

Dental mesowear patterns challenge the hypothesis of a 1.7 Ma transition to open grasslands in South Africa's Cradle of Humankind

Megan Malherbe^{a,b,*}, Martin Haeusler^a, Robyn Pickering^{b,c}, Deano Stynder^d

^a Institute of Evolutionary Medicine, University of Zürich, 190 Winterthurerstrasse, Zürich, Switzerland

^b Human Evolution Research Institute, University of Cape Town, University Avenue, Rondebosch, Cape Town, South Africa

^c Department of Geological Sciences, University of Cape Town, University Avenue, Rondebosch, Cape Town, South Africa

^d Department of Archaeology, University of Cape Town, University Avenue, Rondebosch, Cape Town, South Africa



ARTICLE INFO

Editor: Howard Falcon-Lang

Keywords:

Palaeoecology
Palaeontology
Palaeoenvironmental reconstruction
Cradle of Humankind
Dental mesowear

ABSTRACT

The assessment of palaeoenvironmental conditions in South Africa's Cradle of Humankind has traditionally relied on two main lines of evidence: the identification of fossil herbivore taxa and the stable carbon isotopic signatures preserved in their dental enamel. However, interpretations drawn from taxonomic composition often depend on taxonomic analogy – that is, the assumption that extinct species had similar diets and habitat preferences as their modern relatives. This assumption can be problematic as ecological roles can shift significantly over evolutionary time. Furthermore, many of these studies were conducted within broad chronological frameworks, which may obscure important temporal and spatial variability in vegetation structure. The traditional model is that the Cradle experienced a transition from woodlands to open grasslands around 1.7 million years ago. While foundational, this model rests on assumptions about ecological continuity and inexact chronological resolution that can mask finer-scale environmental differences. Here, we assess the hypothesis of an abrupt environmental shift at 1.7 Ma by comparing dental mesowear profiles across seven of the most important Cradle sites spanning the time period 3.2–1.3 Ma. These uranium-lead dated sites are: Cooper's Cave, Drimolen, Haagsgat, Hoogland, Malapa, Sterkfontein, and Swartkrans. We analysed mesowear signatures from fossil bovids ($n = 623$) across seven bovid tribes. All deposits exhibit similar mesowear scores, consistently reflecting a stronger grazing than browsing signal. Findings do not support a transition from woodlands to grasslands ca. 1.7 Ma. Instead, they are consistent with a heterogeneous landscape that remained unchanged from 3.2 to 1.3 Ma. We also identify variation in dietary ecology between members of the same tribe (e.g. *Alcelaphini*) in the same deposit (e.g. Swartkrans Member 2), indicating generalist tendencies among some tribes. Moreover, certain tribes (*Tragelaphini*, *Reduncini*, *Antilopini*) differ substantially in feeding preference compared to their modern counterparts. Our study highlights the importance of a regional approach to reconstructions of the South Africa Plio-Pleistocene, and the value of conducting such studies within an accurate, local and direct chronological framework.

1. Introduction

The Pliocene-Pleistocene transition (at 2.58 Ma) marks a period in time when the global climate shifted from relatively warm and stable conditions to those that were colder, drier and more variable (deMenocal 2004; Ravelo et al. 2004). The climate-driven environmental changes during this time have often been posited as a driver of mammalian and hominin evolution, reflected particularly in the fossil record of the African continent and in the spread of the genera *Homo* and *Paranthropus* (deMenocal 1995; Vrba 1995; Trauth et al. 2021). The

formation of large ice sheets in high-latitude regions marked the onset of major ice age cycles, which began to exert a growing influence on global climate (Shackleton et al. 1990; deMenocal & Rind 1993; deMenocal 1995; Clarke et al. 1999). Palaeoclimate records from marine sediments in particular indicate a global reduction in temperature and increase in aridity between 3 and 1 Ma (Tiedemann et al. 1994; deMenocal 1995; Zachos et al. 2001; deMenocal 2004).

On a regional scale, multi-basin records of lake phases in eastern Africa show a long-term aridification trend, punctuated by rapid fluctuations between extended humid and arid periods (Williams et al.

* Corresponding author at: Institute of Evolutionary Medicine, University of Zürich, 190 Winterthurerstrasse, Zürich, Switzerland.

E-mail address: megan.malherbe@iem.uzh.ch (M. Malherbe).

1979; Feibel 1999; Ashley and Hay, 2002; Behrensmeyer et al. 2002; Trauth et al. 2005). Similarly, vegetation changes indicated by the carbon isotopic composition of plant wax biomarkers, reveal a dynamic vegetative structure with an overall increase in C₄ plants in eastern Africa from the Pliocene to the Pleistocene (Rose et al. 2016; Uno et al. 2016a; Uno et al. 2016b; Lupien et al. 2021). Stable carbon isotope analysis of pedogenic carbonates also reveal a drying trend, as well as periods of strong evaporation, which appear to increase at ~2 Ma (Levin et al. 2004; Wynn 2004; Quinn et al. 2007; Lepre & Quinn 2022). African ecosystems were evidently shaped by the global shifts in climate, influencing both vegetation and animal community structures. Variations in resource availability and landscape configuration affected the foraging strategies, mobility, and adaptive behaviours of numerous mammalian species, including hominins.

One of the most effective ways to gain insight into how an increase in aridity reshaped palaeoecosystems across the African continent is through the study of fossil faunal communities. Bovids have occupied a central role in this regard, because their fossil remains are abundant and well-preserved, their species occupy a wide range of ecological niches, and their relatively stable diets generally provide reliable reflections of the environments they inhabited (Vrba 1975; Vrba 1980; Sponheimer et al. 1999; Luyt & Lee-Thorp 2003). Although bovid diets were traditionally considered fixed and highly specific, recent studies have shown that some species, such as reduncins and antilopins, display notable dietary flexibility that varies with environmental conditions, while dietary specificity remains well-supported for others, including certain cephalophin and hippotragin species (Codron et al. 2019; Sewell et al. 2019; Blondel et al. 2022). Despite this variability, the taxonomic diversity, abundance, and broad habitat range of bovids continue to make them valuable proxies for palaeoenvironmental reconstruction (Vrba 1975; Vrba 1980; Reed 1997; van der Merwe & Thackeray 1997; Luyt & Lee-Thorp 2003; Badenhorst et al. 2011; Steininger 2011; van Zyl et al. 2016).

Taxonomy-based analyses of fossil bovid assemblages have played a central role in reconstructing past environments in Africa, particularly through studies of species presence/absence and patterns of abundance (Reed 2013). Shifts in the presence of fossil species at archaeological sites are often interpreted as evidence of climate and habitat change – an approach that relies on the assumption that extinct taxa had similar ecological preferences to their modern relatives (Dodd & Stanton 1990). For example, around 2 million years ago in the Turkana Basin, Hadar, and the Lower Omo Valley, there was an increased presence of bovid tribes now typically found in dry grasslands, such as Alcelaphini, Antilopini, and Hippotragini (Bobe et al. 2002). Concurrently, woodland-adapted fossil mammals like *Theropithecus brumpti* disappeared from these regions (Behrensmeyer et al. 1997; Reed 2008). This presence/absence shift has been interpreted as representing a transition from more closed, wet environments to more open, arid ones. Patterns of bovid species abundance also indicate an environmental shift during this period. A general rise in African bovid species abundance, accompanied by rapid episodes of taxonomic change reflects an increasing dominance of arid-adapted species (Vrba 1985; Vrba 1995; Bobe & Eck 2001; Alemseged, 2003; Bobe et al. 2007). These trends indicate ecological restructuring across Africa, likely driven by increasing aridity and the expansion of open grassland habitats.

South Africa's Cradle of Humankind (hereafter the Cradle), recognised as a UNESCO World Heritage Site, is home to the world's richest concentration of hominin sites and plays a crucial role in constructing the history of human evolution. Notably, unique discoveries such as *Australopithecus sediba* and *Homo naledi* have been unearthed here, species that are exclusive to this region (Berger et al. 2010; Berger et al. 2015). Swartkrans, a cave site within the Cradle, boasts the largest collection of *Paranthropus robustus* fossils, comprising over 100 individual specimens (Pickering et al. 2012). Research interest in the Cradle has extended beyond its rich hominin fossil record, with studies increasingly investigating the environmental conditions under which

hominins in the region evolved. Specifically, palaeoenvironmental reconstructions suggest a marked transition towards more variable and open grassland environments from ~1.7 Ma onward, replacing previously predominantly wooded habitats (Bamford 1999; Kuman & Clarke 2000; Luyt & Lee-Thorp 2003; Lee-Thorp et al. 2007; Sewell et al. 2019).

Palaeoenvironmental reconstructions of the seven uranium-lead (U-Pb) dated sites included in this study – Cooper's Cave, Drimolen, Haasgat, Hoogland, Malapa, Sterkfontein, and Swartkrans – have varied depending on the methods applied (Table 1; U-Pb chronology from Pickering et al., 2019). When assessed chronologically through taxonomic identifications, Hoogland (~3.2 Ma) emerges as one of the most taxonomically diverse localities within the Cradle of Humankind, although the limited faunal assemblage constrains definitive palaeoenvironmental interpretations (Adams et al., 2010). Earlier research on Sterkfontein Member 4 (2.6–2.0 Ma) characterized the depositional environment as predominantly forested (Vrba, 1975, 1980), but subsequent analyses focusing on faunal abundance and ecological indicators have suggested a more heterogeneous, mosaic environment (Reed, 1997; Avery, 2001). The Drimolen environment (~2.6–1.8 Ma) is a challenge to reconstruct, due to the paucity of identifiable craniodontal specimens from both the Main Quarry and the Makondo deposit (Rovinsky et al. 2015; Murszewski et al. 2020). Haasgat (~2.2–1.8 Ma) preserves a plethora of primate fossils, with some contesting palaeoenvironmental reconstructions based on other faunal data – the high prevalence of *Pelea capreolus* suggest grassland but *Cercopithecoides williamsi* and *Kobus* sp. are more representative of forests/swamps (Keyser 1991; Plug & Keyser 1994). Swartkrans Member 1 represented either a mesic, closed woodland (Benefit & McCrossin 1990), or a more mosaic environment (Watson 1993; Reed 1997). Malapa (~1.98 Ma), currently the only site where *A. sediba* has been recovered, is home to an ecologically diverse carnivore assemblage (Kuhn et al. 2011; Kuhn et al. 2016), Viverridae, which support forest habitats (van der Merwe et al. 2021) and bovids which support more grassland (Brophy et al. 2016). Sterkfontein Member 5 East and West (~2.0–0.8 Ma) are regarded as the deposits that best mark the transition from closed, wet conditions to open, dry environments at ~1.7 Ma. This reconstruction is based on the presence of *Equus*, *Pedetes* and *Struthio* (Kuman & Clarke 2000), as well as *Theropithecus oswaldi* (Pickering 1999; Reynolds & Kibii 2011). Fauna from Swartkrans Members 2 and 3 (1.6–0.6 Ma) are considered more open-adapted than that from Sterkfontein, though with riverine woodland-adapted species also present (Vrba 1974; Vrba 1975; Vrba 1980; Reed 1997; Avery 2001; de Ruiter et al. 2008). The Cooper's Cave assemblage (<1.3 Ma) has been reconstructed as a relatively mosaic environment based on the diverse nature of the carnivore (Kuhn et al. 2017; O'Regan & Steininger 2017) and bird assemblages (Pavia et al. 2022).

More recently, studies employing largely taxon-independent analytical methods have begun to challenge the hypothesis of a rapid and pronounced shift towards grassland-dominated environments around 1.7 Ma in South Africa. A dental microwear study of *Australopithecus africanus* and *P. robustus* from various Cradle sites revealed divergences in microwear variables between the species but, interestingly, no significant differences within *P. robustus* samples from Swartkrans, Kromdraai or Drimolen (Peterson et al. 2018). Given that these sites fall within the timeframe of the supposed habitat shift at 1.7 Ma, a difference in microwear between Swartkrans Member 1 and Members 2 and 3 would be expected. However, despite taxonomic analogy suggesting environmental differences between these members, the microwear evidence indicates dietary continuity. It is also worth noting that generalist hominins may not be the ideal indicator for habitat type, as their diets are heterogeneous at any given time. Multi-proxy analyses (including mesowear, microwear and carbon isotopes) of *Antidorcas* dentition from Sterkfontein and Swartkrans did suggest increased grassland presence from 1.7 Ma, however Swartkrans Member 2 is more heterogeneous (Sewell et al. 2019), and sits on the boundary at 1.63–1.41 Ma (Pickering et al. 2019). Moreover, pooled stable isotopic

Table 1

Faunal-based palaeoenvironmental reconstructions provided for the Cradle deposits included in this study. Only macromammal studies using the following methods are included: stable carbon isotopes, dental mesowear (MSW) and microwear (MCW), and taxonomic uniformitarianism (TU), which also includes faunal abundance analyses. Reconstructions differ slightly from one publication to another and have been simplified here for straightforwardness and ease of reading.

Site	Palaeoenvironment	Method	Publication
Cooper's Cave	Mosaic	TU, isotopes, MCW	Steininger 2011, Kuhn et al. 2017, Badenhorst and Steininger 2019
	Grassland & partly woodland	TU	de Ruiter et al., 2009, Hanon et al., 2022
			Adams and Rovinsky, 2018
Drimolen Haasgat	Mosaic	TU	Keyser 1991
	Grassland with forest	TU	McKee, 1991, Plug and Keyser 1994
	Mosaic	TU	Adams, 2012, Adams et al., 2013, Adams and Rovinsky, 2018
Hoogland	Grassland & partly woodland	TU, isotopes	Adams et al., 2010
	Mosaic	TU	
	Woodland & arid grassland	TU	Kuhn et al. 2011, 2016
Malapa	Grassland & partly woodland	Isotopes	Henry et al. 2012
	Woodland/forest	TU	Lazagabaster et al. 2018, van der Merwe et al. 2021
	Mosaic	TU	Brophy et al. 2016
Sterkfontein M4	Woodland & partly grassland	TU, isotopes	Vrba 1975, 1980, 1985, Reed 1997, Lee-Thorp et al. 2007
		Isotopes, MSW, MCW, TU	McKee 1991, Luyt 2001, Sewell et al. 2019
	Mosaic	TU, isotopes	Kuman and Clarke 2000, Luyt and Lee-Thorp 2003
	Woodland	TU	Benefit and McCrossin 1990
Sterkfontein M5	Grassland	TU	Pickering 1999, Luyt and Lee-Thorp 2003, Lee-Thorp et al. 2007
	Grassland	TU, isotopes	
	Grassland & partly woodland	Isotopes, MSW, MCW, TU	Kuman and Clarke 2000, Sewell et al. 2019
Swartkrans M1	Woodland & partly grassland	Isotopes	Lee-Thorp et al. 2007
	Grassland & partly woodland	TU	Watson 1993
		TU, isotopes, MCW	Vrba 1975, 1980, McKee 1991, Brain and Watson 1992, Reed 1997, Lee-Thorp et al. 2007, Steininger 2011
Swartkrans M2	Grassland	TU	Benefit and McCrossin 1990
	Grassland	TU	Lee-Thorp et al. 1989, de Ruiter 2003
	Mosaic	TU, isotopes	
Swartkrans M3	Grassland	TU	Vrba 1975, Reed 1997
	Grassland & partly woodland	TU, isotopes, MSW, MCW	Watson 1993, de Ruiter et al., 2008, Sewell et al. 2019
	Mosaic	TU, isotopes, MCW	de Ruiter, 2003, Lee-Thorp et al. 2007, Steininger 2011
	Grassland	TU, isotopes, MSW, MCW	de Ruiter et al., 2008, Sewell et al. 2019
	Grassland & partly woodland	TU	Watson 1993
	Mosaic	TU, isotopes, MCW	de Ruiter, 2003, Steininger 2011

data from bovid specimens across multiple studies in the Cradle of Humankind indicate that the relative proportions of browsers, mixed feeders, and grazers remain broadly consistent across stratigraphic sequences. Notably, the oldest deposit - Swartkrans Member 1 - exhibits the lowest proportion of C₃ plant feeders, suggesting a comparatively more open or grass-dominated environment at that time (Peterson et al., 2018).

The variable diet of *P. robustus* in the Cradle is well documented, particularly compared to the C₄-dominated diets of eastern African *P. boisei* (Lee-Thorp et al. 1994; Scott et al. 2005; Sponheimer et al. 2006; Cerling et al. 2011; Ungar & Sponheimer 2011; Cerling et al. 2013). Despite both species being recorded across the 1.7 Ma period, their dietary differences are thought to stem from the greater abundance of C₄ vegetation at eastern African sites, whereas the Cradle habitat appears to have favoured a higher intake of C₃ vegetation for *P. robustus*. This reliance on C₃ resources is suggested to have persisted even in the youngest Cradle deposits where *P. robustus* is found, signifying a continued absence of extensive grasslands and the persistence of a mosaic environment (Paine et al. 2019; Sponheimer et al. 2023). These direct dietary evidences from the Cradle, along with emerging findings from other parts of Africa (Blumenthal et al. 2017; Kaya et al. 2018; Negash & Barr 2023) challenge the hypothesis of a sudden shift to grasslands and highlight the need for a systematic analysis of the dietary habits of Cradle bovid assemblages. Understanding these patterns is essential for reconstructing the environmental forces that shaped hominin evolution in this region.

Previous environmental reconstructions from Cradle sites are constrained by the limitations of taxonomic approaches and broad or unclear site chronologies. When relying on taxonomic analogy, there is no guarantee that the dietary habits of fossil species closely mirror those of their modern counterparts (Schubert et al. 2006; Stynder 2009; Stynder 2011). Early isotopic analyses found a discrepancy of over 25 % between actual diets of African fossil mammalian taxa vs. what had been assumed in the literature (Cerling et al. 1999; Sponheimer et al. 1999; Sponheimer et al. 2001). A notable example is fossil colobines, which carbon isotope analyses identified as C₄ grass consumers (Codron et al., 2005), despite the fact that their extant relatives are primarily folivorous and restricted to closed woodland habitats. Nevertheless, the presence of colobines in fossil assemblages has frequently been interpreted as indicative of forested environments (WoldeGabriel et al., 1994), illustrating the risks of relying solely on taxonomic analogy in palaeoenvironmental reconstructions. A further limitation of taxonomic methods is that they do not provide data on the diets of extinct species with no modern descendants.

Obtaining an accurate and constrained chronology across Cradle sites (Table 2) has further complicated efforts to reconstruct the Plio-Pleistocene Cradle habitats. Established radiometric methods such as potassium-argon or argon-argon are inapplicable for dating Cradle deposits, due to the lack of volcanic tuff layers. Thus, traditionally only broad age ranges could be provided, which limited environmental interpretations. Additionally, sites have frequently been dated using faunal comparisons to well-dated sites in eastern Africa; a method which, while useful, also has limitations such as the inability to pinpoint regional speciation/extinction events. While the previous isotopic studies conducted on herbivores from various Cradle deposits have been inarguably valuable in understanding Plio-Pleistocene palaeoenvironments, these studies are either based on broad age estimates (Lee-Thorp & Van der Merwe 1993; Luyt & Lee-Thorp 2003), or on eastern African faunal comparisons (Lee-Thorp et al. 2007). Consequently, specific instances of a shift in landscape and vegetation could not be drawn with certainty. This, as well as differences in sample selection, has led to some discrepancies between isotopic studies at Cradle sites. Different baboon specimens from Swartkrans, for example, revealed a C₄-dominated diet in one study (Codron et al. 2005) and both C₃ and C₄ in another (Lee-Thorp et al. 1989). There have also been differences in carbon isotope results from small mammals (Leichliter et al. 2017) compared to larger

Table 2

Proposed date ranges and methods used to obtain dates for each Cradle deposit included in analysis. Overall date range below each deposit name represents overall estimate across all published studies.

Site and deposit	Published date	Method	Authors
Cooper's Cave	1.9 - ~1.4 Ma	Biochronology	Steininger et al. 2008, de Ruiter et al. 2009
	1.9–1.6 Ma	Primate biochronology	Frost et al. 2022
	1.6–1.4 Ma	U-Pb	de Ruiter et al. 2009, Pickering et al., 2011a
range: 1.9–1.3 Ma	1.3 Ma	U-Pb	Pickering et al. 2019
	2.0–1.5 Ma	Biochronology	Moggi-Cecchi et al., 2010
	1.7 Ma	ESR	Herries et al. 2020
Drimolen: Main Quarry	2.0–1.82 Ma	U-Pb	Pickering et al. 2019
	2.04–1.95 Ma	ESR + U-Pb	Martin et al. 2021
	~2.5–1.9 Ma	Biochronology	Keyser 1991, Adams, 2012
Haasgat	1.5–1 Ma	Biochronology	Plug and Keyser 1994
	2.6–1.8 Ma	Palaeomagnetism	Herries et al. 2014
	2.17–1.82 Ma	U-Pb	Pickering et al. 2019
range: 2.6–1.0 Ma	3.12–2.58 Ma	Biochronology + palaeomagnetism	Adams et al., 2010
	3.08–2.83 Ma	U-Pb	Pickering et al. 2019
	2.36–1.5 Ma	Biochronology	Dirks et al. 2010
Hoogland	~2.3–2.0 Ma	Primate biochronology	Gilbert et al., 2015
	1.95–1.78 Ma	U-Pb	Dirks et al. 2010, Pickering et al., 2011b
	2.0–1.82 Ma	U-Pb	Pickering et al. 2019
Malapa	2.8–2.4 Ma	Bovid biochronology	Vrba 1975, 1980
	~2.5 Ma	Primate biochronology	Delson 1984, 1988
	~2.1 Ma	ESR	Schwarz et al. 1994
range: 2.3–1.78 Ma	2.15–2.14 Ma	Palaeomagnetism	Partridge 2005
	2.8–2.0 Ma	ESR + palaeomagnetism	Herries and Shaw 2011
	2.65–2.01 M	U-Pb + U-Th	Pickering and Kramers 2010
Sterkfontein: Member 4	2.61–2.07 Ma	ESR + U-Pb	Pickering and Herries 2022
	2.0–1.7 Ma	Biochronology + archaeology	Kuman and Clarke 2000
	1.4–1.2 Ma	ESR + palaeomagnetism	Herries and Shaw 2011
Sterkfontein: Member 5 East	2.1 Ma	Cosmogenic nuclides	Granger et al. 2015
	1.4–1.1 Ma	Dating seriation	Herries et al. 2009
	2.0–1.82 Ma	U-Pb	Pickering et al. 2019
Sterkfontein: Member 5 West	1.7–1.4 Ma	Biochronology + archaeology	Kuman and Clarke 2000
	1.3–1.1 Ma	ESR + palaeomagnetism	Herries and Shaw 2011
	1.3–0.8 Ma	Dating seriation	Herries et al. 2009
Swartkrans:	<1.9 Ma	Primate biochronology	Delson 1988
	~2–1 Ma	Bovid biochronology	Vrba 1975
	1.73 Ma	Equid biochronology	Churcher and Watson 1993

Table 2 (continued)

Site and deposit	Published date	Method	Authors
	2.2–1.8 Ma	Cosmogenic nuclides	Gibbon et al. 2014, Kuman et al. 2021
	~2.25 Ma	U-Pb	Pickering et al., 2011a
Swartkrans:			
Member 1	1.8–1.5 Ma	Biochronology	Vrba 1985
Hanging Remnant	~2.11 Ma - 1.6 Ma	ESR	Curnoe et al. 2001
combined range: 2.25–1.5 Ma	1.8–1.71 Ma	U-Pb	Pickering et al., 2011a, Pickering et al., 2012
Swartkrans:			
Member 2	1.6–1 Ma	Biochronology	Brain and Watson 1992, Vrba 1995, de Ruiter, 2003
range: 1.63–1.0 Ma	1.63–1.41	U-Pb	Pickering et al. 2019
Swartkrans:			
Member 3	700–600 ka	Biochronology	Vrba 1995
	~1.6 Ma	Primate biochronology	Delson 1988, de Ruiter 2003
	960 ka	Cosmogenic nuclides	Gibbon et al. 2014
range: 1.6–0.6 Ma			

mammals (Lee-Thorp et al. 2007; Sewell et al. 2019) at Sterkfontein, Swartkrans and Malapa. These differences are likely not due to methodological issues but rather stem from variations in sample selection or previously variable chronologies.

More recently, advancements in absolute dating techniques have led to an improved understanding of the chronological framework of the Cradle (see Pickering et al. 2007; de Ruiter et al. 2009; Dirks et al. 2010; Pickering & Kramers 2010; Pickering et al. 2011a; Pickering et al. 2011b; Edwards et al., 2019; Edwards et al., 2020; Herries et al. 2020; Edwards et al. 2023 for a detailed breakdown of site members and dates). Many prior discrepancies in age ranges have since been resolved, and age brackets for periods of deposition have been reduced. U-Pb dating of cave speleothems at eight of the Cradle's fossil sites revealed a contemporaneous formation of flowstones across various deposits (Pickering et al. 2019). The flowstones are therefore able to provide a regional framework for faunal occupation in a similar manner to the volcanic tuffs in eastern Africa (Pickering & Herries 2022). Consequently, many sites within the Cradle with previously broad age assignments, now have narrower windows of deposition associated with the fossils. Cooper's Cave, for example, originally deemed anywhere between 1.9 – <1.4 Ma based on faunal assemblages (Steininger et al. 2008; de Ruiter et al. 2009), has since been constrained to <1.32 Ma (Pickering et al. 2019). Likewise, a combination of relative and absolute methods resulted in the Drimolen Main Quarry being assigned the range of 2.04–1.82 (Pickering et al. 2019; Martin et al. 2021). While stratigraphic complexity is undoubtedly still present, the multidisciplinary application of U-Pb, palaeomagnetic and biochronological dating has transformed the chronology of Cradle caves in recent years. More importantly, the direct dating of the caves and narrowing of age ranges across Cradle sites now provides a foundation for revisiting the hypothesis of a sudden habitat shift around 1.7 Ma, using direct dietary methods on a regional scale.

1.1. Using mesowear for palaeoenvironmental reconstruction

In this study, we apply the dental mesowear method to reconstruct the dietary profiles of fossil bovid communities from seven U-Pb dated Cradle sites spanning 3.2 to 1.3 Ma. These sites – Cooper's Cave, Drimolen, Haasgat, Hoogland, Malapa, Sterkfontein, and Swartkrans (Fig. 1) – provide a framework for investigating environmental

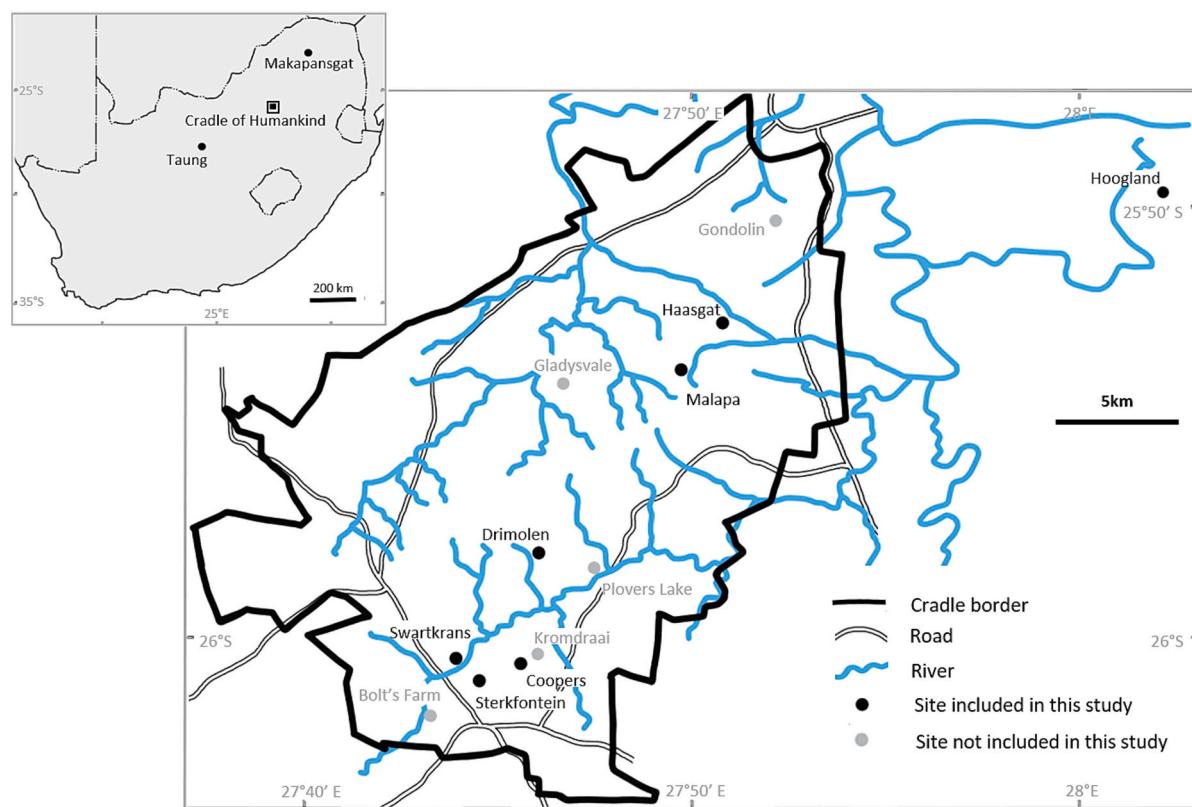


Fig. 1. Map of the Cradle of Humankind, South Africa. Sites included in analyses are shown in bold.

conditions in the Cradle during this pivotal period. Mesowear, a method for measuring macroscopic wear patterns of ungulate dentition, has been successfully applied to a range of ungulate species (Fortelius & Solounias 2000), and has proven an effective proxy for reconstructing palaeodietary patterns (Rivals et al. 2007; Viranta & Mannermaa 2014). In contrast to dental microwear, which reflects short-term dietary signals from the final days or weeks before death, and stable isotope analyses of tooth enamel, which represent dietary intake during the period of tooth mineralization (typically spanning several months), mesowear is well suited for identifying long-term feeding behaviours, as it reflects the cumulative effects of dietary abrasiveness over much of an individual's life (Kaiser & Solounias, 2003; Rivals et al., 2007).

Dental mesowear captures the relative contribution of attrition and abrasion to tooth wear in herbivores. Attrition creates facets on sele-nodont teeth – which are characterized by crescent-shaped ridges adapted for grinding plant material (Ungar 2010) – and abrasion eradicates them due to food wearing the enamel tissue down during mastication (Blondel et al. 2010). The degree to which either attrition or abrasion affects occlusal surfaces is determined by the physical properties of plant foods consumed (Kaiser and Schulz, 2006; Kaiser et al. 2013; Ungar 2015; Kaiser et al. 2016; Ackermans et al., 2020). Plants that are rich in phytoliths, such as monocotyledons, are highly abrasive. Consequently, ungulates that primarily consume monocotyledons, typically grazers, are most affected by abrasion (Damuth & Janis 2014; Karme et al. 2016). In contrast, dicotyledonous plants such as shrubs are less abrasive, and are typically consumed by browsers, whose tooth wear is more strongly influenced by attrition (Schulz & Kaiser, 2012). Tooth abrasion can also be influenced by elements external to the mechanical properties of the types of plants consumed, i.e. surface grit, soil type, proximity to the ground, aridity/rainfall levels (Winkler et al. 2019). However, little correlation has been shown between dry, high-grit environments and high mesowear scores (Desantis et al. 2012; Kubo & Yamada 2014; Ackermans et al., 2018).

While mesowear, isotope, and microwear analyses have previously

been applied to faunal assemblages at the Cradle (Luyt & Lee-Thorp 2003; Lee-Thorp et al. 2007; Schubert 2007; Sewell et al. 2019), these studies have typically focused on single sites or members, limiting the ability to detect broader patterns of ecological change. By comparing bovid assemblages across both spatial and temporal scales, this study adopts a more integrated approach that enables the identification of dietary shifts potentially linked to changes in ecological structure. Assessing the diversity of fossil bovid diets within a regionally and chronologically constrained framework offers a robust means of reassessing palaeoenvironmental conditions at Plio-Pleistocene sites, thereby advancing our understanding of environmental dynamics in the Cradle during a key period in hominin evolution (e.g., Bibi et al., 2013). In order to evaluate the established hypothesis of a stark environmental shift ca. 1.7 Ma, we test the following hypothesis: dental mesowear profiles of fossil bovids will show a temporal shift from browsing-dominated to grazing-dominated signatures, consistent with a transition from woodland to open grassland environments. In addition to this overarching hypothesis, the study also investigates whether ecological structure varies across different members or sites, providing deeper insight into local environmental heterogeneity and its potential implications for habitat use and resource availability.

2. Materials and methods

2.1. Mesowear data collection

Mesowear categorizes cusp wear based on two variables: occlusal relief and cusp shape (Fig. 2). Occlusal relief is scored as either high (h) or low (l), depending on the relative height of the cusps above the surrounding valleys. Due to the fact that bluntness can be an artefact of wear whereas sharpness is never (Fortelius & Solounias 2000), the sharper of the two cusps was measured to account for this and also potential preservation issues. Cusp shape is classified as either sharp (s), round (r), or blunt (b) depending on the degree of facet development.

		Steep valley	H
		Shallow valley	
		Sharp	S
		Round	
		No distinct facets	B

Fig. 2. The mesowear scoring convention for ungulate cheek teeth. Occlusal relief (OR) is scored as 'high' (H) or 'low' (L); cusp shape (CS) is classified as 'sharp' (S), 'round' (R), or 'blunt' (B). Modified after Merceron et al. (2007).

For the same preservation-related reasons, the sharper of the two cusps was measured and used for analysis. The two mesowear variables measured are not entirely independent from one another, and converge at the grazing end of the spectrum where teeth that are blunt have little to no relief (Rivals et al. 2009). For measurement of variation within the mesowear signal, and for an analysis free of modern taxonomic comparison, we combined cusp shape and occlusal relief into a single numerical mesowear score based on possible combinations (see Mihlbachler & Solounias, 2006; Rivals et al., 2007; Rivals et al., 2009; Blondel et al., 2022).

The scoring system used in this study follows Kaiser et al. (2009, 2013) and represents different wear stages: teeth with both sharp cusps and high relief were assigned a score of 0; teeth with both rounded cusps and high relief were assigned a score of 1; teeth with sharp cusps and low relief were assigned a score of 2; teeth with rounded cusps and low relief were assigned a score of 3; and teeth with blunt cusps and low relief were assigned a score of 4 (Fig. 3). This scoring system has also been utilised by Marín-Leyva et al. (2016), Blondel et al. (2022) and Dumouchel & Bobe (2020).

2.2. Fossil data

A total of 623 teeth were analysed, representing seven major bovid tribes: Alcelaphini, Antilopini, Neotragini, Tragelaphini, Reduncini, Hippotragini, and Bovini (Table 3). To investigate dietary changes over time, fossil bovids were assessed by both depositional unit and taxonomic tribe across 11 distinct time intervals (Table 4). The analysis primarily emphasizes depositional units, as this approach offers stronger temporal resolution and is supported by the dominance of Alcelaphini and Antilopini, which together account for over 80 % of the sample.

Upper and lower second molar (M2 and m2) teeth were used wherever possible following Kaiser & Solounias (2003), and only adult

specimens were utilised to avoid age structure discrepancies noted in previous studies (Fortelius & Solounias 2000; Rivals et al. 2007). We examined teeth with light and moderate wear stages following Fortelius & Solounias (2000) and Kaiser and Fortelius (2003), who show that wear in ungulates is stable during the lifespan, except for the earliest and latest stages. Post-depositional processes can affect occlusal surfaces, but taphonomic alterations are easy to identify with careful screening. Therefore, all teeth were screened prior to analysis, and those with obvious taphonomic alterations were excluded. The mesowear signal is considered reliable with the inclusion of a minimum of ten specimens, and stable after twenty (Fortelius & Solounias 2000; Green & Croft 2018). Malapa is the only deposit in this study with fewer than 10 specimens ($n = 6$), while Sterkfontein Member 4 has the next smallest sample, with 12 specimens. Many more teeth are available from Sterkfontein, but they were excluded due to uncertain provenience within these deposits. While the mesowear signals from these sites are still informative, it is worth noting that they are less secure than for sites with larger samples. Inter-observer error is known to be insignificant in mesowear analyses (Kaiser et al. 2000), but to reduce any possibilities of error, scoring was only conducted by one of us (MM). Reliability was evaluated and ensured by repeating measurements on randomly chosen specimens. Scoring consistency was further maintained by adhering closely to the original character definitions and comparative examples provided in the abovementioned scoring schemes. All individual mesowear scores were averaged according to deposit (Table 3a), and mean and median scores were obtained for each assemblage, and by extension, time period. The same was done for scores according to tribe (Table 3b), and averages were compared with extant data from Kaiser et al. (2013) and Blondel et al. (2018). Since averaging mesowear scores assumes equal intervals between categories, medians are also reported and where the median substantially differs from the mean, this deviation is noted and discussed in the text.

2.3. Statistical analysis

Statistical tests to analyse differences in mesowear scores between chronological phases were performed using the statistical software PaSt v.4.10 (Palaeontological Statistics) (Hammer & Harper 2001) and R v.4.0.4 (R Core Team R, 2023). Individual species of different tribes were not considered separately in statistical analyses. Non-parametric tests (Kruskal-Wallis) and associated post hoc comparisons were used to identify significant variation between deposits for each parameter. Pairwise differences were assessed using both Benjamini-Hochberg and the more conservative Bonferroni corrections. We employed these statistical approaches instead of the commonly used hierarchical cluster classification based on Euclidean distances, because incorporating fossils with unknown dietary preferences into an existing hierarchical classification may introduce bias based on the classifications of extant samples (Blondel et al. 2010). Furthermore, the mesowear method should function as a taxon-free tool, yet specimens within modern comparative samples are often misclassified in terms of diet, potentially

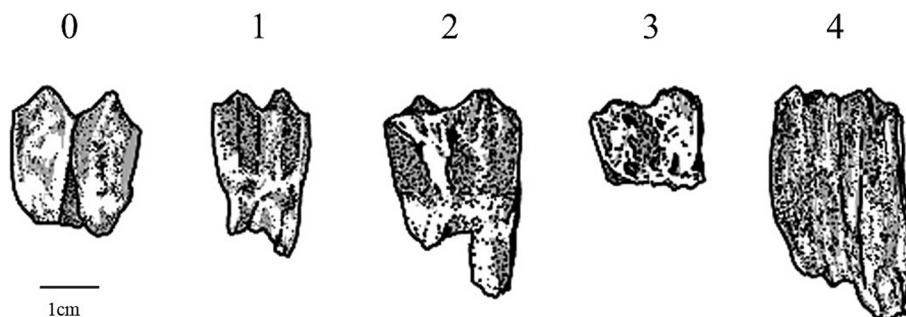


Fig. 3. Illustration of cusp shape and occlusal relief numerical scores. Adapted from Dumouchel & Bobe (2020).

Table 3

Mesowear scorings of the fossil bovids at the Cradle, separated a) by deposit and b) by tribe. N: number of specimens, MWS: mesowear score, std. dev: standard deviation, std. error: standard error, MB: member, W: West, E: East.

a) Deposit	N	% High	% Low	% Sharp	% Round	% Blunt	MWS	Mean	Median	Std dev	Std error
Cooper's Cave	92	85,6	14,4	18	82	0	1848	2,0	1079	0,112	
Drimolen Main	23	21	79	50,6	49,4	0	2043	2,0	0,767	0,160	
Haasgat	62	13	87	3	97	0	2419	3,0	0,879	0,112	
Hoogland	37	22,8	77,2	8,8	91,2	0	2270	3,0	1045	0,172	
Malapa	6	44	56	0	100	0	2000	2,0	1095	0,447	
Sterkfontein MB5 W	33	52,6	47,4	20,8	79,2	0	2030	3,0	1104	0,192	
Sterkfontein MB5 E	46	30	70	19,5	80,5	0	1761	1,0	1158	0,171	
Sterkfontein MB4	12	32	68	4,5	45,5	50	2000	1,5	1128	0,326	
Swartkrans MB1	85	16	84	7	91,7	1,3	2094	3,0	1065	0,115	
Swartkrans MB3	45	39	61	39,75	60,25	0	2200	3,0	1036	0,154	
Swartkrans MB2	182	23,4	76,6	15	85	0	2357	3,0	0,951	0,071	
b) Tribe	N	% High	% Low	% Sharp	% Round	% Blunt	MWS	Mean	Median	Std dev	Std error
Alcelaphini	425	46,25	53,75	6,25	93,45	0,3	2035	3,0	1062	0,052	
Antilopini	112	15	85	18	73	9	2518	3,0	0,890	0,084	
Bovini	4	89	11	0	100	0	1500	1,5	1000	0,500	
Hippotragini	13	41	59	0	100	0	1769	1,0	1013	0,281	
Neotragini	38	100	0	31	69	0	2684	3,0	0,471	0,076	
Reduncini	14	32,4	67,6	20	80	0	2214	3,0	1122	0,300	
Tragelaphini	17	52	48	35	65	0	1882	2,0	1054	0,256	

leading to substantial errors (Green & Croft 2018). In conducting pairwise comparisons between fossil bovids of different deposits, no prior assumptions are made regarding the diets of each tribe. To contextualize the fossil mesowear data, we compared the average mesowear scores of fossil taxa with published mesowear averages of extant ungulate tribes. Additionally, we conducted a comparative analysis of fossil and extant (Supp. Table S1) mesowear scores by tribe, calculating 95 % confidence intervals (CIs) for each group and assessing the overlap of these intervals to determine statistical significance. Our comparison of extant and fossil taxa is indeed based on their reported mesowear scores rather than assigned dietary categories of the extant animals so as not to incorporate any prior assumptions on species-specific preferences.

Lastly, it is known that tooth wear proxies, such as mesowear, can exhibit a phylogenetic signal due to the close relationship between diet and phylogeny (Fraser et al. 2018). However, this does not compromise their utility for dietary inference, as wear patterns reflect diet consistently across taxa (DeSantis et al., 2018), and functional methods such as mesowear offer the opportunity to recognise differences that might be less detectable via morphological methods. Accordingly, we did not use phylogenetic comparative methods as its presence is expected and not problematic for interpreting broad dietary patterns (DeSantis et al., 2018).

3. Results

3.1. Comparative analysis of fossil and extant bovid mesowear

The mean mesowear score for the fossil tragelaphin sample ($n = 17$) is 1.88 ± 0.25 , 95 % CI: 1.38–2.38 which is significantly higher than that of all extant tragelaphin species included in the comparison (four species with a combined mean of 0.52 ± 0.1 , 95 % CI: 0.31–0.73) (Fig. 4, Table 5). Similarly, the fossil reduncin sample ($n = 14$) has a mean mesowear score of 2.21 ± 0.29 and a median of 3.0, whereas the combined mean of the two extant reduncin species is 1.12 ± 0.08 , 95 % CI: 0.95–1.23. Both fossil alcelaphin ($n = 425$) and hippotragin ($n = 13$) samples, on the other hand, fall within the range of their modern counterparts (Table 5). The mean mesowear score of fossil alcelaphins in the Cradle (2.04 ± 0.05 , 95 % CI: 1.93–2.14) is closest to that of extant *Alcelaphus buselaphus* (1.92 ± 0.16), a grazer known to include no less than 80 % grass in its diet throughout the year (Schuette et al. 1998).

The median of Cradle alcelaphins is 3.0, suggesting a high grazing signal. The fossil hippotragin mean (1.77 ± 0.28 , 95 % CI: 1.22–2.32) and median (1.0) is the lowest of all Cradle tribes analysed, and clusters closest with modern *Hippotragus niger* (1.45 ± 0.25). Overall, the biggest discrepancy between fossil Cradle taxa and modern species is between antilopin ($n = 112$) with a high (grazing) mesowear score average of 2.25 ± 0.08 , 95 % CI: 2.52–2.35 (median = 3.0), and the extant springbok *Antidorcas marsupialis* with a much lower average of 0.35 ± 0.11 , 95 % CI: 0.13–0.57. Of the seven fossil tribes included in the analyses, the highest mesowear score mean is that of the neotragin ($n = 38$) with 2.68 ± 0.08 , 95 % CI: 2.53–2.83. The modern comparative sample for neotragin comes from Kaiser et al. (2013), with the three included species having a combined mesowear score of 1.07 (standard deviation not provided).

3.2. Comparative analysis of bovid mesowear across deposits

Haasgat (2.41 ± 0.11) and Swartkrans Member 2 (2.36 ± 0.07) have the highest mean mesowear score values, both reflecting strong grazing signals (Fig. 5). All three Swartkrans members, Sterkfontein Member 5 West, Haasgat and Hoogland have the highest median scores (3.0). The lowest average scores were recorded at Cooper's Cave (1.85 ± 0.11) and Sterkfontein Member 5 East (1.76 ± 0.17), indicating the weakest grazing signals. However, median scores suggest that Sterkfontein Member 5 East and Sterkfontein Member 4 had the lowest values, with 1.0 and 1.5 respectively, reflecting slight differences in score distribution. Notably, Sterkfontein Member 5 East, despite its low mesowear score, is slightly older than the high-scoring Swartkrans Member 2. The former is dated to approximately 2.0–1.4 Ma (Herries & Shaw 2011; Pickering et al. 2019), a period often linked to an expansion of open vegetation.

The overall mesowear score means for every deposit are >1.5 , typically closer to 2 and with just under 2.5 as the highest. Similarly, median scores are between 1.0 and 3.0, with the majority at the higher end. All deposits exhibit similar mesowear scores, consistently reflecting a stronger grazing than browsing signal. However, there is no clear trend indicating a progressive increase in grazing behaviour over time. In fact, the youngest site (Cooper's Cave) is the most varied overall. Specifically, the mesowear score means of alcelaphin and antilopin teeth at this site ($n = 61$ and $n = 41$ respectively) do not overlap (Fig. 5), suggesting

Table 4

Mesowear scorings of fossil bovids for each tribe within each deposit at the Cradle. N: number of specimens, MWS: mesowear score, std. dev: standard deviation, std. error: standard error, MB: member.

Deposit	Age (Ma)	Tribe	N	% Low	% High	% Sharp	% Round	% Blunt	MWS			
				Mean	Median	Std dev	Std error					
Hoogland	3.12–2.29	Tragelaphini	2	100	0	0	100	0	3	3	0	0
		Neotragini	3	100	0	0	100	0	3	3	0	0
		Alcelaphini	15	67	33	0	100	0	2333	3	0,976	0,252
		Reduncini	8	63	37	0	100	0	2,25	3	1,04	0,366
		Antilopini	9	56	44	44	56	0	1778	2	1,3	0,434
Sterkfontein MB4	2.8–2.0	Alcelaphini	11	36	64	9	91	0	1818	1	0,982	0,296
		Antilopini	1	100	0	0	0	100	4	4	N/A	N/A
Drimolen Main	2.04–1.5	Alcelaphini	10	50	50	10	90	0	1,9	1,5	0,994	0,314
		Neotragini	5	100	0	80	20	0	2,2	2	0,447	0,2
Haasgat	2.6–1.0	Tragelaphini	8	88	12	62	38	0	2125	2	0,641	0,227
		Alcelaphini	28	46	54	0	100	0	1929	1	1,02	0,192
		Neotragini	22	100	0	18	82	0	2818	3	0,395	0,084
		Tragelaphini	2	100	0	0	100	0	3	3	0	0
		Antilopini	5	100	0	0	100	0	3	3	0	0
Malapa	2.3–1.78	Hippotragini	1	100	0	0	100	0	3	3	N/A	N/A
		Reduncini	4	75	25	0	100	0	2,5	3	1	0,5
		Alcelaphini	3	67	33	0	100	0	2333	3	1,15	0,667
		Antilopini	1	100	0	0	100	0	3	3	N/A	N/A
		Tragelaphini	2	0	100	0	100	0	1	1	0	0
Sterkfontein MB5 Oldowan	2.1–1.1	Antilopini	4	100	0	25	75	0	2,75	3	0,5	0,25
		Alcelaphini	42	40	60	14	86	0	1667	1	1,16	0,179
Swartkrans MB5 West	1.7–0.8	Antilopini	3	100	0	0	100	0	3	3	0	0
		Alcelaphini	24	54	46	4	96	0	2042	3	1,08	0,221
		Tragelaphini	1	0	100	100	0	0	0	0	N/A	N/A
		Bovini	3	33	67	0	100	0	1667	1	1,15	0,667
		Hippotragini	2	50	50	0	100	0	2	2	1,41	1
Swartkrans MB1	2.25–1.5	Alcelaphini	79	52	48	1	95	4	2038	3	1,08	0,121
		Antilopini	5	100	0	20	80	0	2,8	3	0,447	0,2
Swartkrans MB2	1.63–1.0	Neotragini	1	100	0	0	100	0	3	3	N/A	N/A
		Alcelaphini	125	68	32	4	96	0	2,24	3	1	0,09
		Antilopini	44	95	5	14	86	0	2773	3	0,677	0,102
		Reduncini	1	100	0	0	100	0	3	3	N/A	N/A
		Hippotragini	5	20	80	0	100	0	1,4	1	0,894	0,4
Swartkrans MB3	1.6–0.6	Neotragini	7	100	0	57	43	0	2429	2	0,535	0,202
		Alcelaphini	27	63	37	15	85	0	2,26	3	1,06	0,204
		Antilopini	16	81	19	44	56	0	2189	2	0,911	0,228
		Reduncini	1	0	100	100	0	0	0	0	N/A	N/A
		Hippotragini	1	100	0	0	100	0	3	3	N/A	N/A
Cooper's Cave	1.9–1.3	Alcelaphini	61	43	57	7	93	0	1789	1	1,08	0,139
		Antilopini	24	4	96	33	67	0	2208	2	1,02	0,208
		Bovini	1	0	100	0	100	0	1	2	N/A	N/A
		Tragelaphini	2	0	100	50	50	0	0,5	0,5	0,707	0,5
		Hippotragini	4	25	75	0	100	0	1,5	1	1	0,5

occupation of different dietary niches. Swartkrans Members 1 and 2 (2.0–1.4 Ma) and Sterkfontein Member 5 East (2.0–1.8 Ma), perhaps in part due to the larger sample sizes for these deposits, evidence the largest separation in mesowear scores between individuals of the same tribe (Fig. 5). This appears to be the case particularly for alcelaphin specimens, which score on both ends of the spectrum in the same deposit. However, antilopin teeth in these three deposits consistently reflect a strong grazing pattern.

Regarding specific site differences, Cooper's Cave mesowear scores (the youngest site at ~1.3 Ma) are significantly different from those at both Haasgat (2.0–1.81 Ma) and Swartkrans Member 2 (1.63–1.41 Ma) with both the Benjamini-Hochberg and Bonferroni tests (Table 6), presenting an overall lower signal. Sterkfontein Member 5 East (2.0–1.4 Ma) differs significantly from Swartkrans Member 2 (with Benjamini-Hochberg and Bonferroni tests), also presenting an overall lower signal. Sterkfontein Member 5 East shows more divergence from this deposit than to Member 5 West, which demonstrates no significant difference to the East deposit. Across all deposits, individuals plot closer to 0 (browsers) than they do to 4 (grazers), though the mean and median is still higher on average and suggestive of grassland vegetation presence during fossil deposition.

4. Discussion

We conducted a dental mesowear analysis of fossil bovid molars from seven sites within South Africa's Cradle of Humankind, spanning an age range from 3.2 to 1.3 Ma. Taking advantage of the robust chronology now available for the majority of Cradle sites, we utilised our results to assess two questions. Firstly, is there a shift from woodland towards open, grassland-dominated environments around 1.7 Ma, as proposed in certain earlier studies? Secondly, are there noticeable differences in ecological structure among the study sites/members, and how might these distinctions (or lack thereof) be interpreted?

Our mesowear analysis across bovid tribes and depositional units reveals no consistent increase in grazing behaviour over time, providing no evidence for a shift towards grazing-dominated habitats around 1.7 Ma – or at any other point within the studied intervals (Fig. 6). Sewell et al. (2019) conducted mesowear analysis on *Antidorcas* specimens from Swartkrans and Sterkfontein, noting a slight increase in grazing between Sterkfontein Member 4 and Member 5, and no clear shift between Swartkrans members. However, because mesowear scores were not provided and their sample sizes differed from ours ($n = 91$ from Sterkfontein in our study vs. $n = 15$ in theirs), direct comparison is not straightforward. Nonetheless, based on occlusal relief and cusp shape percentages, our results are broadly in agreement with theirs. Moreover,

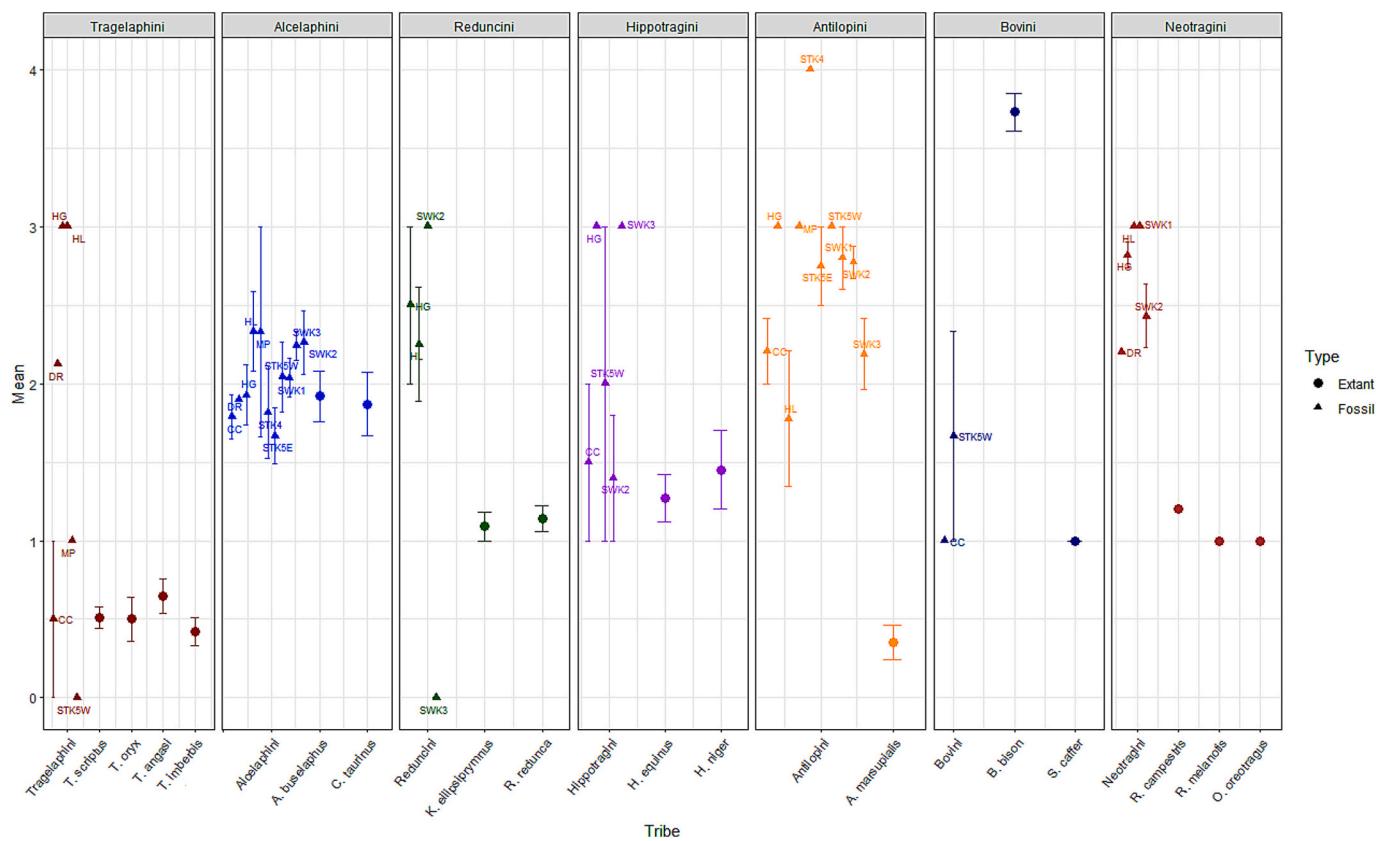


Fig. 4. Distribution of mesowear scores per tribe for Cradle fossil and modern samples. Modern data come from Blondel et al. (2018), except for Neotragini that are taken from Kaiser et al. (2013). Dots and triangles represent the mean MWS, error bars represent standard error of the mean. CC: Cooper's Cave, DR: Drimolen, HG: Haagsgat, HL: Hoogland, MP: Malapa, STK: Swartkrans.

Table 5
Comparative analysis of fossil and extant mesowear scores by tribe, including 95 % Confidence Intervals (CI) and CI overlap assessment.

Tribe	Group	n	Mean	95 % CI lower	95 % CI upper	CI overlap
Alcelaphini	Extant (2 species)	128	1895	1,54	2,25	Yes
	Fossil	425	2035	1934	2136	
	Extant (1 species)	26	0,35	0,134	0,566	
Antilopini	Fossil	112	2518	2353	2683	No
	Extant (2 species)	46	2365	2199	2531	
	Fossil	4	1,5	0,52	2,48	
Bovini	Extant (2 species)	46	1,36	0,956	1764	Yes (wide range)
	Fossil	13	1769	1219	2,32	
	Extant (3 species)	17	1067	(no SEs)	(no SEs)	
Hippotragini	Fossil	38	2684	2534	2834	No
	Extant (2 species)	99	1115	0,948	1282	
	Fossil	14	2214	1627	2802	
Neotragini	Extant (4 species)	112	0,52	0,313	0,727	No
	Fossil	17	1882	1381	2383	
	Extant (3 species)	17	1882	1381	2383	

their mesowear analysis did not contain data from Sterkfontein Member 5 East, and the Member 5 West and Member 4 sample sizes were $n = 5$ and $n = 10$ respectively, which may explain why they noted a clearer shift in ecological structure around 1.7 Ma.

Isotopic research by Luyt (2001) identified a notable environmental

shift from more wooded to more open habitats around 1.8 Ma, based on data from the older Sterkfontein Member 4, younger Sterkfontein Member 5 and Swartkrans Member 1. However, this shift was not framed within a robust chronological framework: the dates used for each deposit were approximations without reported ranges (they use an age of 2.6 Ma for Sterkfontein Member 4 and ~1.7 Ma for Member 5). In their study, the shift was associated with deposits dated to ~1.7 Ma, but more recent dating shows these deposits accumulated between ~2.0 and 1.8 Ma (Pickering et al. 2019). Moreover, Sterkfontein Member 4, assigned to ~2.6 Ma in their study, has since been dated to as young as 2.12 Ma. These updated chronologies help explain the more consistent results we observe across all three deposits. Luyt & Lee-Thorp (2003) indicated a shift specifically in Sterkfontein Member 5 West, where we also observed an increase in grazing. Lee-Thorp et al. (2007) determined a shift to open environments at 1.7 Ma based on isotopes from herbivores at Sterkfontein, Swartkrans and Makapanvlei; however, they caution that the dates for each site are of low resolution and uncertain periods of accumulation. No specific age range is supplied for Swartkrans Member 1, the deposit in which the shift supposedly becomes evident. Furthermore, their study notes that the primary result is an increase in grazers from Swartkrans Member 1, and while this is the case, the proportion of browsers between the older Sterkfontein Member 4 and the younger Swartkrans Member 1 remains almost identical – suggesting not necessarily a loss of woodlands, but rather an expansion of grassy habitats alongside persistent sources of browse. Overall, the broader dates and overall chronological uncertainties reported in earlier research explain why a more pronounced shift in vegetation at the Cradle was previously observed. In contrast, our conclusion of no overt change is informed by a wide range of sites and a direct, regional chronology.

Our second question looks at the ecological variability between sites.

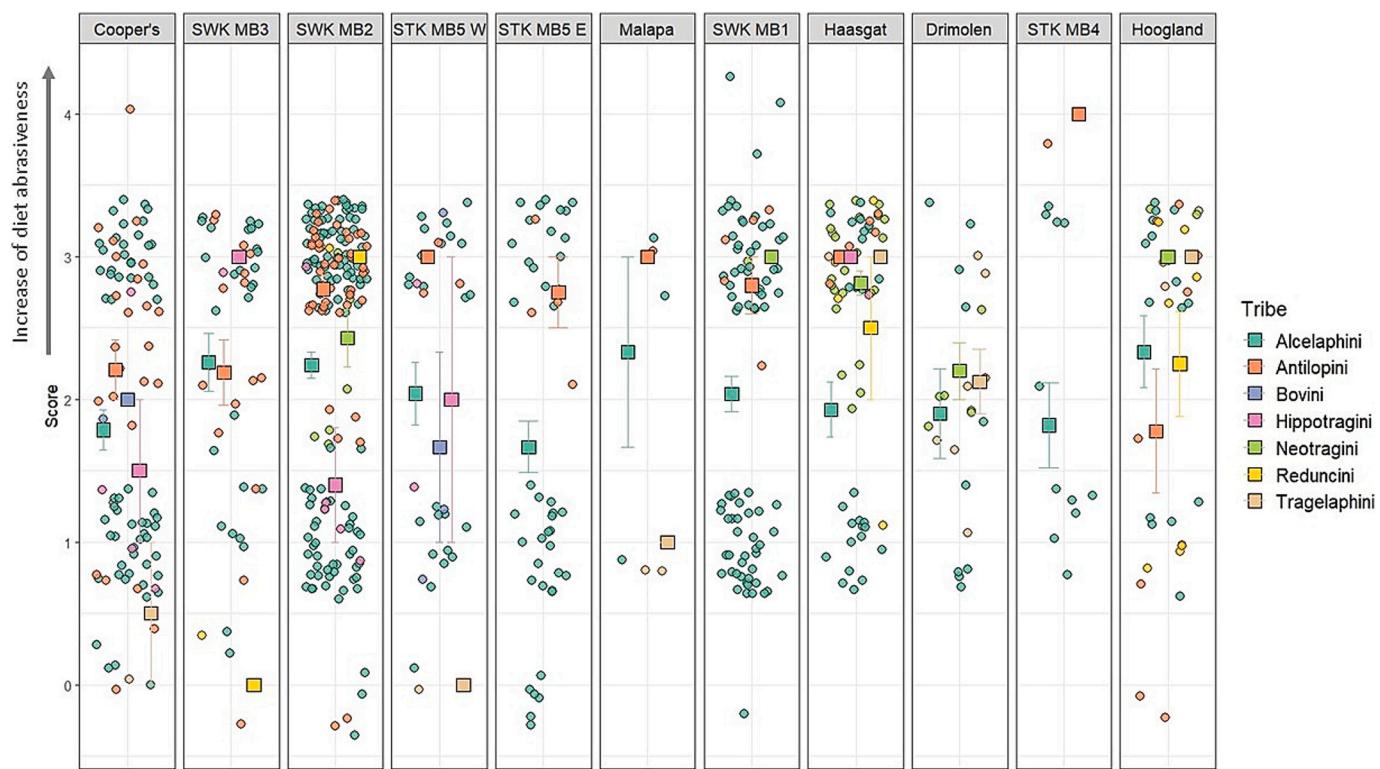


Fig. 5. Individual fossil mesowear scores per deposit. Points represent individual specimen, squares with error bars represent the mean value and standard error of each sample. Deposits are shown chronologically, with the youngest on the left.

Table 6

a) Kruskal-Wallis comparison of mesowear scores between Cradle deposit members, and b) results of pairwise comparisons between deposits. Numbers provided are from Benjamini-Hochberg procedure. Numbers in bold indicate significant differences, and are shown in solely bold for Benjamini-Hochberg and in bold with underline for both Benjamini-Hochberg and Bonferroni tests. df: degrees of freedom, SWK: Swartkrans, STK: Sterkfontein, MB: Member.

a) Kruskal-Wallis	df	H	p-value							
Between deposits	10	27.199	0.00242							
Between tribes	6	30.0218	0.00004							
b) Benjamini-Hochberg										
Cooper's	Cooper's									
Drimolen	0,84,923	Drimolen								
Haasgat	<u>0,01867</u>	0,34,914	Haasgat							
Hoogland	0,30,133	0,66,078	0,84,167	Hoogland						
Malapa	0,84,923	0,93,344	0,73,954	0,84,167	Malapa					
STK MB4	0,84,923	0,93,344	0,6228	0,75,987	0,98,346	STK MB4				
STK MB5 E	0,84,923	0,84,167	<u>0,0253</u>	0,30,133	0,84,923	0,84,167	STK MB5 E			
STK MB5 W	0,73,954	0,84,923	0,39,416	0,73,954	0,93,344	0,93,344	0,70,507	STK MB5 W		
SWK MB1	0,40,014	0,84,167	0,34,914	0,73,954	0,90,017	0,84,923	0,39,416	0,90,017	SWK MB1	
SWK MB2	<u>0,00752</u>	0,34,914	0,84,923	0,84,923	0,75,987	0,66,078	<u>0,01867</u>	0,40,014	0,34,914	SWK MB2
SWK MB3	0,34,914	0,73,954	0,70,507	0,84,923	0,84,923	0,84,167	0,34,914	0,84,167	0,84,923	0,73,954

Although changes were observable in our data within bovid tribes and site members, the overall ecological signal remains heterogenous across time. According to our analysis, the Swartkrans Member 2 infill is one of the most open environments at the Cradle. However, the difference between Member 2 and Member 3 is inconsequential – in fact, these two members appear to be among the most similar of all the deposits studied. These data indicate a lack of discernible difference in vegetation between the two Swartkrans Members, in agreement with previous faunal analyses and pointing to an open-to-mixed vegetative structure. Moreover, all three Swartkrans members are often reported as indistinguishable in terms of faunal evidence (Brain 1993; Avery 2001; Elton 2001; de Ruiter 2003), though not all studies agree with this interpretation (e.g., Reed 1997).

Mixed-feeding appears to have played a dominant role across many

Cradle sites, with bovids from Drimolen, Cooper's Cave, and Swartkrans exhibiting strong mixed-feeding signals. This suggests a generalised dietary strategy during the focus period, highlighting the flexibility of these species and underscoring the importance of mixed feeders in vegetation dynamics. Interestingly, certain sites also demonstrate a more bimodal distribution of mesowear signals (Fig. 5). Evidence from Hoogland, Haasgat and Sterkfontein suggests that bovids were alternating between grazing and browsing, with a stronger emphasis on grazing. This pattern may reflect significant shifts in vegetative structure, and further suggests that bovids of the same tribe were adapting their diet in response to changing ecological conditions. Overall, mesowear signals across deposits do not differ substantially from each other (Table 3a) and mostly point to a heterogenous environment between 3 and 1 Ma.

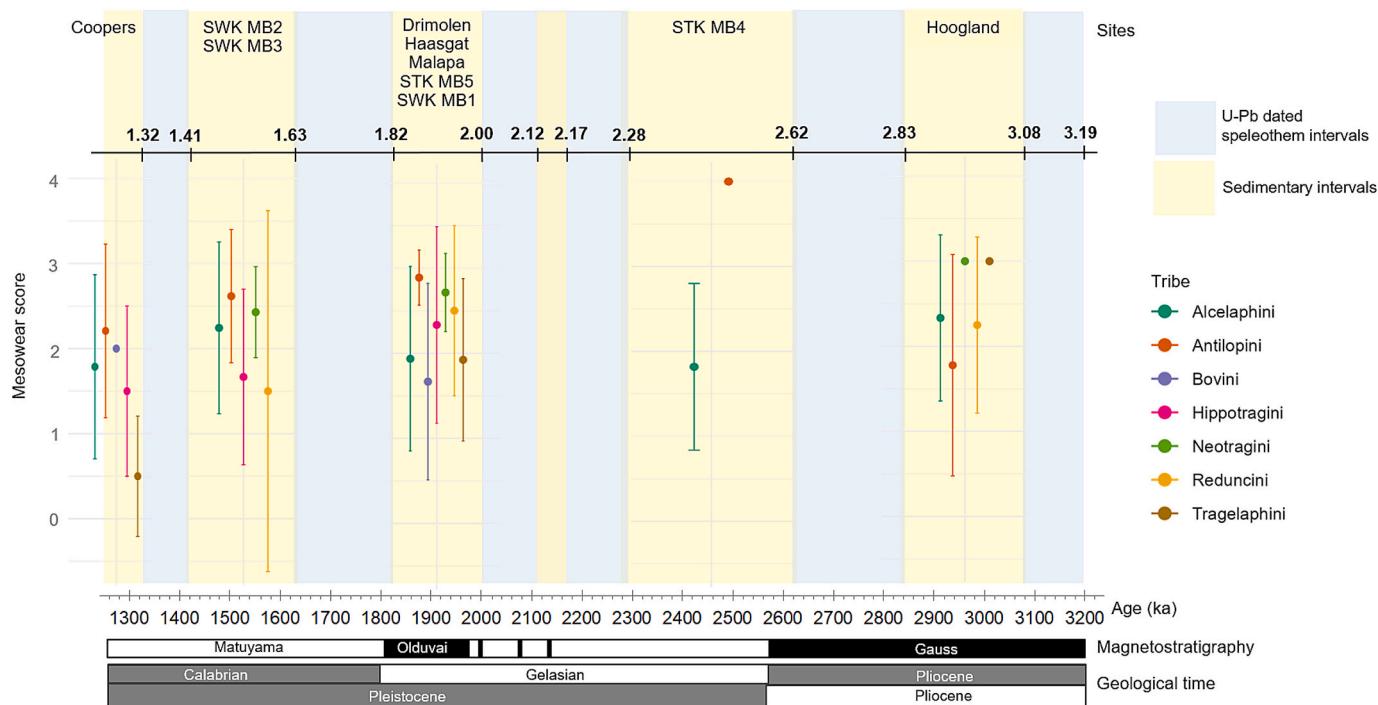


Fig. 6. Mean mesowear scores and standard deviations for each bovid tribe plotted against the chronological framework for the deposits in the Cradle of Humankind. Age ranges are constrained by U-Pb dating of interbedded flowstones (Pickering et al. 2019). Sites are grouped within their respective depositional intervals. Magnetostratigraphic polarity zones are also shown here. STK: Sterkfontein, SWK: Swartkrans, MB: Member.

Our analysis includes new mesowear data from sites which have not been included before in studies exploring environmental shifts at the Cradle, and whose age ranges fall directly across the period when the change is deemed the most pronounced. These sites are Haasgat (2.17–1.8 Ma), which presents a grazing signal with some inclusion of browse; Drimolen Main Quarry (2.04–1.8 Ma); and Malapa (1.98 Ma), both of which indicate mixed feeding. The inclusion of these previously unstudied sites provides a more complete and nuanced perspective on environmental change at the Cradle, filling in a picture of stable but heterogeneous palaeoecology through the Plio-Pleistocene.

The majority of bovid specimens across all sites belong to the Alcelaphins and Antilopins (>80 %), making their feeding ecologies the primary drivers of the overall dietary signal. The ecological preferences of these tribes have long informed palaeoenvironmental reconstructions in the Cradle. In her influential study, Vrba (1985) used consensus data from nine modern bovid tribes in sub-Saharan Africa to draw what she described as “remarkable and consistent” (Vrba 1985: 64) associations between alcelaphins and antilopins, and open grassland habitats. Since then, the relative abundance of these tribes at early hominin sites has often been treated as a reliable proxy for vegetation structure. However, the assumption that all bovids belonging to the Alcelaphini or Antilopini tribes (ancient or modern) are strict grazers, feeding solely on phytolith-rich, predominantly C₄ grasses, is now recognised as an oversimplification. Antilopins, for example, and southern African springbok species in particular, are now widely recognised as mixed feeders both in the fossil record (Luyt 2001; Sewell et al. 2019) and in the one remaining extant species *Antidorcas marsupialis* (Castelló 2016). Therefore, the abundant presence of these fossil tribes does not necessitate a dominant grassland, a finding reflected in our results. Across all deposits, these bovid tribes are shown to have consumed a mixed diet (or alternate between graze and browse), though with a more prominent grazing signal overall. The mixed-feeding behaviour observed in these two tribes illustrates a greater dietary flexibility than previously assumed. Specifically, in Swartkrans Members 1 and 2 and Sterkfontein Member 5 East, a clear separation is observed within Alcelaphins in the same deposit, with some individuals grazing and some browsing. We

therefore argue that the bovids occupying these Plio-Pleistocene landscapes were adapted to changes in vegetation and seasonal shifts in ecology, as reflected in their fossil signals preserving both browsing and grazing signals. The climatic shifts of the Plio-Pleistocene were variable and often unstable (Potts 1998; Trauth et al. 2021), which may also explain these signals. The depositional time windows of both these deposits are long, on the order of several hundred thousand years, meaning that local hydroclimatic conditions would have varied during these times, driving associated change in the vegetation and thus the feeding ecology of these herbivores.

Between 3.2 and 1.3 Ma, Cradle bovids overall appear to have occupied a greater diversity of environments – or more mosaic environments – than their eastern African counterparts. Alcelaphins, in particular, exhibit stronger mesowear signals indicative of grazing at Plio-Pleistocene sites such as Laetoli, Tanzania (Kaiser 2011), and Kibish, Ethiopia (Dumouchel & Bobe 2020), than their counterparts do at sites in the Cradle. Tragelaphins and hippotragins, by contrast, display a more browse-dominated mesowear signal at eastern African sites than they do in the Cradle, where they appear to exhibit mixed feeding or grazing tendencies. Most of the Cradle’s tragelaphin sample, dating to 2.6–1.8 Ma, reflects a mixed to grazing signal. In comparison, mesowear scores from tragelaphins in Members C, E, F, and G of the Shungura Formation – dating to approximately 2.9–1.9 Ma – indicate a predominantly browsing diet (Blondel et al. 2018). Reduncins from the same Shungura members, while not browsing as strictly as Tragelaphins (Blondel et al. 2022), still indicate a more browse dominated mesowear signal than those at the Cradle, which lean more towards grazing. Neotragins, which have the most abrasive mesowear signal at the Cradle (Fig. 4), exhibit a more intermediate signature in the ~2.6 Ma Laetoli deposits (Kaiser 2011). Similarly, Cradle Antilopins present strong grazing signals, in contrast to the predominantly browsing signal seen in their Laetoli counterparts. These differences indicate regional variation in bovid dietary ecology, with the Laetoli taxa consuming more browse and South African versions of the same tribes displaying more abrasive diets in these two tribes. Given the vast geographic separation and distinct climatic and environmental regimes – both in the Plio-

Pleistocene and today – these differences are unsurprising. The effects of precipitation, grit levels, grass length and grassland type are all features that further influence the overall more mixed signal observed within the Cradle bovids. Importantly, these kinds of direct, large scale and time-equivalent comparisons across regions were previously not possible due to limited or inconsistent datasets, highlighting the scope and potential of this expanded mesowear data from the Cradle.

These regional contrasts also reveal distinct lineage-specific patterns of dietary stability and transformation across the Plio-Pleistocene. While tribes such as the Alcelaphini maintain relatively consistent grazing tendencies across fossil and modern samples, others exhibit more marked shifts or regional divergence. For instance, Antilopins in the Cradle already display strong grazing signals, aligning more closely with their modern counterparts than do the browsing-dominated fossil antelopins of eastern Africa, perhaps suggesting an earlier shift towards abrasive diets in the south. Neotragins in the Cradle also show a more abrasive mesowear signal than both their fossil relatives at Laetoli and their modern forms, potentially reflecting localized niche expansion or heightened environmental abrasion. In contrast, Hippotragins show greater ecological continuity in the Cradle, with fossil mesowear values broadly overlapping those of modern counterparts. Cradle specimens exhibit greater levels of dental abrasion than their Laetoli counterparts. Given that the Laetoli deposits are Pliocene in age, the observed dietary divergence likely reflects a combination of temporal and regional environmental differences. While Cradle fossils do not fully converge with their extant counterparts, in several tribes they appear more directionally aligned with modern dietary signals than do equivalent-aged fossils from eastern Africa. This may reflect either earlier shifts in feeding strategy in the south, or more persistent regional differences in vegetation structure and environmental pressures. These patterns underscore the value of spatially and temporally integrated datasets for reconstructing palaeoecology, revealing how some lineages track consistent dietary strategies, while others adapt to shifting ecological conditions.

Beyond regional trends, site-specific comparisons reveal key patterns, as well as unexpected deviations. Though geochronological evidence does not suggest an explicit separation for the dates of Sterkfontein Member 5 East vs West (Herries et al. 2009; Herries & Shaw 2011; Pickering et al. 2019), the latter is evidently younger based on various other lines of evidence (Kuman & Clarke 2000; Herries & Shaw 2011), specifically stone tools. In line with the younger age as well as isotopic evidence, we observed a shift towards more open grasslands from Member 5 East to Member 5 West, though the change was not considerable.

Cooper's D is the youngest site included in this study, and we expected to find the highest mesowear scores indicating a dominant grazing signal. However, the average mesowear score across all tribes at Cooper's D reflected a mixed feeding strategy – incorporating both browsing and grazing – compared to other sites. Additionally, most tribes exhibited distinct mesowear patterns from one another, suggesting resource partitioning among generalist feeders. This pattern suggests that, despite overlapping dietary flexibility, these taxa were able to exploit different niches within the same environment, reducing direct competition and reflecting a diverse and heterogeneous habitat structure. Similarly, with Hoogland as the oldest site included in this study, we expected a low mesowear score, but in fact it was among the highest, indicating a landscape that supports grazing. Swartkrans Member 1 has previously been reconstructed as relatively open, with a dominance of C₄ grasses (Vrba 1985; Reed 1997; Lee-Thorp et al. 2007), particularly when compared to Sterkfontein Member 4. We do not find this pattern. Indeed, whilst our Sterkfontein Member 4 sample was relatively small ($n = 12$) and we urge a level of caution against over interpretation, Swartkrans Member 1 exhibited only a slightly higher mesowear score, and the difference between the two was not statistically significant ($p = 0.849$). More recent isotopic analysis on small mammals from Swartkrans has indicated a more closed environment for Member 1 (Leichliter

et al. 2017), in line with taxonomic conclusions (Benefit & McCrossin 1990).

A potential caveat of this study is the use of tribal-level resolution in the mesowear analysis. While this approach allows for broad ecological interpretations over long time spans and large samples, it necessarily groups multiple species that may have exhibited distinct dietary adaptations. Such taxonomic aggregation can obscure intra-tribal ecological diversity and contribute to higher inter-individual variability within the dataset. We acknowledge this limitation and note that while general dietary patterns (e.g., Alcelaphins as fresh grass grazers, Reduncins as wet grass grazers) are informative at this scale, they do not capture potential niche partitioning at the species level. The possibility that some tribes contained species with differing or shifting diets should be kept in mind when interpreting the results. An additional interpretive caution is warranted regarding the apparent stability of dietary patterns in mixed feeders. The absence of clear mesowear shifts in these taxa should not be taken as definitive evidence of ecological or climatic stability. Mixed feeders are, by definition, dietary generalists that can maintain similar mesowear signatures across a range of environmental conditions. For instance, an individual might maintain the same mesowear signal despite shifting from a diet of 60 % grass to one of 40 %, depending on available vegetation and seasonal needs. Thus, stable mesowear signals in mixed feeders may mask underlying environmental changes and should be interpreted with this flexibility in mind.

Overall, the findings of this study contribute to debates on Plio-Pleistocene environmental reconstructions at the Cradle by including more study sites, especially those around the 1.7-million-year mark. This period is thought to be a time of significant transition to grassland habitats, but our analysis did not find any evidence of such a shift. Additionally, by applying a single methodological approach across seven sites and examining vegetation patterns within a regional chronological framework, our findings revealed that all deposits show evidence of heterogeneous conditions, encompassing both mosaic and grassland landscapes. A study of this nature – examining more than two sites within the context of a new direct chronological framework – has not previously been undertaken. Our findings suggest that hominin evolution and speciation in the Cradle during the Plio-Pleistocene did not occur in response to a steady increase in open grassland environments. Instead, these processes unfolded within a dynamic and environmentally heterogeneous landscape. Dental microwear, which examines tooth wear on a more short-term scale than mesowear, would be a valuable next step in providing a more integrated and comparative perspective on past environmental change. Applying the method across the same bovids and Cradle sites explored here could offer a more refined understanding of ecological patterns and habitat shifts between 3 and 1 Ma, particularly due to its ability to capture short-term signals of dietary behaviour. For instance, while the current mesowear study reveals broad dietary tendencies and long-term alternations in feeding strategies within the same taxonomic groups, microwear could help determine whether these reflect genuine environmental shifts or short-term resource partitioning among sympatric species. Combining both methods would thus allow us to test for intra-member dietary variability and better evaluate the stability or fluctuation of available resources at finer temporal and ecological scales.

5. Conclusions

This study is the first to apply mesowear analysis across more than three Plio-Pleistocene Cradle sites and the first to incorporate the absolute ages for the deposits on a regional scale. The regional chronology, based on a model of flowstone formation, indicates consistent fluctuations between wet and dry cycles from 3.2 to 1.3 Ma. This record has a major wet phase between 1.8 and 1.6 Ma, centred on 1.7 Ma, as evidenced by a period of major flowstone formation at five of the caves. Following this, from 1.6 Ma onwards, there is a shift towards drier conditions, with only one last wet period of flowstone formation at 1.3

Ma. To better understand the palaeoenvironmental conditions at the Cradle of Humankind during this period, we analysed dental mesowear in various bovid tribes across seven sites – Cooper's Cave, Drimolen, Haasgat, Hoogland, Malapa, Sterkfontein, and Swartkrans. Despite previous hypotheses suggesting a major shift towards open grassland environments around 1.7 Ma, our findings reveal no clear transition of this kind, indicating instead a more complex and variable ecological backdrop with consistent shifts in browsing and grazing activity within the bovid community. Notably, tribes that dominate certain sites, e.g., Alcelaphini and Antilopini at Cooper's Cave, appeared to have utilised different resources within the same deposit. Our study indicates that the majority of bovid tribes were dietarily flexible, enabling them to adjust to the fluctuating and unstable conditions that defined the Plio-Pleistocene. Additionally, we noted that some fossil bovid tribes (e.g., Tragelaphini and Antilopini) consumed more graze than their modern counterparts. We provide evidence that the palaeoenvironmental conditions in the Cradle, on a regional level, consisted of a grassland-mosaic landscape, with no clear shift towards dominant open grasslands at a precise point in time.

CRediT authorship contribution statement

Megan Malherbe: Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Martin Haeusler:** Writing – review & editing, Validation, Supervision, Resources. **Robyn Pickering:** Writing – review & editing, Visualization, Validation, Supervision, Investigation, Conceptualization. **Deano Stynder:** Writing – review & editing, Validation, Supervision, Project administration, Methodology.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank the Ditsong National Museum of Natural History and the Evolutionary Studies Institute at the University of the Witwatersrand for access to their collections. Funding was also provided in order to support this research by the Swiss Society for Anthropology and the Graduate Research Campus at the University of Zurich. This research contributes towards the output of the Biogeochemistry Research Infrastructure Platform (BIOGRIP), supported by the South African Department of Science, Technology and Innovation.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2025.113199>.

Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

References

- Ackermans, N.L., Winkler, D.E., Schulz-Kornas, E., Kaiser, T.M., Muller, D.W.H., Kircher, P.R., Hummel, J., Clauss, M., Hatt, J.M., 2018. Controlled feeding experiments with diets of different abrasiveness reveal slow development of mesowear signal in goats (*Capra aegagrus hircus*). *J. Exp. Biol.* 221. <https://doi.org/10.1242/jeb.186411>.
- Ackermans, N.L., Martin, L.F., Codron, D., Hummel, J., Kircher, P.R., Richter, H., Kaiser, T.M., Clauss, M., Hatt, J.-M., 2020. Mesowear represents a lifetime signal in sheep (*Ovis aries*) within a long-term feeding experiment. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 553. <https://doi.org/10.1016/j.palaeo.2020.109793>.
- Adams, J.W., 2012. A revised listing of fossil mammals from the Haasgat cave system ex situ deposits (HGD), South Africa. *Palaeontol. Electron.* 15, 1–88.
- Adams, J.W., Rovinsky, D.S., 2018. Taphonomic interpretations of the Haasgat HGD assemblage: a case study in the impact of sampling and preparation methods on reconstructing South African karstic assemblage formation. *Quat. Int.* 495, 4–18. <https://doi.org/10.1016/j.quaint.2018.01.036>.
- Adams, J.W., Herries, A.I., Hemingway, J., Kegley, A.D., Kgasi, L., Hopley, P., Reade, H., Potze, S., Thackeray, F., 2010. Initial fossil discoveries from Hoogland, a new Pliocene primate-bearing karstic system in Gauteng Province, South Africa. *J. Hum. Evol.* 59, 685–691. <https://doi.org/10.1016/j.jhevol.2010.07.021>.
- Adams, J.W., Kegley, A.D., Krigbaum, J., 2013. New faunal stable carbon isotope data from the Haasgat HGD assemblage, South Africa, including the first reported values for *Papio anubis* and *Cercopithecus haasgati*. *J. Hum. Evol.* 64, 693–698. <https://doi.org/10.1016/j.jhevol.2013.02.009>.
- Alemseged, Z., 2003. An integrated approach to taphonomy and faunal change in the Shungura formation (Ethiopia) and its implication for hominid evolution. *J. Hum. Evol.* 44, 451–478. [https://doi.org/10.1016/s0047-2484\(03\)00012-5](https://doi.org/10.1016/s0047-2484(03)00012-5).
- Ashley, G.M., Hay, R.L., 2002. Sedimentation patterns in a Plio-Pleistocene volcaniclastic rift-platform basin, Olduvai Gorge, Tanzania. In: Renaut, R.W., Ashley, G.M. (Eds.), *Sedimentation in Continental Rifts*. Society for Sedimentary Geology, pp. 107–122.
- Avery, D.M., 2001. The Plio-Pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. *J. Hum. Evol.* 41, 113–132. <https://doi.org/10.1006/jhev.2001.0483>.
- Badenhorst, S., Steininger, C.M., 2019. The equidae from Cooper's D, an early Pleistocene fossil locality in Gauteng, South Africa. *PeerJ* 7, e6909. <https://doi.org/10.7717/peerj.6909>.
- Badenhorst, S., Senegas, F., Gommery, D., Potze, S., Kgasi, L., Thackeray, F., 2011. Pleistocene faunal remains from Garage Ravine cave, Bolt's Farm in the Cradle of Humankind World Heritage Site area, Gauteng South Africa. *Ann. Ditsong Natl. Mus. Nat. Hist.* 1, 33–40.
- Bamford, M., 1999. Pliocene fossil woods from an early hominid cave deposit, Sterkfontein, South Africa. *S. Afr. J. Sci.* 95, 231–237.
- Behrensmeyer, A.K., Potts, R., Deino, A., Ditchfield, P.W., 2002. Olorgesailie, Kenya: a million years in the life of a Rift Basin. In: Renaut, R.W., Ashley, G.M. (Eds.), *Sedimentation in Continental Rifts*. Society for Sedimentary Geology, pp. 97–106.
- Behrensmeyer, A.K., Todd, N.E., Potts, R., McBrinn, G.E., 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. *Science* 278, 1589–1594.
- Benefit, B., McCrossin, M., 1990. Diet, species diversity and distribution of African fossil baboons. *Kroeger Anthropol. Soc. Pap.* 71, 77–93.
- Berger, L.R., de Ruiter, D., Churchill, S.E., Schmid, P., Carlson, K.J., Dirks, P., Kibii, J.M., 2010. *Australopithecus sediba*: a new species of *Homo-like* Australopith from South Africa. *Science* 328, 195–204.
- Berger, L.R., Hawks, J., de Ruiter, D.J., Churchill, S.E., Schmid, P., Delezene, L.K., Kivell, T.L., Garvin, H.M., Williams, S.A., DeSilva, J.M., Skinner, M.M., Musiba, C.M., Cameron, N., Holliday, T.W., Harcourt-Smith, W., Ackermann, R.R., Bastir, M., Bogin, B., Bolter, D., Brophy, J., Cofran, Z.D., Congdon, K.A., Deane, A.S., Dembo, M., Drapeau, M., Elliott, M.C., Feuerriegel, E.M., Garcia-Martinez, D., Green, D.J., Gurtov, A., Irish, J.D., Kruger, A., Laird, M.F., Marchi, D., Meyer, M.R., Nalla, S., Negash, E.W., Orr, C.M., Radovcic, D., Schroeder, L., Scott, J.E., Throckmorton, Z., Tocheri, M.W., VanSickle, C., Walker, C.S., Wei, P., Zipfel, B., 2015. *Home Naledi*, a new species of the genus *Home* from the Dinaledi Chamber, South Africa. *eLife* 4, 1–35. <https://doi.org/10.7554/eLife.09560>.
- Bibi, F., Souron, A., Bocherens, H., Uno, K., Boissier, J.R., 2013. Ecological change in the lower Omo Valley around 2.8 Ma. *Biol. Lett.* 9, 20120890. <https://doi.org/10.1098/rsbl.2012.0890>.
- Blondel, C., Merceron, G., Andossa, L., Taisso, M.H., Vignaud, P., Brunet, M., 2010. Dental mesowear analysis of the late Miocene Bovidae from Toros-Menala (Chad) and early hominid habitats in Central Africa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 292, 184–191. <https://doi.org/10.1016/j.palaeo.2010.03.042>.
- Blondel, C., Merceron, G., Rowan, J., Surault, J., Boissier, J.-R., 2022. Dietary ecology of Reduncini (Bovidae) from the Shungura Formation, lower Omo Valley, Ethiopia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 587. <https://doi.org/10.1016/j.palaeo.2021.110789>.
- Blondel, C., Rowan, J., Merceron, G., Bibi, F., Negash, E., Barr, W.A., Boissier, J.-R., 2018. Feeding ecology of Tragelaphini (Bovidae) from the Shungura Formation, Omo Valley, Ethiopia: Contribution of dental wear analyses. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 496, 103–120. <https://doi.org/10.1016/j.palaeo.2018.01.027>.
- Blumenthal, S.A., Levin, N.E., Brown, F.H., Brugal, J.P., Chritz, K.L., Harris, J.M., Jehle, G.E., Cerling, T.E., 2017. Aridity and hominin environments. *Proc. Natl. Acad. Sci. USA* 114, 7331–7336. <https://doi.org/10.1073/pnas.1700597114>.
- Bobe, R., Behrensmeyer, A.K., Chapman, R.E., 2002. Faunal change, environmental variability and late Pliocene hominin evolution. *J. Hum. Evol.* 42, 475–497. <https://doi.org/10.1006/jhev.2001.0535>.
- Bobe, R., Behrensmeyer, A.K., Chapman, R.E., 2007. Patterns of abundance and diversity in late Cenozoic bovids from the Turkana and Hadar Basins, Kenya and Ethiopia. In: Bobe, R., Alemseged, Z., Behrensmeyer, A.K. (Eds.), *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence*. Springer, Dordrecht, The Netherlands, pp. 129–157.
- Bobe, R., Eck, G.G., 2001. Responses of African bovids to Pliocene climatic change. *Paleobiology* 27, 1–48. <https://doi.org/10.1666/0094-8373>.
- Brain, C.K., 1993. Structure and stratigraphy of the Swartkrans cave in the light of the new excavations. In: Brain, C.K. (Ed.), *Swartkrans: A Cave's Chronicle of Early Man*. Transvaal Museum, Pretoria, pp. 23–33.
- Brain, C.K., Watson, V., 1992. A guide to the Swartkrans early hominid cave site. *Ann. Transv. Mus.* 35, 343–365.

- Brophy, J.K., de Ruiter, D., Fortelius, M., Bamford, M., Berger, L.R., 2016. Pleistocene Bovidae (Mammalia) from Malapa, Gauteng province, South Africa. *Palaeontol. Electron.* 19, 1–22.
- Castello, J.R., 2016. *Bovids of the World: Antelopes, Gazelles, Cattle, Goats, Sheep, and Relatives*. Princeton University Press.
- Cerling, B.W., Harris, J., Leakey, M.G., 1999. Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. *Oecologia* 120, 364–374.
- Cerling, T.E., Manthi, F.K., Mbua, E.N., Leakey, L.N., Leakey, M.G., Leakey, R.E., Brown, F.H., Grine, F.E., Hart, J.A., Kalemie, P., Roche, H., Uno, K.T., Wood, B.A., 2013. Stable isotope-based diet reconstructions of Turkana Basin hominins. *Proc. Natl. Acad. Sci. USA* 110, 10501–10506. <https://doi.org/10.1073/pnas.1222568110>.
- Cerling, T.E., Mbua, E., Kirera, F.M., Manthi, F.K., Grine, F.E., Leakey, M.G., Sponheimer, M., Uno, K.T., 2011. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proc. Natl. Acad. Sci. USA* 108, 9337–9341. <https://doi.org/10.1073/pnas.1104627108>.
- Churcher, C.S., Watson, V., 1993. Additional fossil equidae from Swartkrans. In: Brain, C. K. (Ed.), *Swartkrans: A Cave's Chronicle of Early Man*. Transvaal Museum, Pretoria, pp. 137–150.
- Clarke, P.U., Alley, R.B., Pollard, D., 1999. Northern Hemisphere ice-sheet influences on global climate change. *Science* 286, 1104–1111.
- Codron, D., Hofmann, R.R., Clauss, M., 2019. Morphological and physiological adaptations for browsing and grazing. In: Gordon, I.J., Prins, H.H.T. (Eds.), *The Ecology of Browsing and Grazing II*. Springer, Cham, Switzerland, pp. 81–125.
- Codron, D., Luyt, C.J., Lee-Thorp, J., Sponheimer, M., de Ruiter, D., Codron, J., 2005. Utilization of savanna-based resources by Plio-Pleistocene baboons. *S. Afr. J. Sci.* 101, 245–248.
- Curnoe, D., Grun, R., Taylor, L., Thackeray, F., 2001. Direct ESR dating of a Pliocene hominin from Swartkrans. *J. Hum. Evol.* 40, 379–391. <https://doi.org/10.1006/jhev.2000.0459>.
- Damuth, J., Janis, C.M., 2014. A comparison of observed molar wear rates in extant herbivorous mammals. *Ann. Zool. Fenn.* 51, 188–200. <https://doi.org/10.5735/086.051.0219>.
- Delson, E., 1984. *Cercopithecoid biochronology of the African plio-pleistocene: correlation among eastern and southern hominid-bearing localities*. Cour. Forsch.-Inst. Senckenberg 69, 199–218.
- Delson, E., 1988. Chronology of South African australopith site units. In: Grine, F.E. (Ed.), *Evolutionary History of the Robust Australopithecines*. Aldine De Gruyter, New York, pp. 317–324.
- de Ruiter, D., 2003. Revised faunal lists for members 1-3 of Swartkrans, South Africa. *Ann. Transv. Mus.* 40, 29–41.
- de Ruiter, D., Pickering, R., Steininger, C.M., Kramers, J.D., Hancox, P.J., Churchill, S.E., Berger, L.R., Backwell, L., 2009. New *Australopithecus robustus* fossils and associated U-Pb dates from Cooper's Cave (Gauteng, South Africa). *J. Hum. Evol.* 56, 497–513. <https://doi.org/10.1016/j.jhevol.2009.01.009>.
- de Ruiter, D.J., Sponheimer, M., Lee-Thorp, J.A., 2008. Indications of habitat association of *Australopithecus robustus* in the Bloubank Valley, South Africa. *J. Hum. Evol.* 55, 1015–1030. <https://doi.org/10.1016/j.jhevol.2008.06.003>.
- deMenocal, P.B., 1995. Plio-pleistocene African climate. *Science* 270, 53–59.
- deMenocal, P.B., 2004. African climate change and faunal evolution during the Pliocene–Pleistocene. *Earth Planet. Sci. Lett.* 220, 3–24. [https://doi.org/10.1016/s0012-821x\(04\)00003-2](https://doi.org/10.1016/s0012-821x(04)00003-2).
- deMenocal, P.B., Rind, D., 1993. Sensitivity of Asian and African climate to variations in seasonal insolation, glacial ice cover, sea surface temperature, and Asian orography. *J. Geophys. Res.* 98 (D4), 7265–7287.
- Desantis, L.R., Schubert, B.W., Scott, J.R., Ungar, P.S., 2012. Implications of diet for the extinction of saber-toothed cats and American lions. *PLoS One* 7, e52453. <https://doi.org/10.1371/journal.pone.0052453>.
- DeSantis, L.R., Fortelius, M., Grine, F.E., Janis, C., Kaiser, T.M., Merceron, G., Purnell, M. A., Schulz-Kornas, E., Saarinen, J., Teaford, M., Ungar, P.S., 2018. The phylogenetic signal in tooth wear: what does it mean? *Ecol. Evol.* 8 (22), 11359–11362.
- Dirks, P., Kibbi, J.M., Kuhn, B.F., Steininger, C., Churchill, S.E., Kramers, J.D., Pickering, R., Farber, D.L., Meriaux, A., Herries, A.I., King, G., Berger, L.R., 2010. Geological setting and age of *Australopithecus sediba* from Southern Africa. *Science* 328, 205–208.
- Dodd Jr., J.R., Stanton, R.J., 1990. *Paleoecology: Concepts and Applications*. John Wiley & Sons, New York.
- Dumouchel, L., Bobe, R., 2020. Paleoenvironmental implications of dental mesowear and hypodonty in fossil ungulates from Kanapoi. *J. Hum. Evol.* 140, 102548.
- Edwards, T.R., Armstrong, B.J., Birkett-Rees, J., Blackwood, A.F., Herries, A.I.R., Penzo-Kajewski, P., Pickering, R., Adams, J.W., 2019. Combining legacy data with new drone and DGPS mapping to identify the provenance of Plio-Pleistocene fossils from Bolt's Farm, Cradle of Humankind (South Africa). *PeerJ* 7, e6202. <https://doi.org/10.7717/peerj.e6202>.
- Edwards, T.R., Pickering, R., Mallett, T.L., Herries, A.I., 2020. Reconstructing the depositional history and age of fossil-bearing palaeokarst: a multidisciplinary example from the terminal Pliocene Aves Cave complex, Bolt's farm, South Africa. *Results Geophys. Sci.* 1–4. <https://doi.org/10.1016/j.rggs.2020.100005>.
- Edwards, T.R., Pickering, R., Mallett, T.L., Herries, A.I.R., 2023. Challenging the antiquity of the Cradle of Humankind, South Africa: Geochronological evidence restricts the age of *Eurotamys bolti* and *Parapapiro* to less than 2.3 Ma at Waypoint 160, Bolt's Farm. *J. Hum. Evol.* 178, 103334. <https://doi.org/10.1016/j.jhevol.2023.103334>.
- Elton, S., 2001. Locomotor and habitat classifications of Cercopithecoid postcranial material from Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2, South Africa. *Palaeontol. Afr.* 37.
- Feibel, C.S., 1999. Basin evolution, sedimentary dynamics and hominid habitats in East Africa: an ecosystem approach. In: Bromage, T.G., Schrenk, F. (Eds.), *African Biogeography, Climate Change, and Human Evolution*. Oxford University Press, Oxford, pp. 276–281.
- Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *Am. Mus. Novit.* 3301, 1–36.
- Fraser, D., Haupt, R.J., Barr, W.A., 2018. Phylogenetic signal in tooth wear dietary niche proxies. *Ecol. Evol.* 8, 5355–5368.
- Frost, S.R., White, F.J., Reda, H.G., Gilbert, C.C., 2022. Biochronology of South African hominin-bearing sites: a reassessment using cercopithecoid primates. *Proc. Natl. Acad. Sci. USA* 119, e2210627119. <https://doi.org/10.1073/pnas.2210627119>.
- Gibbon, R.J., Pickering, T.R., Sutton, M.B., Heaton, J.L., Kuman, K., Clarke, R.J., Brain, C.K., Granger, D.E., 2014. Cosmogenic nuclide burial dating of hominin-bearing Pleistocene cave deposits at Swartkrans, South Africa. *Quat. Geochronol.* 24, 10–15. <https://doi.org/10.1016/j.quageo.2014.07.004>.
- Gilbert, C.C., Steininger, C.M., Kibbi, J.M., Berger, L.R., 2015. Papio cranium from the hominin-bearing site of Malapa: Implications for the evolution of modern baboon cranial morphology and South African Plio-Pleistocene biochronology. *PLOS ONE* 10, e0133361. <https://doi.org/10.1371/journal.pone.0133361>.
- Granger, D.E., Gibbon, R.J., Kuman, K., Clarke, R.J., Bruxelles, L., Caffee, M.W., 2015. New cosmogenic burial ages for Sterkfontein Member 2 *Australopithecus* and Member 5 Oldowan. *Nature* 522, 85–88. <https://doi.org/10.1038/nature14268>.
- Green, J.L., Croft, D.A., 2018. Using dental mesowear and microwear for dietary inference: a review of current techniques and applications. *Methods Paleoccol.* 53–73.
- Hammer, Ø., Harper, D.A., 2001. Past: paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* 4, 1.
- Hanon, R., Pean, S., Prat, S., Rector, A.L., Steininger, C., 2022. Fossil Bovidae from the Hominini-bearing site of Cooper's D (Bloubank Valley, South Africa): implications for *Paranthropus robustus* Broom, 1938 and early Homo Linnaeus, 1758 habitat preferences. *C. R. Palevol* 21, 431–450. <https://doi.org/10.5852/cr-palevol2022v21a21>.
- Henry, A.G., Ungar, P.S., Passey, B.H., Sponheimer, M., Rossouw, L., Bamford, M., Sandberg, P., de Ruiter, D.J., Berger, L., 2012. The diet of *Australopithecus sediba*. *Nature* 487, 90–93. <https://doi.org/10.1038/nature11185>.
- Herries, A.I., Curnoe, D., Adams, J.W., 2009. A multi-disciplinary seriation of early *Homo* and *Paranthropus* bearing palaeocaves in southern Africa. *Quat. Int.* 202, 14–28. <https://doi.org/10.1016/j.quaint.2008.05.017>.
- Herries, A.I., Shaw, J.C., 2011. Palaeomagnetic analysis of the Sterkfontein palaeocave deposits: implications for the age of the hominin fossils and stone tool industries. *J. Hum. Evol.* 60, 523–539. <https://doi.org/10.1016/j.jhevol.2010.09.001>.
- Herries, A.I., Kappens, P., Kegley, A.D.T., Patterson, D., Howard, D.L., De Jonge, M.D., Potze, S., Adams, J.W., 2014. Palaeomagnetic and synchrotron analysis of >1.95 Ma fossilbearing palaeokarst at Haasgat, South Africa. *S. Afr. J. Sci.* 110, 1–12. <https://doi.org/10.1590/sajs.2014/20130102>.
- Herries, A.I.R., Martin, J.M., Leece, A., Adams, J.W., Boschian, G., Joannes-Boyau, R., Edwards, T.R., Mallett, T., Massey, J., Murszewski, A., Neubauer, S., Pickering, R., Strait, D.S., Armstrong, B.J., Baker, S., Caruana, M., Denham, T., Hellstrom, J., Moggi-Cecchi, J., Mokobane, S., Penzo-Kajewski, P., Rovinsky, D.S., Schwartz, G.T., Stammers, R.C., Wilson, C., Woodhead, J., Menter, C.G., 2020. Contemporaneity of *Australopithecus*, *Paranthropus*, and early *Homo erectus* in South Africa. *Science* 368. <https://doi.org/10.1126/science.aaw7293>.
- Kaiser, T.M., 2011. Feeding ecology and niche partitioning of the Laetoli ungulate faunas. In: Harrison, T. (Ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context*. Vol. I: Geology, Geochronology, Paleoecology and Paleoenvironment. Springer, Berlin, Germany, pp. 329–354.
- Kaiser, T.M., Brasch, J., Castell, J.C., Schulz, E., Clauss, M., 2009. Tooth wear in captive wild ruminant species differs from that of free-ranging conspecifics. *Mamm. Biol.* 74, 425–437. <https://doi.org/10.1016/j.mambio.2008.09.003>.
- Kaiser, T.M., Clauss, M., Schulz-Kornas, E., 2016. A set of hypotheses on tribology of mammalian herbivore teeth. *Surf Topogr Metrol Prop* 4. <https://doi.org/10.1088/2051-672x/4/1/014003>.
- Kaiser, T.M., Fortelius, M., 2003. Differential mesowear in occluding upper and lower molars: opening mesowear analysis for lower molars and premolars in hypodont horses. *J. Morphology* 258, 67–83. <https://doi.org/10.1002/jmor.10125>.
- Kaiser, T.M., Müller, D.W.H., Fortelius, M., Schulz, E., Codron, D., Clauss, M., 2013. Hypodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates: implications for understanding tooth wear. *Mammal Rev.* 43, 34–46. <https://doi.org/10.1111/j.1365-2907.2011.00203.x>.
- Kaiser, T.M., Schulz, E., 2006. Tooth wear gradients in zebra as an environmental proxy – a pilot study. *Mitt. Hamb. Zool. Mus. Inst.* 103, 187–210.
- Kaiser, T.M., Solounias, N., 2003. Extending the tooth mesowear method to extinct and extant equids. *Geodiversitas* 25, 321–345.
- Kaiser, T.M., Solounias, N., Fortelius, M., Bernor, R.L., Schrenk, F., 2000. Tooth mesowear analysis on *Hippotherium primigenium* from the Vallesian Dinotherien-sande (Germany) - a blind study. *Carolinae* 58, 103–114.
- Karme, A., Rannikko, J., Kallonen, A., Clauss, M., Fortelius, M., 2016. Mechanical modelling of tooth wear. *J. R. Soc. Interface* 13. <https://doi.org/10.1098/rsif.2016.0399>.
- Kaya, F., Bibi, F., Zilobaite, I., Eronen, J.T., Hui, T., Fortelius, M., 2018. The rise and fall of the Old World savannah fauna and the origins of the African savannah biome. *Nat. Ecol. Evol.* 2, 241–246. <https://doi.org/10.1038/s41559-017-0414-1>.
- Keyser, A.W., 1991. The palaeontology of Haasgat: a preliminary account. *Palaeontol. Afr.* 28, 29–33.

- Kubo, M.O., Yamada, E., 2014. The inter-relationship between dietary and environmental properties and tooth wear: comparisons of mesowear, molar wear rate, and hypsodonty index of extant Sika deer populations. *PLoS One* 9, e90745. <https://doi.org/10.1371/journal.pone.0090745>.
- Kuhn, B.F., Hartstone-Rose, A., Lacruz, R.S., Herries, A.I.R., Werdelin, L., Bamford, M.K., Berger, L.R., 2016. The carnivore guild circa 1.98 million years: biodiversity and implications for the palaeoenvironment at Malapa, South Africa. *Palaeobiodivers. Palaeoenviron.* 96, 611–616. <https://doi.org/10.1007/s12549-016-0245-0>.
- Kuhn, B.F., Werdelin, L., Hartstone-Rose, A., Lacruz, R.S., Berger, L.R., 2011. Carnivore remains from the Malapa hominin site, South Africa. *PLoS One* 6, e26940. <https://doi.org/10.1371/journal.pone.0026940>.
- Kuhn, B.F., Werdelin, L., Steininger, C., 2017. Fossil Hyaenidae from Cooper's Cave, South Africa, and the palaeoenvironmental implications. *Palaeobiodivers. Palaeoenviron.* 97, 355–365. <https://doi.org/10.1007/s12549-016-0247-y>.
- Kuman, K., Clarke, R.J., 2000. Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. *J. Hum. Evol.* 38, 827–847. <https://doi.org/10.1006/jhev.1999.0392>.
- Kuman, K., Granger, D.E., Gibbon, R.J., Pickering, T.R., Caruana, M.V., Bruxelles, L., Clarke, R.J., Heaton, J.L., Stratford, D., Brain, C.K., 2021. A new absolute date from Swartkrans Cave for the oldest occurrences of *Paranthropus robustus* and Oldowan stone tools in South Africa. *J. Hum. Evol.* 156, 103000. <https://doi.org/10.1016/j.jhevol.2021.103000>.
- Lazagabaster, I.O., Brophy, J.K., Sanisidro, O., Pineda-Munoz, S., Berger, L.R., 2018. A new partial cranium of *Metridiochoerus* (Suidae, Mammalia) from Malapa, South Africa. *J. Afr. Earth Sci.* 145, 49–52. <https://doi.org/10.1016/j.jafrearsci.2018.05.005>.
- Lee-Thorp, J., Van der Merwe, N., 1993. Stable carbon isotope studies of Swartkrans fossils. In: Brain, C.K. (Ed.), *Swartkrans: A Cave's Chronicle of Early Man*. Transvaal Museum Monograph, Pretoria, pp. 251–256.
- Lee-Thorp, J., Van der Merwe, N.J., Brain, C.K., 1989. Isotopic evidence for dietary differences between two extinct baboon species from Swartkrans. *J. Hum. Evol.* 18, 183–189.
- Lee-Thorp, J., van der Merwe, N.J., Brain, C.K., 1994. Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotopic analysis. *J. Hum. Evol.* 27, 361–372.
- Lee-Thorp, J.A., Sponheimer, M., Luyt, C.J., 2007. Tracking changing environments using stable carbon isotopes in fossil tooth enamel: an example from the south African hominin sites. *J. Hum. Evol.* 53, 595–601. <https://doi.org/10.1016/j.jhevol.2006.11.020>.
- Leichliter, J., Sandberg, P., Passey, B., Codron, D., Avenant, N.L., Paine, O.C.C., Codron, J., de Ruiter, D., Sponheimer, M., 2017. Stable carbon isotope ecology of small mammals from the Sterkfontein Valley: Implications for habitat reconstruction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 485, 57–67. <https://doi.org/10.1016/j.palaeo.2017.06.003>.
- Lepre, C.J., Quinn, R.L., 2022. Aridification and orbital forcing of eastern African climate during the Plio-Pleistocene. *Glob. Planet. Chang.* 208. <https://doi.org/10.1016/j.gloplacha.2021.103684>.
- Levin, N.E., Quade, J., Simpson, S.W., Semaw, S., Rogers, M., 2004. Isotopic evidence for Plio-Pleistocene environmental change at Gona, Ethiopia. *Earth Planet. Sci. Lett.* 219, 93–110. [https://doi.org/10.1016/s0012-821x\(03\)00707-6](https://doi.org/10.1016/s0012-821x(03)00707-6).
- Lupien, R.L., Russell, J.M., Yost, C.L., Kingston, J.D., Deino, A.L., Logan, J., Schuh, A., Cohen, A.S., 2021. Vegetation change in the Baringo Basin, East Africa across the onset of Northern Hemisphere glaciation 3.3–2.6 Ma. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 570. <https://doi.org/10.1016/j.palaeo.2019.109426>.
- Luyt, C.J., 2001. Revisiting the palaeoenvironments of the South African hominid-bearing plio-pleistocene sites: new isotopic evidence from sterkfontein. PhD thesis, University of Cape Town, South Africa.
- Luyt, C.J., Lee-Thorp, J., 2003. Carbon isotope ratios of Sterkfontein fossils indicate a marked shift to open environments c. 1.7 Myr ago. *S. Afr. J. Sci.* 99, 271–273.
- Marín-Leyva, A.H., DeMiguel, D., García-Zepeda, M.L., Ponce-Saaedra, J., Arroyo-Cabrales, J., Schaaf, P., Alberdi, M.T., 2016. Dietary adaptability of late Pleistocene Equus from West Central Mexico. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 441, 748–757. <https://doi.org/10.1016/j.palaeo.2015.10.019>.
- Martin, J.M., Leece, A.B., Neubauer, S., Baker, S.E., Mongle, C.S., Boschian, G., Schwartz, G.T., Smith, A.L., Ledogar, J.A., Strait, D.S., Herries, A.I.R., 2021. Drimolen cranium DNH 155 documents microevolution in an early hominin species. *Nat. Ecol. Evol.* 5, 38–45. <https://doi.org/10.1038/s41559-020-01319-6>.
- McKee, J.K., 1991. Palaeo-ecology of the Sterkfontein hominids: a review and synthesis. *Palaeontol. Afr.* 28, 41–51.
- Merceron, G., Schulz, E., Kordos, L., Kaiser, T., 2007. Paleoenvironment of *Dryopithecus brancoi* at Rudabanya, Hungary: evidence from dental meso- and micro-wear analyses of large vegetarian mammals. *J. Hum. Evol.* 53, 331–349.
- Mihlbachler, M.C., Solounias, N., 2006. Coevolution of tooth crown height and diet in oreodonts (merycoidodontidae, artiodactyla) examined with phylogenetically independent contrasts. *J. Mamm. Evol.* 13, 11–36. <https://doi.org/10.1007/s10914-005-9001-3>.
- Moggi-Cecchi, J., Menter, C., Bocccone, S., Keyser, A.W., 2010. Early hominin dental remains from the Plio-Pleistocene site of Drimolen, South Africa. *J. Hum. Evol.* 58, 374–405. <https://doi.org/10.1016/j.jhevol.2010.01.006>.
- Murszewski, A., Boschian, G., Herries, A.I.R., 2020. Complexities of assessing palaeocave stratigraphy: reconstructing site formation of the approximately 2.61 Ma Drimolen Makondo fossil site. *PeerJ* 8, e10360. <https://doi.org/10.7717/peerj.10360>.
- Negash, E.W., Barr, W.A., 2023. Relative abundance of grazing and browsing herbivores is not a direct reflection of vegetation structure: implications for hominin paleoenvironmental reconstruction. *J. Hum. Evol.* 177, 103328. <https://doi.org/10.1016/j.jhevol.2023.103328>.
- O'Regan, H.J., Steininger, C., 2017. Felidae from Cooper's Cave, South Africa (Mammalia: Carnivora). *Geodiversitas* 39, 315–332. <https://doi.org/10.5252/g2017n2a8>.
- Paine, O.C.C., Koppa, A., Henry, A.G., Leichliter, J.N., Codron, D., Codron, J., Lambert, J. E., Sponheimer, M., 2019. Seasonal and habitat effects on the nutritional properties of savanna vegetation: potential implications for early hominin dietary ecology. *J. Hum. Evol.* 133, 99–107. <https://doi.org/10.1016/j.jhevol.2019.01.003>.
- Partridge, T.C., 2005. Dating of the Sterkfontein hominids: progress and possibilities. *Trans. R. Soc. S. Afr.* 60, 107–109. <https://doi.org/10.1080/00359190509520486>.
- Pavia, M., Val, A., Carrera, L., Steininger, C.M., 2022. Fossil birds from Cooper's Cave in reconstructing the early Pleistocene paleoenvironment in the Cradle of Humankind (Gauteng, South Africa). *J. Hum. Evol.* 167, 103185. <https://doi.org/10.1016/j.jhevol.2022.103185>.
- Peterson, A., Abella, E.F., Teaford, M.F., Ungar, P.S., 2018. Microwear textures of *Australopithecus africanus* and *Paranthropus robustus* molars in relation to paleoenvironment and diet. *J. Hum. Evol.* 119, 42–63. <https://doi.org/10.1016/j.jhevol.2018.02.004>.
- Pickering, R., Hancock, P.J., Lee-Thorp, J.A., Grun, R., Mortimer, G.E., McCulloch, M., Berger, L.R., 2007. Stratigraphy, U-Th chronology, and paleoenvironments at Gladysvale Cave: insights into the climatic control of South African hominin-bearing cave deposits. *J. Hum. Evol.* 53, 602–619. <https://doi.org/10.1016/j.jhevol.2007.02.005>.
- Pickering, R., Herries, A.I., 2022. New multi-disciplinary age estimates for the Sterkfontein Member 4 australopithecines. In: Ward, C., Richmond, B., Zipfel, B. (Eds.), *Hominin Postcranial Remains from Sterkfontein, South Africa*. Oxford University Press, Oxford, pp. 21–30.
- Pickering, R., Herries, A.I.R., Woodhead, J.D., Hellstrom, J.C., Green, H.E., Paul, B., Ritzman, T., Strait, D.S., Schoville, B.J., Hancock, J.P., 2019. U-Pb-dated flowstones restrict South African early hominin record to dry climate phases. *Nature* 565, 226–229. <https://doi.org/10.1038/s41586-018-0711-0>.
- Pickering, R., Kramers, J.D., 2010. Re-appraisal of the stratigraphy and determination of new U-Pb dates for the Sterkfontein hominin site, South Africa. *J. Hum. Evol.* 59, 70–86. <https://doi.org/10.1016/j.jhevol.2010.03.014>.
- Pickering, R., Kramers, J.D., Hancock, P.J., de Ruiter, D., Woodhead, J.D., 2011a. Contemporary flowstone development links early hominin bearing cave deposits in South Africa. *Earth Planet. Sci. Lett.* 306, 23–32. <https://doi.org/10.1016/j.epsl.2011.03.019>.
- Pickering, R., Dirks, P.H., Jinnah, Z., De Ruiter, D.J., Churchill, S.E., Herries, A.I., Woodhead, J.D., Hellstrom, J.C., Berger, L.R., 2011b. *Australopithecus sediba* at 1.977 Ma and implications for the origins of the genus *Homo*. *Science* 333 (6048), 1421–1423.
- Pickering, T.R., 1999. *Taphonomic Interpretations of the Sterkfontein Early Hominid Site (Gauteng, South Africa) Reconsidered in Light of Recent Evidence*. PhD thesis, The University of Wisconsin, Madison, WI, USA.
- Pickering, T.R., Heaton, J.L., Clarke, R.J., Sutton, M.B., Brain, C.K., Kuman, K., 2012. New hominin fossils from Member 1 of the Swartkrans formation, South Africa. *J. Hum. Evol.* 62, 618–628. <https://doi.org/10.1016/j.jhevol.2012.02.003>.
- Plug, I., Keyser, A.W., 1994. Haasgat cave, a Pleistocene site in the Central Transvaal: geomorphological, faunal and taphonomic considerations. *Ann. Transv. Mus.* 39, 139–145.
- Potts, R., 1998. Variability selection in hominin evolution. *Evol. Anthropol.* 7, 81–96.
- Quinn, R.L., Lepre, C.J., Wright, J.D., Feibel, C.S., 2007. Paleogeographic variations of pedogenic carbonate delta 13C values from Koobi Fora, Kenya: implications for floral compositions of Plio-Pleistocene hominin environments. *J. Hum. Evol.* 53, 560–573. <https://doi.org/10.1016/j.jhevol.2007.01.013>.
- R Core Team R, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ravelo, A., Andreassen, D., Lyle, M., Lyle, A., Wara, M., 2004. Regional climate shifts caused by gradual global cooling in the Pliocene epoch. *Nature* 429, 263–267.
- Reed, K.E., 1997. Early hominin evolution and ecological change through the African Plio-Pleistocene. *J. Hum. Evol.* 289–322.
- Reed, K.E., 2008. Paleoenvironmental patterns at the Hadar hominin site, Afar Regional State, Ethiopia. *J. Hum. Evol.* 54, 743–768. <https://doi.org/10.1016/j.jhevol.2007.08.013>.
- Reed, K.E., 2013. Multiproxy paleoecology: Reconstructing evolutionary context in paleoanthropology. In: Begun, D.R. (Ed.), *A Companion to Paleoanthropology*. Blackwell Publishing, Hoboken, NJ, pp. 203–225.
- Reynolds, S.C., Kibii, J.M., 2011. Sterkfontein at 75: review of palaeoenvironments, fauna and archaeology from the hominin site of Sterkfontein (Gauteng Province, South Africa). *Palaeontol. Afr.* 46, 59–88.
- Rivals, F., Mihlbachler, M.C., Solounias, N., 2007. Effect of ontogenetic-age distribution in fossil and modern samples on the interpretation of ungulate paleodiets using the mesowear method. *J. Vertebr. Paleontol.* 27, 763–767.
- Rivals, F., Schulz, E., Kaiser, T.M., 2009. A new application of dental wear analyses: estimation of duration of hominin occupations in archaeological localities. *J. Hum. Evol.* 56, 329–339. <https://doi.org/10.1016/j.jhevol.2008.11.005>.
- Rose, C., Polissar, P.J., Tierney, J.E., Filley, T., deMenocal, P.B., 2016. Changes in northeast African hydrology and vegetation associated with Pliocene–Pleistocene sapropel cycles. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 371.
- Rovinsky, D.S., Herries, A.I., Menter, C.G., Adams, J.W., 2015. First description of in situ primate and faunal remains from the Plio-Pleistocene Drimolen Makondo palaeocave infill, Gauteng, South Africa. *Palaeontol. Electron.* 18, 1–21.
- Schubert, B.W., 2007. Dental mesowear and the paleodiets of bovids from Makapansgat Limeworks Cave, South Africa. *Palaeontol. Afr.* 42, 43–50.
- Schubert, B.W., Ungar, P.S., Sponheimer, M., Reed, K.E., 2006. Microwear evidence for Plio-Pleistocene bovid diets from Makapansgat Limeworks cave, South Africa.

- Palaeogeogr. Palaeoclimatol. Palaeoecol. 241, 301–319. <https://doi.org/10.1016/j.palaeo.2006.04.004>.
- Schuette, J., Leslie, D., Lochmiller, R., Jenks, J., 1998. Diets of hartebeest and roan antelope in Burkina Faso: support of the long-faced hypothesis. *J. Mammal.* 79, 426–436.
- Schulz, E., Kaiser, T.M., 2012. Historical distribution, habitat requirements and feeding ecology of the genus *Equus* (Perissodactyla). *Mammal Rev.* 43, 111–123. <https://doi.org/10.1111/j.1365-2907.2012.00210.x>.
- Schwarzch, H.P., Grun, R., Tobias, P.V., 1994. ESR dating studies of the australopithecine site of Sterkfontein, South Africa. *J. Hum. Evol.* 26, 175–181. <https://doi.org/10.1006/jhev.1994.1010>.
- Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M.F., Walker, A., 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436, 693–695. <https://doi.org/10.1038/nature03822>.
- Sewell, L., Mercer, G., Hopley, P., Zipfel, B., Reynolds, S.C., 2019. Using springbok (*Antidorcas*) dietary proxies to reconstruct inferred palaeovegetational changes over 2 million years in Southern Africa. *J. Archaeol. Sci. Rep.* 23, 1014–1028. <https://doi.org/10.1016/j.jasrep.2018.02.009>.
- Shackleton, N.J., Berger, A., Peltier, W., 1990. An alternative astronomical calibration of the lower Pleistocene timescale based on ODP Site 677. *Earth Environ. Sci. Trans. R. Soc. Edinb.* 81, 251–261.
- Sponheimer, M., Daegling, D.J., Ungar, P.S., Bobe, R., Paine, O.C.C., 2023. Problems with *Paranthropus*. *Quat. Int.* 650, 40–51. <https://doi.org/10.1016/j.quaint.2022.03.024>.
- Sponheimer, M., Passey, B., de Ruiter, D., Guatelli-Steinberg, D., Cerling, T.E., Lee-Thorp, J., 2006. Isotopic evidence for dietary variability in the early hominin *Paranthropus robustus*. *Science* 314, 980–982.
- Sponheimer, M., Reed, K.E., Lee-Thorp, J., 1999. Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominin locality. *J. Hum. Evol.* 36, 705–718.
- Sponheimer, M., Reed, K.E., Lee-Thorp, J., 2001. Isotopic palaeoecology of Makapansgat Limeworks Perissodactyla. *S. Afr. J. Sci.* 97, 327–329.
- Steininger, C., 2011. The dietary behaviour of early Pleistocene bovids from Cooper's Cave and Swartkrans, South Africa. PhD thesis. University of the Witwatersrand, Johannesburg, South Africa.
- Steininger, C., Berger, L.R., Kuhn, B.F., 2008. A partial skull of *Paranthropus robustus* from Cooper's Cave, South Africa. *S. Afr. J. Sci.* 104, 143–146.
- Stynder, D.D., 2009. The diets of ungulates from the hominid fossil-bearing site of Elandsfontein, Western Cape, South Africa. *Quat. Res.* 71, 62–70. <https://doi.org/10.1016/j.yqres.2008.06.003>.
- Stynder, D.D., 2011. Fossil bovid diets indicate a scarcity of grass in the Langebaanweg E quarry (South Africa) late Miocene/early Pliocene environment. *Paleobiology* 37, 126–139.
- Tiedemann, R., Sarnthein, M., Shackleton, N., 1994. Astronomic timescale for the Pliocene Atlantic 180 and dust flux records of Ocean Drilling Program site 659. *Paleoceanography* 9, 619–638.
- Trauth, M., Maslin, M., Deino, A., Strecker, M., 2005. Late Cenozoic Moisture history of East Africa. *Science* 309, 2051–2053.
- Trauth, M.H., Asrat, A., Berner, N., Bibi, F., Foerster, V., Grove, M., Kaboth-Bahr, S., Maslin, M.A., Mudelsee, M., Schäbitz, F., 2021. Northern Hemisphere Glaciation, African climate and human evolution. *Quat. Sci. Rev.* 268. <https://doi.org/10.1016/j.quascirev.2021.107095>.
- Ungar, P., 2010. *Mammal Teeth: Origin, Evolution, and Diversity*. Johns Hopkins University Press, Baltimore.
- Ungar, P., Sponheimer, M., 2011. The Diets of early Hominins. *Science* 334, 190–193.
- Ungar, P.S., 2015. Mammalian dental function and wear: a review. *Biosurf. Biotribol.* 1, 25–41. <https://doi.org/10.1016/j.bsb.2014.12.001>.
- Uno, K.T., Polissar, P.J., Jackson, K.E., deMenocal, P.B., 2016a. Neogene biomarker record of vegetation change in eastern Africa. *Proc. Natl. Acad. Sci. USA* 113, 6355–6363. <https://doi.org/10.1073/pnas.1521267113>.
- Uno, K.T., Polissar, P.J., Kahle, E., Feibel, C.S., Harmand, S., Helene, R., deMenocal, P., 2016b. A Pleistocene palaeovegetation record from plant wax biomarkers from the Nachukui Formation, West Turkana, Kenya. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 371. <https://doi.org/10.1098/rstb.2015.0235>.
- van der Merwe, N.J., Thackeray, F., 1997. Stable carbon isotope analysis of Plio-Pleistocene ungulate teeth from Sterkfontein, South Africa. *S. Afr. J. Sci.* 93.
- van der Merwe, R.H., Baker, S.E., Kuhn, B.F., 2021. New Viverridae specimens from the Malapa hominin site and their utility as palaeoenvironmental indicators. *Geobios* 68, 109–123. <https://doi.org/10.1016/j.geobios.2021.04.005>.
- van Zyl, W., Badenhorst, S., Brink, J.S., 2016. Pleistocene Bovidae from X Cave on Bolt's Farm in the Cradle of Humankind in South Africa. *Ann. Ditsong Natl. Mus. Nat. Hist.* 6, 39–71.
- Viranta, S., Mannermaa, K., 2014. Mesowear Analysis on Finnish medieval horses. *Ann. Zool. Fenn.* 51, 119–122. <https://doi.org/10.5735/086.051.0213>.
- Vrba, E., 1974. Description and taxonomy of the Swartkrans Member 1 (SKa) Bovidae, 21. *Transvaal Museum Memoirs*.
- Vrba, E., 1975. Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil Bovidae. *Nature* 254, 301–304.
- Vrba, E., 1980. The significance of bovid remains as indicators of environment and predation patterns. In: Behrensmeyer, A.K., Hill, A.P. (Eds.), *Fossils in the Making*. University of Chicago Press, Chicago.
- Vrba, E., 1985. Ecological and adaptive changes associated with early hominid evolution. In: Delson, E. (Ed.), *Ancestors: The Hard Evidence*. Alan R. Liss, New York, New York, pp. 63–71.
- Vrba, E., 1995. The fossil record of African antelopes (mammalia, bovidae) in relation to human evolution and paleoclimate. In: Vrba, E., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 385–424.
- Watson, V., 1993. Composition of the Swartkrans bone accumulations, in terms of skeletal parts and animals represented. In: Brain, C.K. (Ed.), *Swartkrans: A Cave's Chronicle of Early Man*. Transvaal Museum Monograph, Pretoria, pp. 35–74.
- Williams, M.A.J., Williams, F.M., Gasse, F., Curtis, G.H., Adamson, D.A., 1979. Plio-Pleistocene environments at Gadeb prehistoric site, Ethiopia. *Nature* 282, 29–33.
- Winkler, D.E., Schulz-Kornas, E., Kaiser, T.M., De Cuyper, A., Clauss, M., Tutken, T., 2019. Forage silica and water content control dental surface texture in guinea pigs and provide implications for dietary reconstruction. *Proc. Natl. Acad. Sci. USA* 116, 1325–1330. <https://doi.org/10.1073/pnas.1814081116>.
- WoldeGabriel, G., White, T.D., Suwa, G., Renne, P.R., de Heinzelin, J., Hart, W.K., Heiken, G., 1994. Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature* 371, 330–333.
- Wynn, J.G., 2004. Influence of Plio-Pleistocene aridification on human evolution: evidence from paleosols of the Turkana Basin, Kenya. *Am. J. Phys. Anthropol.* 123, 106–118. <https://doi.org/10.1002/ajpa.10317>.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, Rhythms, and Aberrations in Global climate 65 Ma to present. *Science* 292, 686–693.