* data are more dispersed; one sample, specifically *A. bondi*, plots with the younger cluster, while the other two (*A. marsupialis*), aside from the outlier exhibiting nonclosed system behaviour, align with the older age group. Interestingly, one of these samples falls within the main older group, while the other is positioned between the two clusters, suggesting a possible intermediate age or different diagenetic history. The four specimens in the younger cluster all derive from spits 0–10 cm or 10–20 cm in Beaumont's excavation and come from both 'Rubble' and 'Gravel' labelled bags. The IcPD results suggest, as did the faunal and taphonomic analysis above, that there is no tangible difference between the 'Rubble' and 'Gravel' Strata defined by Beaumont, but should be seen as one assemblage that covers a longer time span than may have been previously recognised. It has been suggested that there is a very small amount of younger lithic material in both the Beaumont excavations (Underhill, 2012) and the MINERVA excavations (Ecker et al., 2021), which would fit with this study, suggesting that the first 20 cm of the find layer includes also a small amount of faunal material from a younger period in the Pleistocene. All four examples measured here are from different squares, suggesting individual inclusions rather than a cluster of younger material.

Of the four younger samples, only one (Alcelaphine ID 9247/360) displayed large differences in duplicated isotope measurements ($\delta^{13}\text{C}$ $\Delta 1.2\%$, $\delta^{18}\text{O}$ $\Delta 7.1\%$). The other three specimens, as well as the IcPD outlier *S. caffra* (ID 431), did

not show any unusual difference in isotope duplicate measurements, suggesting that the isotopic alterations are not linked to the age or protein preservation. As both clusters include typical FLMA species, and with the evidence discussed above, we suggest a Pleistocene age for both clusters, but it is important to recognise that the isotopic results reported do not come from a single short depositional event.

Comparison to other FLMA assemblages

Comparing this study to Hutson's analysis of the collected fauna, some differences become apparent. In addition to mammals, Hutson's list includes a reptile, *C. niloticus*, and a large bird. There are no carnivores in the material analysed here, while Hutson lists two hyaenids. There were four additional species in this study: *A. marsupialis*, *C. taurinus*, *K. ellipsiprymnus* and *T. oryx*. An unidentified Proboscidean is listed by Hutson, but no elephants were identified in the excavation material. The overall environmental interpretations are very similar. This could be seen as a confirmation of Beaumont's assumption that the faunal remains from the diamond-digging dumps originated from Stratum 3, but they might be mixed with material originating from different time periods. In contrast, the assemblage studied here comes from a controlled excavation context. Hutson analysed the high diversity of species in the assemblage, the presence of mammalian and reptilian carnivores, as well as the presence of a bird and of mammals of different size classes that possibly reflect the actual faunal community at Pniel 6 in the Middle Pleistocene, while the excavation material analysed in this study mainly contains ungulates, maybe due to other accumulation agents.

The faunal and isotopic results of this study were compared to the Middle Pleistocene sites Florisbad Spring 'Old Collection' (~100–400 ka, Codron et al., 2008), Wonderwerk Cave Stratum 2 (150–240 ka, Chazan et al., 2020), and Kathu Pan 1 (464–700 ka, Mohale et al., 2022) to compare palaeoenvironmental conditions at a regional scale. While the species composition at each site is different, the stable isotope values of all sites reflect similar environmental conditions. In detail, these include a grazing community of *Megalotragus priscus* and *Antidorcas bondi* and the presence of C_4 -plants for Florisbad Spring (Codron et al., 2008) and a water body, indicating relatively wet conditions, mostly C_4 -grasses, but also some C_3 -grasses for Wonderwerk Cave (Chazan et al., 2020), and C_4 -grassland with a significant C_3 -component for Kathu Pan (Mohale et al., 2022). This indicates a larger-scale mixed C_4 and C_3 open grassland in this area (Table 5, Fig. 7). The presence of water-dependent species at each site indicates large permanent water bodies throughout the region. This fits well with studies showing that interior South Africa was wetter than today during the Middle Pleistocene (Lukich and Ecker 2022). All sites represent FLMA fauna, although the composition of species varies by site. Codron et al. (2008) proposed that during the FLMA, herbivores in South Africa increased their C_4 intake. This resulted in fewer mixed-feeding species and feeding niches of C_4 grazing or C_3 browsing. For Alcelaphini, a predominant C_4 -component in the diets is evident by $\delta^{13}\text{C}$ values $> -2\%$ for the majority of specimens, with few exceptions (Table 5, Fig. 7). Equidae have consistently lower $\delta^{13}\text{C}$ values than Alcelaphini at all four sites, which suggests that habitat preferences are influencing these values in addition to the dietary intake. Florisbad Spring has, on average, the highest $\delta^{13}\text{C}$ values for its grazing species across all sites, which might be a reflection of

Table 5. Occurrence of species at Pniel 6 (Hutson, 2018 and this study), Kathu Pan 1 (Mohale et al., 2022), Florisbad Spring Old Collection (Brink, 2005) and Wonderwerk Cave Excavation 2 (Chazan et al., 2020).

Species/Taxon	English name	Kathu Pan 1	Pniel 6 (Hutson 2018)	Pniel 6 (this study)	Florisbad Spring	Wonderwerk Cave
Mammalia						
Hominidae						
<i>Homo</i> sp.	Homo sp.				x	
Cercopithecidae						
<i>Papio</i> indet.	Baboon indet.				x	
<i>Cercopithecinae</i> cf. <i>Papio hamadryas</i>	Hamadryas baboon					x
Bovidae						
Bovid I			x			x
Bovid II			x	x		x
Bovid III			x	x		x
Bovid IV			x	x		x
Alcelaphinae						
<i>Alcelaphini</i> undet.				x		x
<i>Alcelaphus</i> sp.	Hartebeest		x			
<i>Alcelaphus buselaphus</i>	Red hartebeest			x	x	x
<i>Damaliscus</i> spec.				x		x
<i>Damaliscus niro</i>	Extinct antelope		x			
<i>Damaliscus dorcas</i>	Blesbok		x			
<i>Damaliscus</i> cf. <i>pygargus phillipsi</i>	Blesbok					x
<i>Connochaetes gnou</i>	Black wildebeest		x	x	x	
<i>Connochaetes taurinus</i>	Blue wildebeest			x		x
<i>Megalotragus priscus</i>	Extinct giant alcelaphine		x	x	x	
Antilopinae						
<i>Antidorcas bondi</i>	Bond's springbok		x	x	x	
<i>Antidorcas marsupialis</i>	Springbok			x	x	x
<i>Oreotragus oreotragus</i>	Klipspringer					x
<i>Raphicerus campestris</i>	Steenbok				x	x
Bovinae						
<i>Syncerus antiquus</i>	Extinct buffalo	x			x	
<i>Syncerus caffer</i>	African buffalo		x	x	x	
<i>Tragelaphus strepsiceros</i>	Greater Kudu					x
<i>Taurotragus oryx</i>	Eland			x	x	
Reduncinae						
<i>Kobus</i> spec.		x				
<i>Kobus ellipsiprymnus</i>	Waterbuck			x		
<i>Kobus leche</i>	Lechwe		x	x	x	x
<i>Pelea capreolus</i>	Grey Rhebok			x		x
Hippotraginae						
<i>Hippotragus</i> sp.	Roan/Sable	x			x	
Equidae						
<i>Indet. Equid</i>			x			
<i>Equus</i> sp.				x		x
<i>Equus lylei</i>		x			x	
<i>Equus capensis</i>	Cape zebra		x	x	x	
<i>Equus quagga</i>	Plains zebra		x	x	x	
Elephantidae						
<i>Indet. proboscidean</i>			x			
<i>Elephas recki</i>	Recks' elephant	x				
Procaviidae						
<i>Procavia capensis</i>	Rock hyrax					x
Hippopotamidae						
<i>Hippopotamus amphibius</i>	Hippopotamus	x	x	x	x	
Rhinocerotidae						
<i>Rhinoceros</i> sp.						x
<i>Ceratotherium simum</i>	White rhinoceros	x		x	x	
Giraffidae		x				
Suidae						
<i>Phacochoerus aethiopicus</i>	Desert warthog				x	
<i>Phacochoerus africanus</i>	Common warthog		x	x	x	
Canidae						
Canid, <i>C. mesomelas</i> size						x
<i>Canis mesomelas</i>	Black-backed jackal				x	x
<i>Lycaon pictus</i>	African wild dog				x	
Herpestidae						
<i>Atilax paludinosus</i>	Marsh mongoose				x	

(Continued)

Table 5. (Continued)

Species/Taxon	English name	Kathu Pan 1	Pniel 6 (Hutson 2018)	Pniel 6 (this study)	Florisbad Spring	Wonderwerk Cave
<i>Galerella sanguinea</i>	Slender mongoose				x	
Hyenidae						
Hyaenid sp.			x			x
<i>Proteles cristata</i>	Aardwolf					x
Felidae						
<i>Panthera leo</i>	Lion				x	
Mustelidae						
<i>Aonyx capensis</i>	Clawless otter				x	
Hystriidae						
<i>Hystrix africaeaustralis</i>	Cape porcupine					x
Leporidae						
Leproid spp.						x
Leproid, <i>Lepus capensis</i> size	Cape hare			x		x
Leproid, <i>Pronolagus rupestris</i> size	Smith's red rock rabbit					x
Pedetidae						
<i>Pedetes capensis</i>	Springhare	x				x
Reptilia						
Crocodylidae						
<i>Crocodylus niloticus</i>	Nile crocodile		x			
Testudinidae						
<i>Stigmochelys pardalis</i>	Leopard tortoise					x
Aves						
Indet. large bird			x			
Small Aves spp.						x
<i>Struthio camelus</i> (eggshell)	Ostrich			x		x

Table 6. All $\delta^{13}\text{C}_{\text{VPDB}}$ and $\delta^{18}\text{O}_{\text{VPDB}}$ mean values of Pniel 6 (this study), Kathu Pan 1 (Mohale et al., 2022), Florisbad Spring (Codron et al., 2008) and Wonderwerk Cave Excavation 2 (Chazan et al., 2020).

Species	Pniel 6			Kathu Pan 1			Florisbad Spring			Wonderwerk Cave		
	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
<i>Antidorcas bondi</i>	3	0.0	3.1				6	-0.4	-0.1			
<i>Alcelaphus buselaphus</i>	4	0.9	0.5							1	-0.5	0.2
<i>Antidorcas marsupialis</i>	1	-5.0	1.3				5	-8.7	1.0	2	-9.1	3.9
<i>Connochaetus gnou</i>	1	-2.1	1.9				5	-0.3	-0.2			
<i>Connochaetus taurinus</i>	1	-1.4	3.9							2	-2	-1.3
<i>Damaliscus</i> sp.	2	0.2	0.0									
<i>Damaliscus niro</i>							5	3.0	0.2			
<i>Damaliscus pygargus</i>							5	-0.2	-0.8	4	-1	0.8
<i>Equus</i> sp.										3	-1.5	1.7
<i>Equus</i> cf. <i>lylei</i>				8	-1.6	-0.4						
<i>Equus capensis</i>	2	-2.7	2.8				5	-0.6	1.1			
<i>Equus quagga</i>	3	-2.1	4.4									
<i>Hippopotamus amphibius</i>	1	-5.7	-2.3	3	-1.3	-3.3	4	-2.2	-0.7			
<i>Kobus</i> sp.				2	-2.2	3.2						
<i>Kobus ellipsiprymnus</i>	3	-1.2	2.5				5	-3.9	-0.8			
<i>Kobus leche</i>	3	-3.9	2.0				5	-1.2	0.5	2	-3.7	-0.9
<i>Megalotragus priscus</i>	2	-1.6	2.9				4	1.2	2.3			
<i>Phacochoerus</i> cf. <i>africanus</i>							5	-0.4	-1.9			
<i>Phacochoerus africanus</i>	4	-0.8	-0.4									
<i>Syncerus</i> sp.												
<i>Syncerus antiquus</i>				5	-1.8	-1	5	2.9	2.1			
<i>Syncerus caffer</i>	1	-2.7	-0.5									
<i>Taurotragus oryx</i>	2	-10.7	4				5	-7.4	3.4			
Large Alcelaphinae	2	-1.0	3.8									
Alcelaphine				4	-1	2.1	19	0.9	0.3			

Variant spelling due to different classifications in the original sources.

the location, with Florisbad Spring being located today in the Grassland Biome, and the other sites in the Savanna Biome.

Considering the ages of the different sites, no clear trend is detected in the $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ values over time. The only

exception is in the *Equus* and *Suidae*, which show a slight trend towards higher $\delta^{13}\text{C}$ values over time, if Kathu Pan 1 and Florisbad Spring are taken as older sites than Wonderwerk Cave Excavation 2 and Pniel 6. Florisbad Spring shows the

highest variation in $\delta^{13}\text{C}$ values overall, while the variation in $\delta^{18}\text{O}$ is highest in Wonderwerk Cave Excavation 2. Florisbad Spring and Wonderwerk Cave Excavation 2 have lower individual, as well as median, $\delta^{18}\text{O}$ values compared to Kathu Pan 1 and Pniel 6 for Alcephini and Reduncini; thus, Kathu Pan 1 and Pniel 6 seem more arid than Florisbad Spring and Wonderwerk Cave (Table 5, Fig. 7). However, the Equidae and *Syncerus* do not show elevated $\delta^{18}\text{O}$ values for Kathu Pan 1, with Pniel 6 being the site with the highest $\delta^{18}\text{O}$ values for Equidae and Florisbad Spring for *Syncerus*. Both Pniel 6 and Wonderwerk Cave Excavation 2 (Chazan et al., 2020) have evidence that the faunal assemblage could have accumulated during more than one period, and the assemblages from all four sites are based on excavations without modern spatial recording. Furthermore, in addition to changes in climate and seasonality, each site has highly fluctuating water sources such as the spring at Florisbad (Toffolo et al., 2017), the river at Pniel 6, the sinkhole at Kathu Pan 1 and evidence for an active pan outside Wonderwerk Cave in the past (Chazan et al., 2020). This limits our ability to form further conclusions about differences between the four sites.

Conclusion

We presented a faunal analysis including stable isotope measurements and IcpD analysis from the Beaumont and MINERVA excavations at Pniel 6. Although the excavations span several areas over different decades, the fauna and lithic industry all suggest a common Middle Pleistocene origin. The highly fragmentary faunal assemblage represents a typical FLMA set of species, similar, but not identical, in composition to the collected fauna from Pniel 6 analysed by Hutson (2018). Our reconstruction suggests C_3 grasses, shrubs and trees existed besides a dominating presence of C_4 grasses at Pniel 6. The faunal composition, preservation and isotopic signals all are comparable to other Pleistocene FLMA sites in interior South Africa, which show a trend towards C_3 browser and C_4 grazer niches, with few mixed-feeding species.

The importance of duplicates to assess diagenetic alteration is highlighted by almost half of the enamel samples measured for carbon and oxygen stable isotope composition having large differences (>1‰ difference) in duplicate measurements. This is in contrast to the subset of samples analysed for IcpD, which showed closed system behaviour in all but two analysed samples. This indicates that intracrystalline proteins are better protected against secondary modification compared to carbonates in enamel. Furthermore, the amino acid geochronology shows a longer period of accumulation than expected, suggesting deposition over at least two different times in the Pniel faunal assemblage. This could explain the small amount of younger looking elements in the Fauresmith lithic assemblage, the partially bleached OSL samples and the geoarchaeological interpretation of a colluvium and alluvium mixed deposit (Ecker et al., 2021). Pniel 6 highlights the complexity that can be hidden in Middle Pleistocene assemblages. A multimethod approach such as shown here is needed to start teasing apart these complexities and establish potential postdepositional changes to FLMA faunal assemblages.

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Conflict of interest—The authors declare no conflicts of interest.

Data Availability Statement

Data in this study has been included in the supplementary information and will be available on the NOAA data repository upon publication: <https://www.ncei.noaa.gov/pub/data/paleo/aar/>. For the purpose of open access, the author has applied a Creative Commons Attribution (CC BY) licence to any Author Accepted Manuscript version arising from this submission.

Supporting information

Additional supporting information may be found in the online version of this article at the publisher's website.

Figure S1: Bovid size classes at Pniel 6 based on bone fragments and teeth.

Figure S2: ID number 510, unidentifiable bone fragment from Pniel 6, Beaumont excavation, with notch.

Figure S3: ID Number 503, Alcelaphine bone fragment from Pniel 6, Beaumont excavation, with pits, potentially gnaw marks.

Figure S4: ID Number 502, bone fragment from Pniel 6, Beaumont excavation, with potential cut mark.

Figure S5: ID Number 497, bone fragment from Pniel 6, Beaumont excavation, potentially flaked.

Figure S6: ID Number 483, bone fragment from Pniel 6, MINERVA excavation Square 3L6a ID4, with notch.

Figure S7: ID Number 466, *Kobus ellipsiprymnus* tooth from Pniel 6, Beaumont excavation.

Figure S8: ID Number 419, *Antidorcas bondi* tooth from Pniel 6, Beaumont excavation.

Figure S9: ID Number 418, *Taurotragus oryx* tooth from Pniel 6, Beaumont excavation.

Figure S10: ID Number 369, *Damaliscus pygargus* humerus fragment from Pniel 6, Beaumont excavation.

Figure S11: ID Number 298, *Phacochoerus africanus* tooth from Pniel 6, Beaumont excavation.

Figure S12: ID Number 258, *Connochaetus taurinus* tooth from Pniel 6, Beaumont excavation.

Figure S13: ID Number 253, *Antidorcas astralagus* from Pniel 6, Beaumont excavation.

Figure S14: ID Number 230, unidentifiable burnt bone fragment from Pniel 6, Beaumont excavation.

Figure S15: ID Number 227, large mammal bone fragment with pits from Pniel 6, Beaumont excavation.

Figure S16: ID Number 215, *Equus quagga* tooth from Pniel 6, Beaumont excavation.

Figure S17: ID Number 177, *Antidorcas marsupialis* tooth from Pniel 6, Beaumont excavation.

Figure S18: ID Number 174, *Megalotragus priscus* (?) ulnar carpal bone from Pniel 6, Beaumont excavation.

Figure S19: ID Number 115, *Lepus capensis* cf. femur fragment from Pniel 6, Beaumont excavation.

Figure S20: ID Number 103, *Alcelaphus buselaphus* tibia fragment from Pniel 6, Beaumont excavation.

Figure S21: ID Number 97, *Equus quagga* tooth from Pniel 6, Beaumont excavation.

Figure S22: ID Number 46, large Alcelaphine tooth from Pniel 6, Beaumont excavation.

Table S1. List of all identified and unidentified faunal remains.

Table S2. Stable isotope measurements on enamel samples from Pniel 6.

Table S3. IcpD data measured on selected Pniel 6 enamel samples.

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