

The palaeoecological context of the Oldowan–Acheulean in southern Africa

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The influence of climatic and environmental change on human evolution in the Pleistocene epoch is understood largely from extensive East African stable isotope records. These records show increasing proportions of C₄ plants in the Early Pleistocene. We know far less about the expansion of C₄ grasses at higher latitudes, which were also occupied by early *Homo* but are more marginal for C₄ plants. Here we show that both C₃ and C₄ grasses and prolonged wetlands remained major components of Early Pleistocene environments in the central interior of southern Africa, based on enamel stable carbon and oxygen isotope data and associated faunal abundance and phytolith evidence from the site of Wonderwerk Cave. Vegetation contexts associated with Oldowan and early Acheulean lithic industries, in which climate is driven by an interplay of regional rainfall seasonality together with global CO₂ levels, develop along a regional distinct trajectory compared to eastern South Africa and East Africa.

The spread of arid grasslands dominated by C₄ plants is often cited as a driver in the evolution of the genus *Homo* in East Africa^{1–3}. However, some recent research studies have challenged both of these factors of long-term ecological change and their connection to the emergence of *Homo* in the Early Pleistocene^{4,5}. In this study, we propose a different hypothesis for the central interior of southern Africa and conclude that the evolution of the local ecosystem differed markedly from that documented in East Africa. Wonderwerk Cave has the longest temporally stratified sequence associated with hominin occupation in southern Africa⁶ (27° 50′ 46″ S, 23° 33′ 19″ E; Fig. 1; Supplementary Information). The cave is located in the Kuruman hills at the southern end of the Kalahari, currently a summer rainfall area, and is now overlooking an open and semi-arid landscape characterized by a mixture of C₄ grasses and scattered C₃ plants, such as thorn bushes, shrubs and patches of small to medium-sized trees. Research has targeted excavation areas (exc.) 1 and 2, which are 20–30 m into the 140-m long cave, to establish the chronology for the Oldowan (stratum 12, exc. 1), Acheulean (strata 11–6, exc. 1) and early Middle Stone Age (MSA) levels (stratum 2, exc. 2), with complimentary analysis of lithic and faunal assemblages^{7,8} (Supplementary Information). From these deposits, 125 teeth from thirteen mammalian species were sampled for bulk enamel carbon and oxygen isotope analysis. We consider the enamel carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) stable isotope results in combination with published ostrich eggshell (OES) stable isotope data that reflect aridity⁹, and grass silica short cell phytolith¹⁰ and micromammal¹¹ abundance data from the same strata to compare for consistency in trends in the local vegetation across multiple proxies.

Results

In the Early Pleistocene (strata 12–10, exc. 1, 1.95 million years ago (Ma) to 0.99 Ma) average grazer $\delta^{13}\text{C}$ values fall between -5.3‰ and -7.4‰ (Fig. 2, Supplementary Table 1 and Supplementary

Dataset 1), suggesting the consumption of a mix of C₃ and C₄ plants. In detail, samples from Alcelaphini have mean $\delta^{13}\text{C}$ values of $-7.2 \pm 2.3\text{‰}$ ($n=8$, stratum 12), $-6.8 \pm 3.7\text{‰}$ ($n=4$, stratum 11) and $-5.3 \pm 0.8\text{‰}$ ($n=2$, stratum 10). Samples from Equidae have mean $\delta^{13}\text{C}$ values of $-5.7 \pm 2.6\text{‰}$ ($n=10$, stratum 12), $-5.8 \pm 2.6\text{‰}$ ($n=4$, stratum 11) and $-6.1 \pm 2.2\text{‰}$ ($n=5$, stratum 10), whereas springhare (*Pedetes* sp.) is represented by samples of two individuals in stratum 12 with a mean $\delta^{13}\text{C}$ value of $-7.4 \pm 3.0\text{‰}$ (Supplementary Figs. 1,2). As all these taxa are morphologically adapted to grazing and their extant equivalents are all grazers, the results indicate they consumed varied proportions of C₃ and C₄ grasses. Currently, C₃ grasses are not a component of the local vegetation, in which C₄ grasses dominate, a feature characteristic throughout the Holocene¹² (Fig. 2). Grass silica short cell phytolith analysis of sediment samples from stratum 12 indicate that a savannah or Nama-Karoo-type grassland existed compared to the modern morphotype ecology, with warm, locally mesic to dry conditions within a predominantly summer rainfall regime^{6,10}. In the micromammalian record for this period, the relative proportions of Gerbillinae to Murinae reflect a drier and more open environment compared to modern morphotype ecology¹¹. However, beginning in the upper part of stratum 12 and continuing through to stratum 10, the absence of saddle morphotypes and a predominance of C₃-affiliated trapezoid morphotypes in the phytolith record indicate a shift to cooler prevailing conditions and a cooler growing season, with vegetation that is similar to the current Succulent Karoo signifying a year-round rainfall regime, which differs from that prevailing in the region today^{6,10}. Changing proportions of micromammals further indicate a shift to less arid environments in stratum 11 compared to stratum 12, potentially as a result of changing rainfall patterns¹¹. Mean enamel $\delta^{18}\text{O}$ values across all sampled species, reflecting animal water intake and physiology (Supplementary Information), are generally below 36‰, considerably lower than throughout the Holocene for the same species¹² (Fig. 2 and Supplementary Tables 1,5). The lowest

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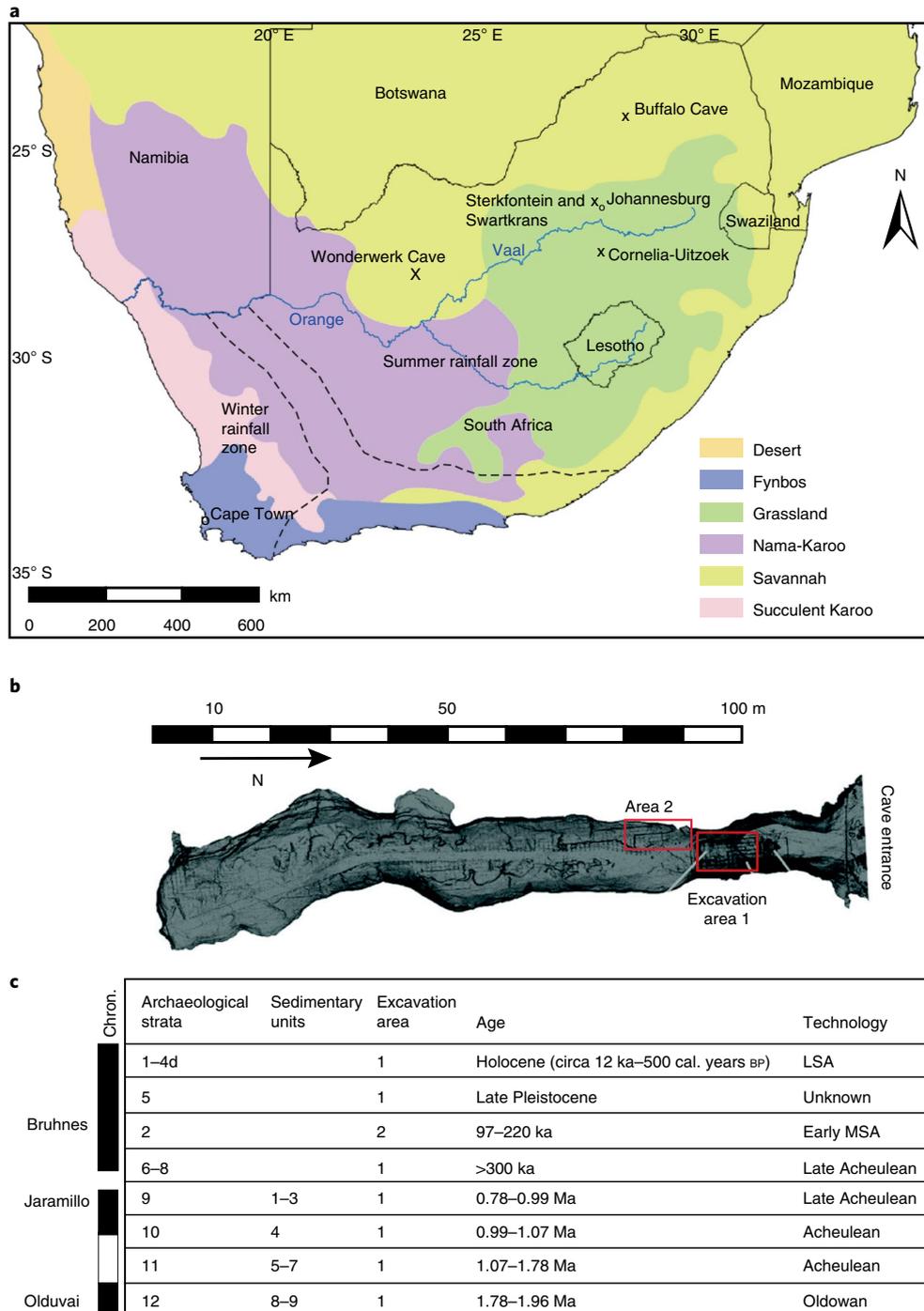


Fig. 1 | Wonderwerk Cave. **a**, Location of Wonderwerk Cave and other sites mentioned in the text within South Africa. The extent of modern biome types and rainfall zones⁴² is indicated. **b**, Laser scan of Wonderwerk Cave with excavation areas 1 and 2 marked. **c**, Stratigraphy of relevant excavation areas from oldest to youngest, including age, palaeomagnetic subchron and associated lithic technology. cal. years BP, calibrated years before present (taken as AD 1950); ka, thousand years ago; LSA, Later Stone Age. Credit: H. Rüter, Zamani Project (**b**).

$\delta^{18}\text{O}$ mean values are in the Early Pleistocene strata (strata 12–10, exc. 1; $25.7\text{--}31.7\text{‰}$), with values in stratum 11 for Alcelaphini (mean $\delta^{18}\text{O}$ $28.8 \pm 2.6\text{‰}$, $n = 4$) and Equidae (mean $\delta^{18}\text{O}$ $26.2 \pm 1.7\text{‰}$, $n = 4$) that are statistically significantly lower compared to the same taxa in the Holocene (Supplementary Table 5). This suggests differences in moisture source and/or rainfall season and, overall, a more humid environment in the Pleistocene. The OES $\delta^{18}\text{O}$ values, although they are suggestive of mostly arid but highly variable conditions (stratum 12 mean $\delta^{18}\text{O}$ $39.4 \pm 1.4\text{‰}$, $n = 5$), show phases of

lower values and hence increased humidity in stratum 11 ($\delta^{18}\text{O}$ 35.2‰ , $n = 1$), 10 (mean $\delta^{18}\text{O}$ $36.0 \pm 2.2\text{‰}$, $n = 16$) and stratum 2, exc. 2^{9,13} (mean $\delta^{18}\text{O}$ $37.1 \pm 4.0\text{‰}$, $n = 18$; Fig. 3). Mean $\delta^{18}\text{O}$ OES values increase from stratum 9 (mean $\delta^{18}\text{O}$ $38.7 \pm 3.7\text{‰}$, $n = 16$) to stratum 6 (mean $\delta^{18}\text{O}$ $40.0 \pm 3.5\text{‰}$, $n = 11$) and are highest in the Holocene^{9,13} (mean $\delta^{18}\text{O}$ $39.0 \pm 3.2\text{‰}$, $n = 196$; Fig. 3). The highest proportions of specimens with low or intermediate $\delta^{13}\text{C}$ values in the enamel isotope record, reflecting C_3 or C_3/C_4 mixed diets occur in stratum 10, whereas phytolith data similarly suggest cool C_3/C_4 grass

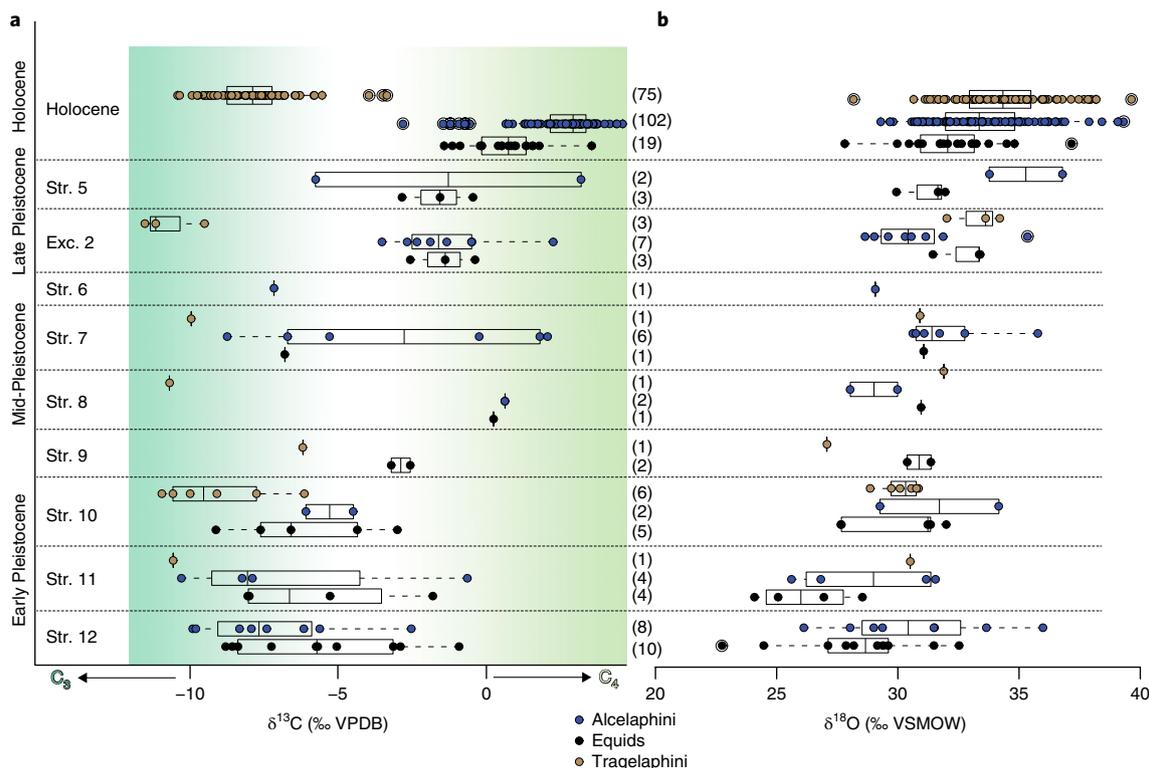


Fig. 2 | Enamel stable isotope results for the three most abundant tribes. Alcelaphini (blue), Tragelaphini (golden) and equids (black), sorted by stratum (Str.) from oldest to youngest. Holocene results were added¹². The box represents the third percentile with the median marked by a line; the points are the individual measurements. Measurements with open circles are identified as outliers in the box plots. Numbers in parentheses in the centre indicate the number of samples. **a**, $\delta^{13}\text{C}$ (‰ Vienna PeeDee Belemnite; VPDB) results. **b**, $\delta^{18}\text{O}$ (‰ Vienna Standard Mean Ocean Water; VSMOW) results.

mixtures in stratum 11 and lower stratum 10 (both exc. 1, Fig. 3). *Kobus leche* (Lechwe), a species that today is restricted to habitats with standing water is represented by samples in stratum 10 (exc. 1) and stratum 2 (exc. 2).

Environmental change at Wonderwerk Cave

When dividing the sampled specimens based on their isotopic values into consumers of predominantly C_3 vegetation, C_4 vegetation and mixed feeders, the percentage of herbivores consuming C_3 vegetation in the Wonderwerk Cave assemblage remains between 20 and 50% throughout the Pleistocene and Holocene. The percentage of specimen consuming predominantly C_4 vegetation increases from 5–22% in strata 12–10 (exc. 1) to 30–47% in the Mid-Pleistocene (strata 9–6, exc. 1, and stratum 2, exc. 2) and Early Holocene, and make up over 60% of samples in the Late Holocene (Supplementary Table 2). These results indicate that a threshold is crossed around 0.9–0.8 Ma, after which the proportions of C_4 grasses increased in the diets of the grazing species (Supplementary Dataset 1). Although final faunal lists are still to be published for some parts of the sequence, a record of all identified dental remains to date (comprising all samples analysed in this study) shows a predominance of Alcelaphini and equids throughout the sequence except for stratum 10, in which browsing species dominate the assemblage. The grass phytolith analysis documents an increase in saddle morphotypes in upper strata 10–9 (exc. 1), forms that are associated with warmer C_3 grass conditions¹⁰. A trend towards higher enamel (Fig. 2) and OES $\delta^{18}\text{O}$ values⁹ in strata 9–6 (exc. 1) suggests greater aridity.

In summary, during the Oldowan occupation (stratum 12, exc. 1), an arid to semi-arid, mostly summer rainfall-dominated climate prevailed with the presence of both C_3 and C_4 grasses. The area became increasingly humid in the early Acheulean (strata 11–10, exc. 1),

showing marked presence of C_3 grasses. These conditions were followed by increasing aridity and favourable conditions for C_4 grass expansions in the late Acheulean (strata 9–6, exc. 1). Occupational hiatuses and unresolved dating of the Mid- and Late Pleistocene strata (strata 9–5, exc. 1) prevent us from establishing whether or how often mesic or C_4/C_3 mixed grass conditions re-occurred. Equally, we cannot know whether similar environmental change happened outside the time periods covered in our sequence. There is convincing evidence for a mesic phase in the early MSA¹⁴ (stratum 2, exc. 2, Fig. 3). Unlike in earlier periods, C_3 grasses do not have a marked presence in the ecosystem at Wonderwerk Cave at that time, suggesting that it is not a simple glacial-interglacial dichotomy that establishes these large-scale changes.

Drivers of environmental change

No analogues exist in southern Africa today for mesic, C_4/C_3 mixed grass environments as suggested for the Early Pleistocene at Wonderwerk Cave. Moreover, it represents a strikingly different environment to that of the Holocene at the site¹². The substantial, albeit variable, presence of C_3 grasses in an area that is today completely dominated by C_4 grass taxa implies different precipitation patterns. First proposed in ref. ¹⁵, the dominant model of rainfall in South Africa during glacials is a northward shift of all circulation systems, expanding the area influenced by winter rainfall from the Atlantic Ocean^{16,17}. These changes in rainfall patterns are reflected in the Wonderwerk Cave herbivore enamel and OES $\delta^{18}\text{O}$ values (strata 11 and 10, exc. 1, stratum 2 exc. 2). Although a summer rainfall regime is suggested for large parts of the sequence (stratum 12, strata 9–6, exc. 1), the influence of inter-seasonal rainfall is highly probable in the early Acheulean (strata 11 and 10, exc. 1) and the early MSA (stratum 2, exc. 2), as indicated by low $\delta^{18}\text{O}$ enamel and OES values. This scenario of increased and/or more regular

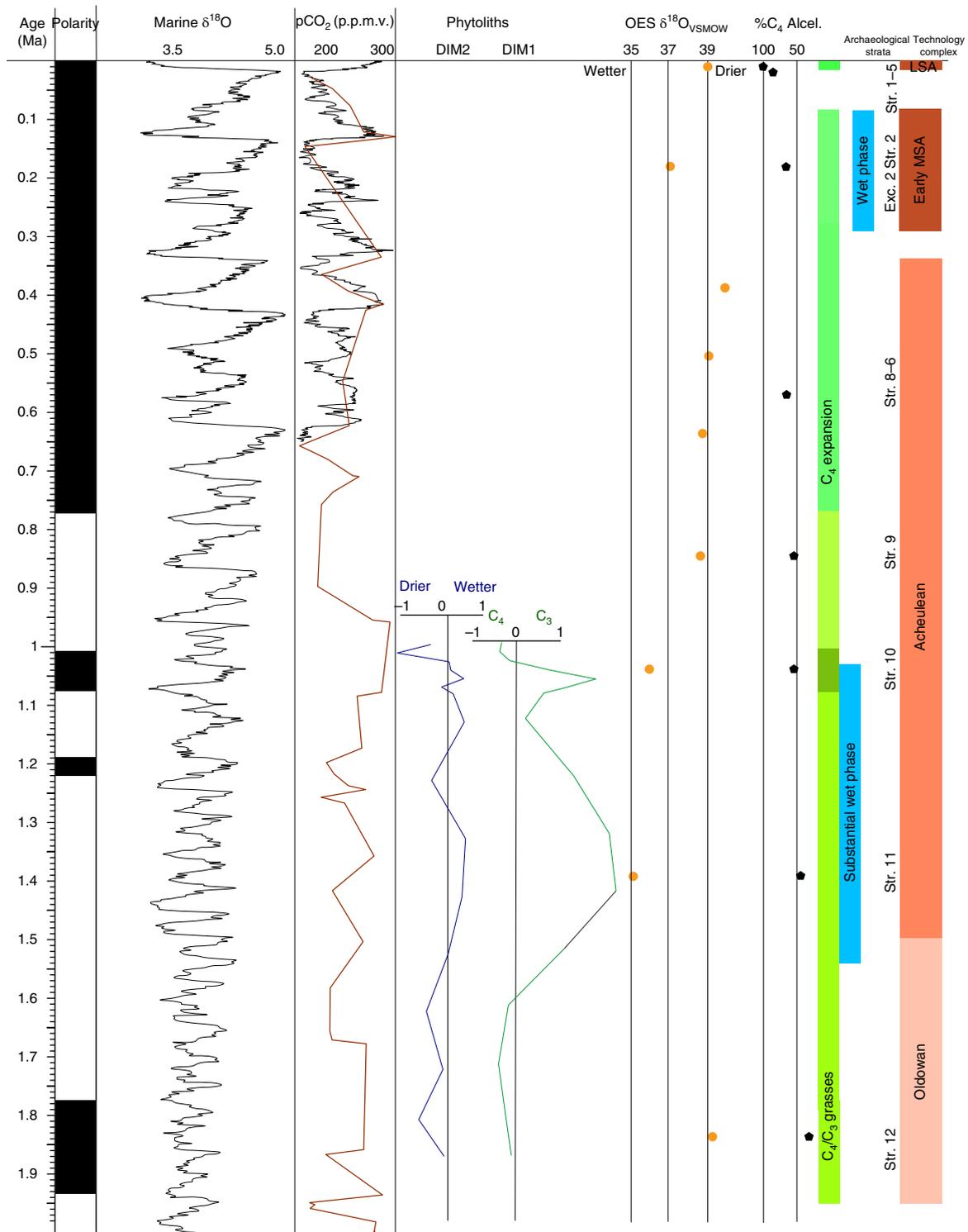


Fig. 3 | Timeline and climate parameters of the past two million years. From left to right: magnetic polarity, $\delta^{18}\text{O}$ (‰) from the LR04 stack of benthic foraminifera⁴³, pCO_2 (in parts per million volume; p.p.m.v.) record from ice cores in Antarctica^{44–48} and boron isotope data²⁹, phytolith principal component analysis loadings for factor 1 (DIM1, which accounts for 68% of the inertia and is interpreted as variation in seasonality) and factor 2 (DIM2, accounts for 20% of the inertia and is interpreted as a reflection of different moisture regimes), based on the percentage values of the morphotypes that strongly associate with mesic- and arid-adapted grasses favouring the C_4 pathway (saddle variant 1 and saddle variant 2 morphotype, respectively) and grasses favouring the C_3 pathway (trapezoid morphotype)¹⁰, OES $\delta^{18}\text{O}_{\text{VSMOW}}$ (‰) from Wonderwerk Cave (orange dots)⁹, percentage of C_4 plants in Alcelaphini (Alcel.) diet per stratum at Wonderwerk Cave (black polygons; Supplementary Table 3). Position of archaeological strata and attribution to lithic technocomplex in Wonderwerk Cave are indicated, as well as interpretation of $\delta^{13}\text{C}$ (vegetation) and $\delta^{18}\text{O}$ (aridity) enamel isotope data. Discontinuities and time-averaging of archaeological strata is discussed in the Supplementary Information.

precipitation provides a context for the year-round presence of lakes and pans, as recovered from several local sediment records^{14,18–20}, including evidence for a fluvial fan system at the time of the Oldowan in Wonderwerk Cave (stratum 12, exc. 1)²⁰. This was followed by a shallow water body in the area in the Early Pleistocene (parallel to Wonderwerk Cave Acheulean strata 11–10, exc. 1), which dried up with lower rainfall and/or a lowering of the groundwater table after 1 Ma, resulting in less available surface water²⁰. In the western Cape, a change in hydrology before the Mid-Pleistocene has been suggested as reason for similar low $\delta^{18}\text{O}$ values in herbivore enamel as at Wonderwerk Cave²¹. Excavations at Kathu, around 50 km from Wonderwerk Cave, of abundant Acheulean stone tools, confirm the use of the palaeolake shores by hominins²². In contrast to tropical areas of Africa, in temperate South Africa winter rainfall influence is one factor limiting the spread of C_4 grasses²³. A threshold response in increasing Antarctic ice volume at 0.9 Ma changed ocean circulation²⁴, which in turn could have strengthened the strong seasonal rainfall regime over South Africa, providing more favourable conditions for C_4 grasses (strata 9–6, exc.1). Further attention should be paid to the influence of atmospheric CO_2 levels, as outlined below.

CO_2 as a driver of environmental change

On the basis of physiological differences between C_3 and C_4 plants in their photosynthetic pathway, a model has previously been proposed²⁵ in which the quantum yield for CO_2 uptake is dependent on the temperature and atmospheric CO_2 concentration. Simulations and growth experiments have shown that C_3 plants at glacial pCO_2 conditions (170–200 p.p.m.) have increased water and nutrient needs²⁶ and reduced biomass production²⁷, confirming the effect of changing CO_2 levels, particularly on C_3 plants. Conversely, C_4 plants are favoured at pCO_2 lower than 350 p.p.m. and at high growing season temperatures²⁵. Therefore, in the low CO_2 conditions of glacials, C_4 plant biomass and growth potential is less affected than C_3 plant biomass²⁸. The harshest glacial periods occurred from around 0.8 Ma onwards, accompanied by a worldwide shift to 100,000-year long orbital cycles. For earlier periods, which are not covered by Antarctic ice core data (Fig. 3), boron isotopes in planktic foraminifer shells provide a proxy for atmospheric partial pressure pCO_2 . The results show very low pCO_2 in successive glacials after 0.8 Ma²⁹ (Fig. 3), compared to previous glacials. Together with a strengthening of the summer rainfall regime, this could have shifted the growing season to the hot summer, and may have periodically imposed conditions that were disadvantageous for C_3 grasses from 0.8 Ma onwards. The increasing $\delta^{13}\text{C}$ values in the grazer diet at Wonderwerk Cave after around 0.8 Ma track the loss of C_3 grasses, and subsequent further spread of C_4 grasses in the region (Fig. 3).

Comparison to other sites

Other parts of southern Africa as well as East Africa have experienced different local vegetation responses to these climatic drivers, despite sharing summer rainfall regimes. When comparing the same mammalian taxa, which were analysed using the same isotopic methods, higher enamel $\delta^{13}\text{C}$ grazer values were found in sites located in the eastern parts of South Africa, for example, at the sites of Sterkfontein, Swartkrans and Cornelia (Fig. 1), compared to Wonderwerk Cave^{30,31} (Fig. 4). This indicates that C_4 grasses were a major part of the local vegetation at these sites during the Early Pleistocene (2–1 Ma). In the Cradle of Humankind, the Buffalo Cave speleothem record shows phases of C_4 expansion at 1.78 to 1.69 Ma³² whereas enamel isotopes³¹ place a shift to open grassy conditions at Sterkfontein and Swartkrans after 1.7 Ma, possibly eliminating any remaining C_3 grasses^{30–33}. This shift coincides with the transition from Oldowan to Acheulean technology in South Africa (Fig. 4). The Western Cape is another region in South Africa for which a number of studies with enamel stable isotope data of mammalian taxa have been published. These

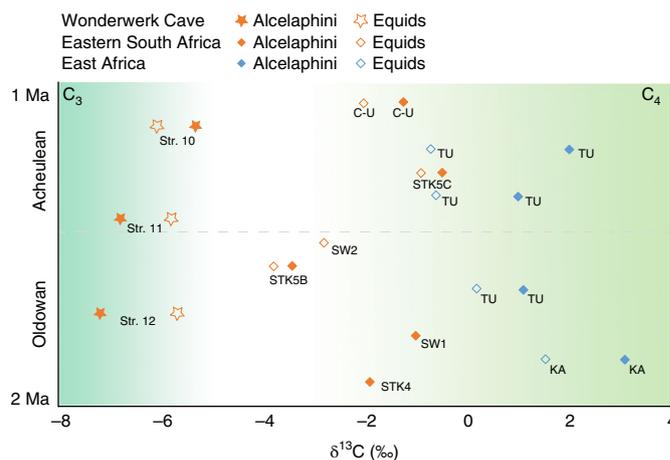


Fig. 4 | Mean $\delta^{13}\text{C}$ (‰) values for equids and Alcelaphini from sites in East and South Africa between 2 and 1 Ma.

The sites are shown in approximate chronological order but have large overlaps. The main distinction is their association with Oldowan or Acheulean lithic technology. From top to bottom: Cornelia-Uitzhoek (C-U)³¹, Wonderwerk Cave Stratum 10 (Str. 10, this study), Turkana Basin 1.3–1.0 Ma (TU, Nachukui Nariokotome and Koobi Fora Chari Formations)³⁷, Sterkfontein Member 5C (STK5C)³⁰, Turkana Basin 1.5–1.3 Ma (TU, Nachukui Natioo and Koobi Fora Okote Formations)³⁷, Wonderwerk Cave Stratum 11 (Str. 11, this study), Swartkrans Member 2 (SW2)³⁰, Sterkfontein member 5B (STK5B)³⁰, Turkana Basin 1.9–1.5 Ma (TU, Nachukui Kaitio and Koobi Fora KBS Formations)³⁷, Wonderwerk Stratum 12 (Str. 12, this study), Swartkrans Member 1 (SW1)³⁰, Kanjera South (KA)³⁸ and Sterkfontein Member 4 (STK4)³⁰.

sites are located in the C_3 -plant-dominated fynbos biome, in the winter rainfall zone, and are therefore following other climatic drivers than sites in the summer rainfall zones of the interior or eastern parts of South Africa. Isotopic analyses of Middle and Late Pleistocene Western Cape sites, for example Elandsfontein^{21,34} or Hoedjiespunt³⁵, have shown that the winter rainfall regime persisted throughout the Pleistocene in this area, which is reflected in the persistence of C_3 values for all mammals.

By contrast, in East Africa, the shift towards a C_4 -dominated environment took place in the Pliocene or very Early Pleistocene³⁶. Stable isotope evidence for the Early Pleistocene shows that C_4 grasses dominated the local vegetation³⁷ in a higher percentage than have been found in South Africa (Fig. 4). The enamel stable isotope data for Alcelaphini and equids from the Turkana Basin (Nachukui and Koobi Fora Formations)³⁷ and Kanjera South³⁸ show markedly higher $\delta^{13}\text{C}$ values in the timespan 2–1 Ma than at Wonderwerk Cave (Fig. 4). Similarly, Alcelaphini at Olduvai in the Oldowan bed I (after 1.78 Ma) and bed II (after 1.83 Ma) have $\delta^{13}\text{C}$ values of 0.2‰ to 3.2‰³⁹, characteristic of a C_4 environment, and so differs markedly from the palaeoenvironment that we have reconstructed for the coeval period at Wonderwerk Cave.

This study demonstrates the persistence of C_3 grasses in the southern Kalahari during the Early Pleistocene, a signature that was probably created because of the unique interplay of regional rainfall seasonality and hydrological conditions together with global drivers such as atmospheric CO_2 levels. Particularly the local environment during the early Acheulean, with lakes and wetlands^{20,22}, as well as C_4 and C_3 grasses and abundant concentrations of stone tool assemblages challenge the narrative of the evolutionary adaptation of early *Homo* to an arid savannah environment, although our data do support the association of hominin occupation and bodies of water⁴⁰. The shift to C_4 environments

takes place at Wonderwerk Cave during the Acheulean and is not related to the shift in lithic technology towards biface production. In line with other local palaeoenvironmental studies, our results challenge global generalizations of climate responses in hominin evolution and highlight the necessity for regional models and appropriate terrestrial records to be able to evaluate drivers and feedbacks.

Methods

Stable isotope analysis. Bulk enamel samples were taken with a diamond-tipped drill along the entire length of the tooth crown. Enamel pre-treatment followed a standard protocol at the Research Laboratory for Archaeology and the History of Art in Oxford, which included soaking of enamel powder in approximately 1.8 ml NaOCl solution (around 2%) for 30 min to remove organics. Samples were centrifuged, decanted and washed with distilled water three times before being soaked in 0.1 M acetic acid (CH₃COOH) for 10 min to remove any exogenous carbonate and washed again three times. Samples were analysed at Bradford University, using a Finnigan Gasbench II, interfaced with a Thermo Delta V Advantage continuous flow isotope ratio mass spectrometer. The reference gas was calibrated against three international standards (NBS 19 (δ¹³C 1.95‰, δ¹⁸O 28.65‰), CO-1 (δ¹³C 2.49‰, δ¹⁸O 28.41‰), CO-8 (δ¹³C -5.76‰, δ¹⁸O 7.55‰)) and three laboratory carbonate standards (MERCK CaCO₃ (δ¹³C -35.45‰, δ¹⁸O 13.35‰), BES (δ¹³C -11.1‰, δ¹⁸O 25.0‰), OES (δ¹³C -10.72‰, δ¹⁸O 25.45‰)), which were interspersed in all runs. The results for both isotopes are expressed as per mil (‰) in the delta (δ) notation versus the international VPDB and VSMOW standard, respectively. Analytical precision as determined from multiple replicates of the laboratory standards was approximately 0.1‰ for δ¹³C and 0.2‰ for δ¹⁸O.

Statistics. To test for homogeneity of variance of the δ¹³C and δ¹⁸O results, a Levene's test was performed in R, with the null hypothesis that all strata variances are equal. Tests were conducted two ways: (1) within each taxon over time and (2) with each taxon within the individual stratum. Statistical differences between all strata were tested for each taxon using a one-way ANOVA with Tukey's HSD post hoc test, with $P < 0.05$ regarded as significant. Because an ANOVA can only be used with parametric values, a Kruskal-Wallis test was used for datasets in which the variables failed the assumptions of the Levene's test. All statistical tests were performed using R⁴¹. Further details and results of the statistical analysis can be found in Supplementary Table 5.

Reporting Summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this article.

Data availability. The data that support the findings of this study are available within this manuscript and the Supplementary Dataset 1.

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Author contributions

M.E., L.K.H., M.C. and J.L.-T. were responsible for research design and M.E. conducted the stable isotope analysis. J.S.B., L.K.H. and L.R. provided material and data. All authors contributed to discussions and writing of the manuscript and approved the final version.

Competing interests

The authors declare no competing interests.

Additional information

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No software was used

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Statistical analysis was performed in R (R Core Team 2013, R Foundation for Statistical Computing, URL <http://www.R-project.org>).

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Life sciences

Study design

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Sample size	After identification of all dental remains from Excavation 1 in Wonderwerk Cave, all herbivore samples that could be identified to tribe or species were chosen for analysis. Sample size is limited by the archaeological excavated collection.
Data exclusions	Excluded were clearly burnt samples and deciduous teeth from juvenile specimen.
Replication	Three samples (ME576, ME619, ME687), identified as outliers after analysis, have been re-run on the mass spectrometer. The results from both runs are within the error range for a single enamel sample for carbon and oxygen isotopes. The mean value from both runs was used in analysis and figures.
Randomization	There was no allocation of samples into groups in the sampling, pretreatment or measurement.
Blinding	Samples were given a successive laboratory number after enamel sampling. It was not possible from this numbering to determine any sample information during pretreatment or measurement without consulting the reference list.

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Unique materials

Obtaining unique materials	All sampled faunal specimen are curated in the McGregor Museum in Kimberley, South Africa, and were sampled with written permission of the curator, Dr. David Morris. All enamel samples were exported under a South African Heritage Resources Agency (SAHRA) permit (Permit ID 1898).
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