Title: A New Paleoecological Context for the Oldowan-Acheulean in Southern Africa

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Abstract: The influence of climatic and environmental change on human evolution in the Pleistocene is understood largely from extensive East African stable isotope records. These records show increasing proportions of C_4 plants in the Early Pleistocene. We know far less about the expansion of C_4 grasses in higher latitudes, which were also occupied by early *Homo* but are more marginal for C_4 plants. Here we show that both C_3 and C_4 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 CO_2 levels, develop along a regional distinct trajectory compared to eastern South Africa and East Africa.

One Sentence Summary: Environmental proxy study at Wonderwerk Cave shows that early *Homo* flourished in a humid C_3 and C_4 grass setting.

Main Text: The spread of arid grasslands dominated by C_4 plants is often cited as a driver in the evolution of the species *Homo* in East Africa[1-3]. However, some recent research challenged both 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 Africa (27°50’46’’S, 23°33’19’’E; Fig. 1; SOM)[6]. The cave is located in the Kuruman hills at the southern end of the Kalahari, currently a summer rainfall area, and is overlooking today an open and semi-arid landscape characterised by a mixture of C_4 grasses and scattered C_3 plants such as thorn bushes, shrubs and patches of small to medium sized trees. Research has targeted Excavation areas (Exc.) 1 and 2, c. 20-30m into the 140m 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 (Supplementary Online Material)[7,8]. From these deposits, 125 teeth from thirteen mammalian species were sampled for bulk enamel carbon and oxygen isotope analysis. We consider the enamel carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) stable isotope results in combination with published ostrich eggshell (OES) stable isotope data that reflect aridity[9], and grass silica short cell phytolith[10] and micromammal[11] abundance data from the same strata to compare consistency for trends in local vegetation over multiple proxies.

Results

In the Early Pleistocene (Strata 10-12, Exc. 1, 1.95Ma to 0.99Ma) average grazer $\delta^{13}C$ values fall between -5.3‰ and -7.4‰ (Fig. 2, Supplementary Table 1 and Supplementary Dataset 1) suggesting the consumption of a mix of C_3 and C_4 plants. In detail, Alcelaphini have mean $\delta^{13}C$ values of -7.2±2.3‰ (n=8, Stratum 12), -6.8±3.7‰ (n=4, Stratum 11) and -5.3±0.8‰ (n=2, Stratum 10). Equidae have mean $\delta^{13}C$ values of -5.7±2.6‰ (n=10, Stratum 12), -5.8±2.6‰ (n=4, Stratum 11) and -6.1±2.2‰ (n=5, Stratum 10), while springhare (*Pedetes* sp.) is represented by two individuals in Stratum 12 with a mean $\delta^{13}C$ value of -7.4±3.0‰ (Supplementary Figures 1 and 2). As all these taxa are morphologically adapted to grazing and their extant equivalents are all grazers, the results indicate consumption of varied proportions of C_3 and C_4 grasses. Currently, C_3 grasses are not a component of the local vegetation, in which C_4 grasses dominate, a feature characteristic throughout the Holocene (Fig. 2)[12]. Grass silica short cell phytolith analysis of Stratum 12 sediment samples indicate a savanna or Nama-Karoo type grassland when compared with modern morphotype ecology, with warm, locally mesic to dry conditions within a predominantly summer rainfall regime[6,10]. In the micromammal record for this period, the relative proportions of Gerbillinae to Murinae reflect a drier and more open environment, when compared to modern morphotype ecology[11]. However, beginning in the upper part of Stratum 12 and continuing through to Stratum 10, the absence of saddle morphotypes and a predominance of C_3-affiliated trapezoid morphotypes in the phytolith record indicate a shift to cooler prevailing conditions and cooler growing season, with a vegetation similar to the current Succulent Karoo signifying a year-round rainfall regime which differs from that prevailing in the region today[6,10]. Changing micromammal proportions further indicate a shift to less arid environments in Stratum 11 compared to Stratum 12, potentially as a result of changing rainfall patterns[11]. Mean enamel $\delta^{18}O$ values across all sampled species, reflecting animal water intake and physiology (Supplementary Online Material), are generally below 36‰, considerably lower than throughout the Holocene for the same species (Fig. 2; Supplementary Tables 1 and 5)[12]. The lowest $\delta^{18}O$ mean values are in the Early Pleistocene strata (Strata 10-12; Exc. 1, 25.7‰ to 31.7‰), with values in Stratum 11 for Alcelaphini (mean $\delta^{18}O$ 28.8±2.6‰, n=8) and Equidae (mean $\delta^{18}O$ 26.2±1.7‰, n=10) 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 $\delta^{18}O$ values, while suggesting mostly arid but highly variable conditions (Strata 12 mean $\delta^{18}O$ 39.4±1.4‰, n=5), show phases of lower values and hence increased humidity in Strata 11 ($\delta^{18}O$ 35.2‰, n=1), 10 (mean $\delta^{18}O$ 36.0±2.2‰, n=16) and Stratum 2, Exc. 2 (mean $\delta^{18}O$ 37.1±4.0‰, n=18) (Fig. 3)[9,13]. Mean $\delta^{18}O$ OES values increase from Stratum 9 (mean $\delta^{18}O$ 38.7±3.7‰, n=16) through to Stratum 6 (mean $\delta^{18}O$ 40.0±3.5‰, n=11) and are highest in the Holocene (mean $\delta^{18}O$ 39.0±3.2‰, n=196) (Fig. 3)[9,13]. The highest proportions of specimens with low or intermediate $\delta^{13}C$ values in the enamel isotope record, reflecting C_3 or C_3/C_4 mixed diets occur in Stratum 10, while phytolith data similarly suggest cool C_3/C_4 grass mixtures in Stratum 11 and lower Stratum 10 (both Exc. 1, Fig. 3). *Kobus leche* (Lechwe), a species that is restricted to habitats with standing water today is represented by samples in Stratum 10 (Exc. 1) and Stratum 2 (Exc. 2).

Environmental change at Wonderwerk Cave

When dividing the sampled specimen 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 10-12 (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 0.9-0.8Ma years ago, 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, where browsing species dominate the assemblage. The grass phytolith analysis documents an increase in saddle morphotypes in upper Stratum 10-9 (Exc. 1), forms that are associated with warmer C_4 grass conditions[10]. A trend towards higher enamel (Fig. 2) and OES $\delta^{18}O$ values[9] in Strata 9-6 (Exc. 1) suggests greater aridity.

To summarise, during the Oldowan occupation (Stratum 12, Exc. 1), an arid to semi-arid, largely 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) preclude us from establishing whether or how often mesic or C_4/C_3 mixed grass conditions reoccurred. Equally, we cannot know if similar environmental change happened outside the time periods covered in our sequence. There is convincing evidence for a mesic phase in the Early MSA (Stratum 2, Exc. 2, Fig. 3)[14]. Unlike in earlier periods, C_3 grasses do not feature significantly 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 site[12]. 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 by van Zinderen Bakker[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 $\delta^{18}O$ 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 likely in the early Acheulean (Strata 11 and 10, Exc. 1) and the Early MSA (Stratum 2 Exc. 2), as attested by low $\delta^{18}O$ enamel and OES values. This scenario of increased and/or more regular 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 1Ma, resulting in less available surface water[20]. In the western Cape, a change in hydrology before the mid-Pleistocene has been suggested as reason for similar low $\delta^{18}O$ values in herbivore enamel as at Wonderwerk Cave[21]. Excavations at Kathu, c. 50km from Wonderwerk Cave, of abundant Acheulean stone tools confirm the use of the paleolake shores by hominins[22]. In contrast to tropical areas of Africa, in temperate South Africa winter rainfall influence is one factor limiting the spread of C_4 grasses[23]. A threshold response in increasing Antarctic ice volume at 0.9ka years ago changed ocean circulation[24], which in turn could have strengthened the strong seasonal rainfall regime over South Africa, providing more favorable conditions for C_4 grasses (Strata 9-6, Exc.1). Further consideration should be paid to the influence of atmospheric CO_2 levels, as outlined below.

CO_2 as a driver of environmental change

Based on physiological difference between C_3 and C_4 plants in their photosynthetic pathway, Ehleringer et al.[25] proposed a model where quantum yield for CO_2 uptake is dependent on temperature and atmospheric CO_2 concentration. Simulations and growth experiments have shown that C_3 plants at glacial pCO_2 conditions (170-200ppm) have increased water and nutrient needs[26] and reduced biomass production[27], confirming the effect of changing CO_2 levels, particularly on C_3 plants. Conversely, C_4 plants are favoured at pCO_2 lower than 350ppm and at high growing season temperatures[25]. Therefore, in the low CO_2 conditions of glacials, C_4 plant biomass and growth potential is less impacted than is C_3 plant biomass[28]. The harshest glacial periods occurred from c. 0.8Ma onwards, accompanied by a worldwide shift to 100,000-year long orbital cycles. For earlier periods, that are not covered by Antarctic ice core data (Fig. 3), boron isotopes in planktic foraminifer shells provide one proxy for atmospheric partial pressure pCO_2. The results show very low pCO_2 in successive glacials after 0.8Ma (Fig. 3)[29], 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 disadvantageous for C_3 grasses from 0.8Ma onwards. The increasing $\delta^{13}C$ values in the grazer diet at Wonderwerk Cave after c. 0.8Ma 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, that were analysed using the same isotopic methods, higher enamel $\delta^{13}C$ grazer values are found in sites located in the eastern parts of South Africa, e.g. 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 (2-1Ma). In the Cradle of Humankind, the Buffalo Cave speleothem record shows phases of C_4 expansion at 1.78 to 1.69 Ma[32] while enamel isotopes[31] place a shift to open grassy conditions at Sterkfontein and Swartkrans after 1.7Ma, 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 enamel stable isotope of mammalian taxa have been studies published. These sites are located in the C_3-plant dominated fynbos biome, in the winter rainfall zone, and are therefore following other climatic drivers than the summer rainfall zone sites 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 Hoedjiespunt[36] have shown that the winter rainfall regime persisted throughout the Pleistocene in this area, as reflected in the persistence of C_3 values for all mammals.

In contrast, in East Africa, the shift towards a C_4 dominated environment took place in the Pliocene or very Early Pleistocene[36]. The stable isotope evidence for the Early Pleistocene is showing C_4 grasses are dominating the local vegetation[37] in a higher percentage than found in South Africa (Fig. 4). The enamel stable isotope data for Alcelaphini and Equids from the Turkana Basin (Nachukui and Koobi Fora)[37] and Kanjera South[38] show markedly higher $\delta^{13}C$ values in the timespan 2-1Ma than at Wonderwerk Cave (Fig. 4). Similarly, Alcelaphini at Olduvai in the Oldowan Bed I (after 1.78Ma) and Bed II (after 1.83Ma) have $\delta^{13}C$ values of 0.2‰ to 3.2‰[40], characteristic of a C_4 environment, and so differs markedly from the paleoenvironment 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 probably created though 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 savanna environment, although our data do support the association of hominin occupation and bodies of water[40]. 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 paleoenvironmental 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 ~1.8 ml NaOCl solution (~2%) for 30 minutes to remove organics. Samples were centrifuged, decanted and washed with distilled water three times before being soaked in 0.1M Acetic Acid (CH_3COOH) for ten minutes 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 ($\delta^{13}C$ 1.95‰, $\delta^{18}O$ 28.65‰), CO-1 ($\delta^{13}C$ 2.49‰, $\delta^{18}O$ 28.41‰), CO-8 ($\delta^{13}C$ -5.76‰, $\delta^{18}O$ 7.55‰)) and three laboratory carbonate standards (MERCK $CaCO_3$ ($\delta^{13}C$ -35.45‰, $\delta^{18}O$ 13.35‰), BES ($\delta^{13}C$ -11.1‰, $\delta^{18}O$ 25.0‰), OES ($\delta^{13}C$ -10.72‰, $\delta^{18}O$ 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 $\delta^{13}C$ and 0.2‰ for $\delta^{18}O$.

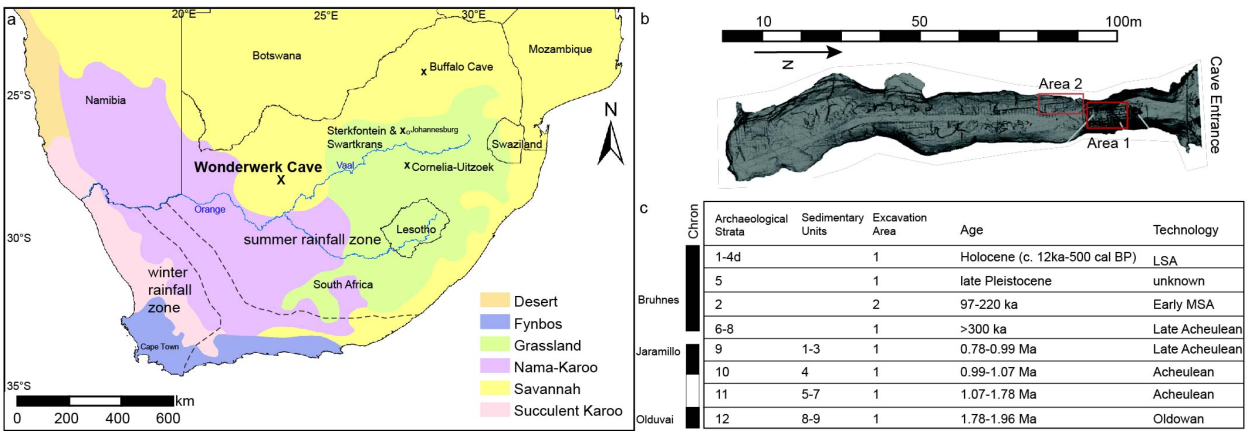
Statistics

To test for homogeneity of variance of the $\delta^{13}C$ and $\delta^{18}O$ 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; 2) with each taxon within the individual Strata. 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. As ANOVA can only be undertaken with parametric values, a Kruskal-Wallis test was used for datasets where variables failed the assumptions of the Levene's test. All statistical tests were performed in R[41]. Further details and results of the statistical analysis can be found in the supplementary Table 5.

Supplementary Online Content and Source Data are available in the online version of the paper; references unique to these sections appear only in the online paper.

Figures and captions



Chron	Archaeological Strata	Sedimentary Units	Excavation Area	Age	Technology
	1-4d		1	Holocene (c. 12ka-500 cal BP)	LSA
	5		1	late Pleistocene	unknown
Bruhnes	2		2	97-220 ka	Early MSA
	6-8		1	>300 ka	Late Acheulean
Jaramillo	9	1-3	1	0.78-0.99 Ma	Late Acheulean
	10	4	1	0.99-1.07 Ma	Acheulean
	11	5-7	1	1.07-1.78 Ma	Acheulean
Olduvai	12	8-9	1	1.78-1.96 Ma	Oldowan

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 zones[42] is indicated. (**b**) Laser scan of Wonderwerk Cave with Excavation Areas 1 and 2 marked (scan courtesy of H. Rüther, Zamani Project); (**c**) Stratigraphy of relevant excavation areas from oldest to youngest, including age, paleomagnetic subchron, and associated lithic technology. MSA=Middle Stone Age, LSA= Later Stone Age.

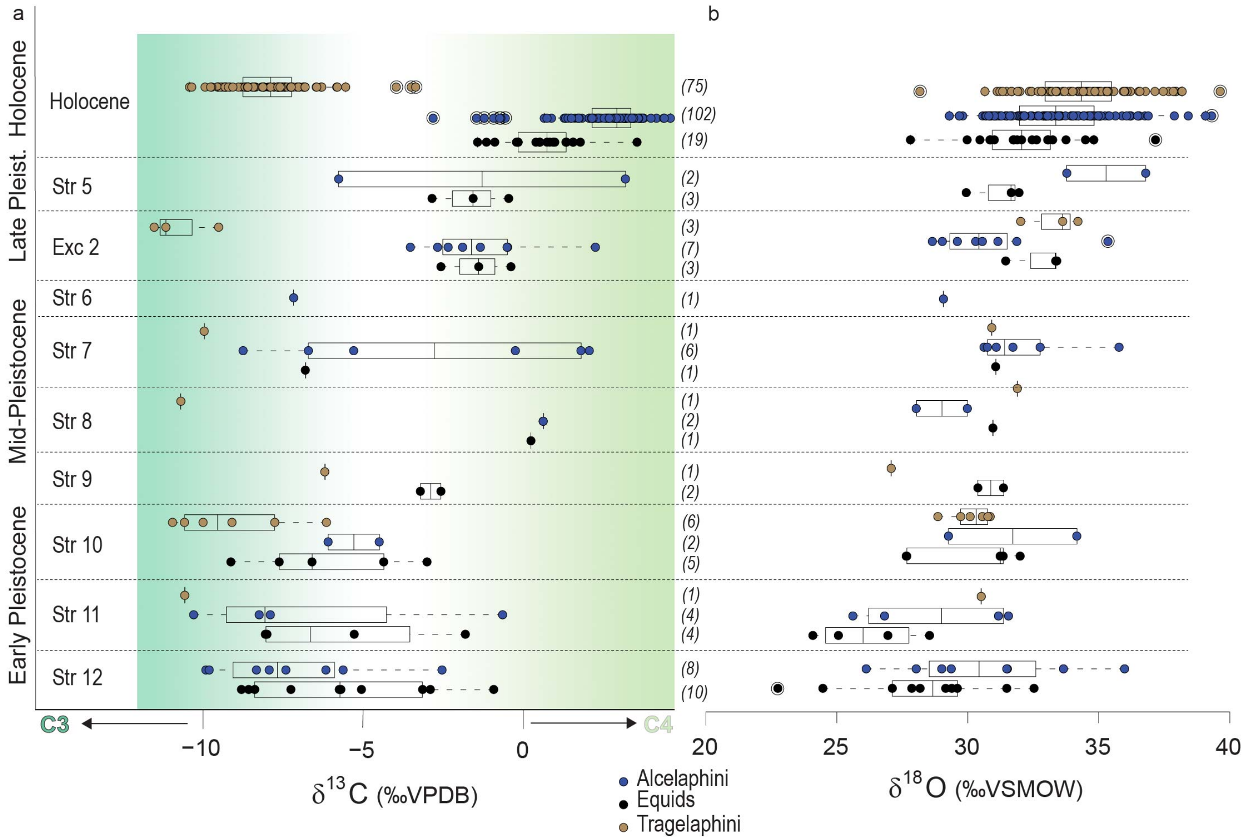


Fig. 2. Enamel stable isotope results for the three most abundant tribes. Alcelaphini (blue), Tragelaphini (golden) and Equids (black), sorted by Stratum from oldest to youngest. Holocene results were added[12]. The box represents the third percentile with the median marked by a line; the points are the individual measurements. Measurements with open circles are identified as outliers in the boxplots. Numbers in parentheses in the centre indicate number of samples. (**a**) $\delta^{13}C$ (‰VPDB) results; (**b**) $\delta^{18}O$ (‰VSMOW) results.

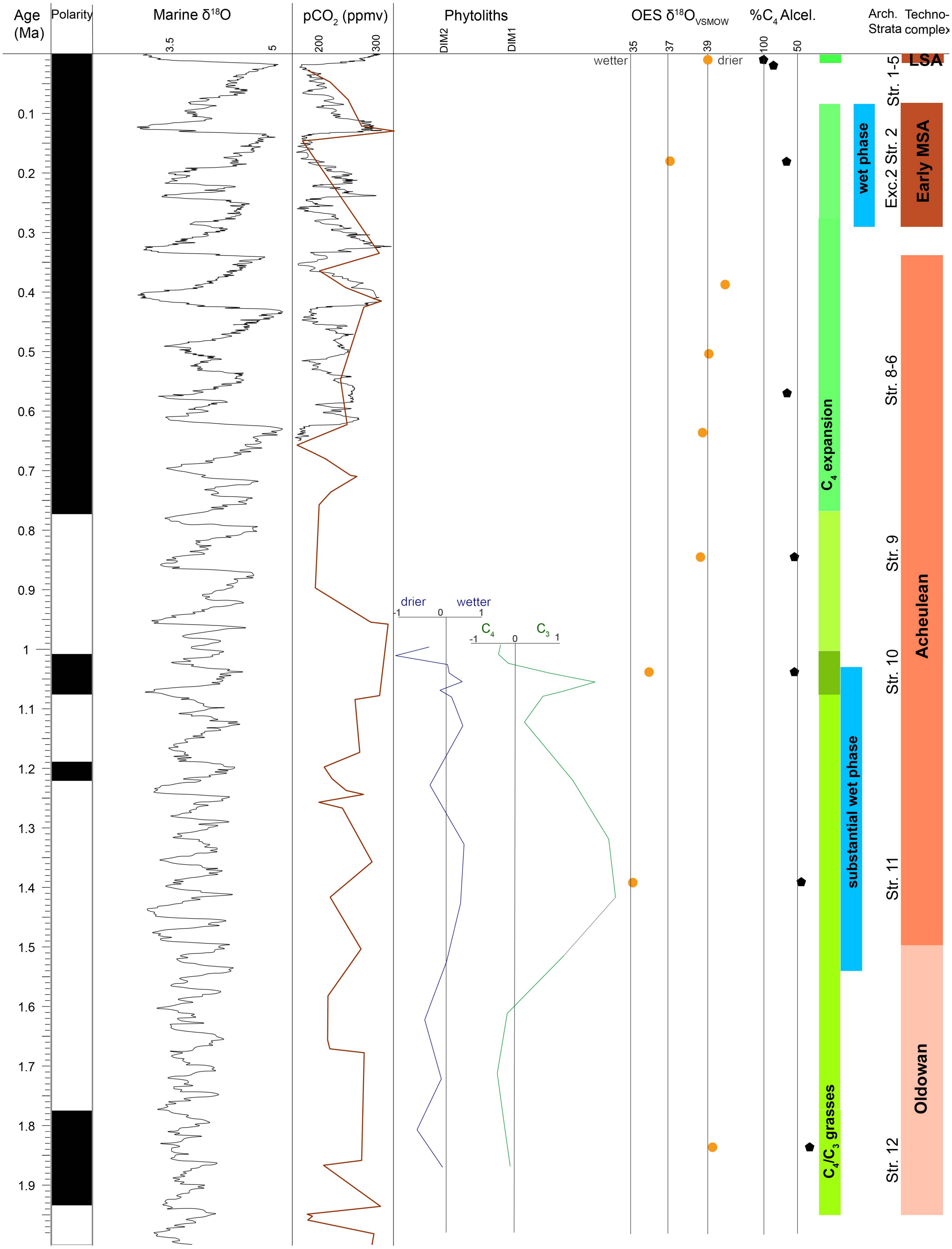


Fig. 3. Timeline and climate parameters of the last two million years. The figure shows from

left to right: magnetic polarity, $\delta^{18}O$ (‰) from the LR04 stack of benthic foraminifera[43], pCO_2 record from ice cores in Antarctica[44-48] and boron isotope data[29], phytolith PCA loadings for factor 1 (accounting for 68% of the inertia; is interpreted as variation in seasonality) and factor 2 (accounting for 20% of the inertia; 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], ostrich eggshell $\delta^{18}O_{SMOW}$ (‰) from Wonderwerk Cave (orange dots)[9], percentage of C_4 plants in Alcelaphini 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 $\delta^{13}C$ (vegetation) and $\delta^{18}O$ (aridity) enamel isotope data. Discontinuities and time-averaging of archaeological strata is discussed in the Supplementary Online Material.

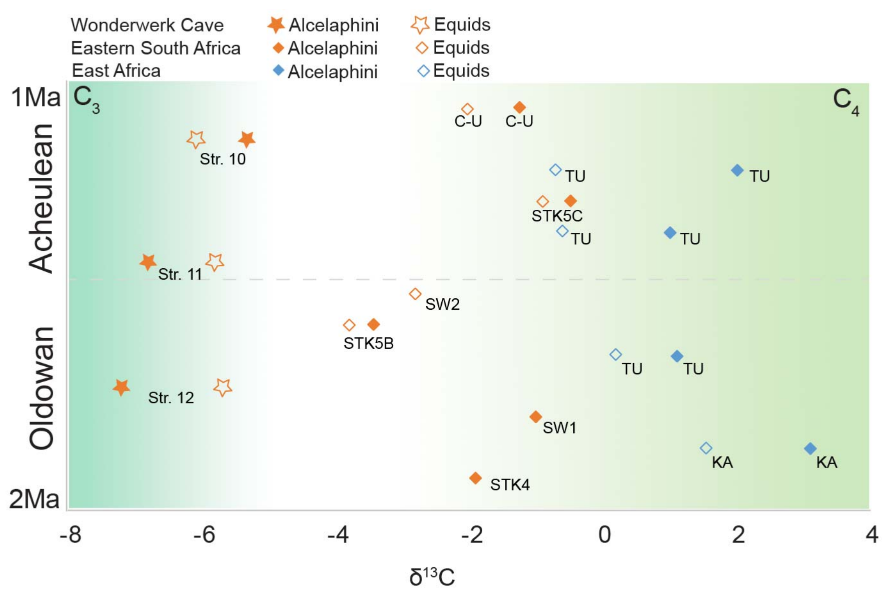


Fig. 4. Mean δ ^{13}C (‰) values for Equids and Alcelaphini from sites in East and South Africa between 2 and 1 million years ago. The sites are shown in approximate chronological order but have large overlaps. The main distinction is their association with Oldowan or Acheulean lithic technology. From top to bottom: Cornelia-Uitzhoek (C-U)[31], Wonderwerk Cave Stratum 10 (Str. 10, this study), Turkana Basin 1.3-1.0Ma (TU, Nachukui Nariokotome and Koobi Fora Chari Formations) [37], Sterkfontein Member 5C (STK5C)[30], Turkana Basin 1.5-

1.3Ma (TU, Nachukui Natoo 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 1.9-1.5Ma (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], Sterkfontein Member 4 (STK4)[30].

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Supplementary information is available in the online version of the paper.

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 ME, LKH, MC and JLT are responsible for research design and ME conducted the stable isotope analysis. JSB, LKH and LR provided material and data. All authors have contributed to discussions and writing of the manuscript and have approved the final version.

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