New site at Olduvai Gorge (AGS, Bed I, 1.84 Mya) widens the range of locations where hominins engaged in butchery

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Outstanding questions about human evolution include systematic connections between critical landscape resources—such as water and food—and how these shaped the competitive and biodiverse environment(s) that our ancestors inhabited. Here, we report fossil n-alkyl lipid biomarkers and their associated δ13C values across a newly discovered Olduvai Gorge site (AGS) dated to 1.84 million years ago, enabling a multiproxy analysis of the distributions of critical local landscape resources across an explicit locus of hominin activity. Our results reveal that AGS was a seasonally waterlogged, largely unvegetated lakeside site situated near an ephemeral freshwater river surrounded by arid-adapted C4 grasses. The sparse vegetation at AGS contrasts with reconstructed (micro)habitats at the other anthropogenic sites at Olduvai Gorge, suggesting that central-provisioning places depended more heavily on water access than vegetation viz. woody plants as is often observed for modern hunter-gatherers. As hominins at AGS performed similar butchering activities as at other Bed I sites, our results suggest they did not need to shelter of trees and thus occupied a competitive position within the predatory guild.

Olduvai Gorge contains one of the most important records of hominin remains, archaeological deposits, and fossil large-mammals in the world1–3. Over the last half century, myriad hominin environments at Olduvai have been interpreted as grasslands to open woodlands with a mosaic of grassy groundcover and thickets4–6. Yet, the spatial distribution of landscape resources and early hominin interactions within their immediate surroundings (microhabitat) remains unresolved.

Previous work at Olduvai focussing on Bed I times (2.0–1.8 Mya) suggests that the vegetation and (hydro)climatic changes documented therein correlate with orbitally (precession) driven cycles superposed on a wider aridification trend8 that continues into the modern day9. Cyclical 19–23 kyr insolation cycles triggered hydro-climate variations in the catchment basin, which in turn drove ecological transitions viz. closed forests during wetter periods to arid C4 graminoid-dominated environments1–6 in-step with transgression–regression phases of the saline, alkaline nearby paleolake Olduvai11,12. Rare species-specific plant remains, including phytoliths and large macrofossils, indicate vegetation was dominated by trees and monocotyledonous vegetation, including palms, sedges and Typha cattails13 among patchy (paleo)wetlands14. The distributions of locally-occurring plants had direct implications on hominin behaviour at Olduvai Gorge and yet remains undiscerned because of limited availability of high-resolution, contiguous samples across discrete archaeological horizons with in situ artifacts and flora indicators15.

Here, we focus on a newly discovered archaeological site at Olduvai, called AGS (Alberto Gómez Site) (Fig. 1B). The uppermost horizon of AGS lies in Bed I below Tuff IC, dated to 1.832 ± 0.003 Ma7, and is isochronous with the clay stratum level 22A (Fig. 1D) that forms much of the coeval Zinj Paleolandscapes16. The Zinj Paleolandcape—which includes FLK Zinj–DS–PTK–AMK and the new AGS site (Fig. 1)—offers an exceptional opportunity to study very-well preserved assemblages over an extensive contiguous area16.
We report the results for a combined lipid biomarker and isotope reconstruction of 24 m² of (hydro)ecological landscape at AGS that, together with existing piecemeal landscape reconstructions around the Zinj Paleolandscape, provides new and high-resolution insight into emerging patterns of hominin local land-use and behavioural dynamics amid human evolution in a changing global climate.

**Results and discussion**

**Plant biomarker distributions.** Plant lipid biomarkers are widely used to reconstruct vegetation and (hydro)climate in ancient environments, and previous studies at Olduvai have used biomarkers in spatial-temporal landscape reconstructions, although not at the resolution of this study (i.e., < 1 m²). Here, we also expand the molecular scope of these earlier studies with an explicit focus on complementary plant biomarkers viz. *n*-alkanes, *n*-alkanols, and *n*-alkanoic (fatty) acids. Combined, these *n*-alkyl lipids offer unique insights into spatial landscape resource distributions well beyond that from any particular individual biomarker class.

**Alkanes and alkanols.** All samples at AGS yielded substantial amounts of homologous *n*-alkanes spread between *n*C₁₆ and *n*C₃₅ (Fig. 2A) with a distinct dominance of long-chain, odd-numbered homologues (ACL = 29.5) (Fig. 6D), indicative of both aquatic and higher plant inputs. With this in mind, *Pₐq* values—a ratio of the aquatic-derived lipids relative to aquatic and terrestrial lipids in toto (Fig. 3A)—indicate the pro-
portional dominance of floating/submerged (i.e., aquatic) macrophytes as compared to emergent macrophytes and terrestrial plants. Samples at AGS feature consistent $P_{aq}$ values of between about 0.1–0.4 (Fig. 3A) indicative of high input from floating and emergent macrophytes such as cattails (*Typha* sp.). $P_{aq}$ values, a ratio of the algal lipids relative to algal plus terrestrial lipids\(^\text{20}\), of < 0.1 further indicate nominal lipid input from algae at AGS (Fig. 6C) that is inconsistent with swamp or salt-marsh habitats, which are rich in edaphic algal biomass\(^\text{6,21}\). Together with intermediate values of the $nC_{33}/nC_{31}$ ratio of 0.2–0.7 (average of ~0.6), in which higher values suggest increasing grass cover\(^\text{22,23}\), we interpret AGS to have been covered in mostly graminoids.

Analysis of intermediate polar (i.e., functionalized) lipid fractions illuminate crucial details about the paleoenvironment at AGS that biomarker $n$-alkanes alone cannot. Major $n$-alcohols in our sample extracts include

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Figure 2. Lipid distributions and the relative abundances of key polarity fractions identified through GC–MS analyses. (A) $n$-Alkanes; (B) $n$-Alkanols; (C) $n$-Alkanoic acids. Diagnostic source associations are also shown\(^\text{19,20,24–26,35,65}\).
mid- (C14 to C22) and long-chained (C24 to C32) with a strong predominance of even-numbered homologues (Fig. 2B). Most samples’ n-alkanol distributions are dominated by nC18OH that is characteristic of bacteria and freshwater algae inputs24–26. However, several distributions are rather dominated by phytoplankton-derived nC24OH24,25 or commonly plant-derived nC28OH25, further clarifying the complex mixture of both aquatic and terrestrial lipid inputs. Common occurrences of nC26OH, typical of freshwater microalgae (Eustigmatophyceae)24,26, further indicates regular inundation with flowing potable water18 at AGS.

Previous studies suggest the ratio of n-hexacosanol (nC26OH) to n-nonacosane (nC29)—called the alcohol preservation index (API)—reflects changes in oxygenation at the sediment depositional interface27,28, wherein smaller values indicate more oxic conditions. At AGS, API values range from 0.2 to 0.4 (Fig. 6A) that fall between average values of hypoxic (API > 0.4) and oxic (API < 0.2) conditions27. Based on these values, we interpret API values at AGS to indicate seasonal flooding pulses across a riparian wetland29 that drove cyclic organic matter oxidation via oxygen exposure at the sediment–water interface after inundation30. Moreover, all samples from AGS lack detectable concentrations of the isoprenoidal lipids pristane and phytane. Because pristane/phytane are dominantly produced from chlorophyll degradation31,32, and (photo)degradation rates are rapid in most fluviolacustrine systems33, lacking pristane/phytane at AGS is consistent with (sub)seasonal redox oscillations, aerobic conditions and high-light intensities characteristic of barren medial floodplain channel deposits with little standing plant biomass34.

n-Alkanoic acids. The polar fractions of AGS lipids show an archetypal bimodal distribution of saturated mid- and long-chain n-alkanoic acids (i.e., n-docosanoic acid [nC22:0] to nC26:0 and nC28:0 to nC32:0, respectively) (Fig. 2C) with an even-over-odd predominance that is indicative of mixed aquatic and terrestrial higher vegetation inputs, respectively35. Even so, shorter-chained homologues viz. nC16:0 and nC18:0 dominate among polar moieties at AGS. These shorter-chain acids are ubiquitous among plants, animals and fungi, but are especially prominent in algae and bacteria35. Therefore, we used the so-called terrigenous to aquatic ratio (TAR FA)—the ratio of long-chain versus shorter-chain alkanoic acids35—for determining proportional lipid input from disparate organic matter sources. Low calculated TAR FA values of 0.05 (Fig. 6F) at AGS indicate aquatic or algal lipids dominated biomass input35 despite its shoreside setting. The diagnostic occurrence of mono- and polyunsaturated nC12 alkanoic acids suggest there was a major input from microbes and freshwater phytoplankton26, with further supports our interpretation of AGS as a riverside wetland that experienced frequent flooding.

Stable carbon isotope signatures among plant biomarkers. Alkane δ13C values. Previous studies report fossil and tenable molecular evidence of lacustrine vegetation viz. aquatic macrophytes in Bed I sediments
at Olduvai, indicating parallelism with wetlands in contemporary East Africa. Molecular isotopes evidence at AGS features similar support through the stable carbon isotopic signatures of \( n \)-hentriacontane (\( \delta^{13}C_{31} \)) that have values of \(-25.0 \pm 1.1\%\) (Figs. 4 and 6H), which we interpret to indicate a complex mixture of C3 and C4 plant inputs. Macrophytes with aquatic (e.g., Hydrilla), floating (e.g., Potamogeton), and emergent (e.g., Cypres and Typha) habits are common in recent East African wetlands, and have similar \( \delta^{13}C \) values as we observe at AGS. However, macrophytic carbon sources are often influenced by partial incorporation of dissolved \( HCO_3^- \) (which causes increased, C4-like \( \delta^{13}C \) values) in aquatic environments, and likewise are affected by physiological differences among plant growth forms and functional types that lead to interpretational difficulties of \( \delta^{13}C_{31} \) values vis-à-vis differentiating plants with bicarbonate uptake mechanisms versus cooccurring graminoids with C4 photosynthetic pathways.

To determine source and input differences among plant-lipid biosignatures, we applied basic analysis of variance (ANOVA) to our measured \( \delta^{13}C \) values for odd-numbered homologues (i.e., \( nC_{23} \), \( nC_{25} \), \( nC_{27} \), \( nC_{29} \), \( nC_{31} \)) in sediments at AGS. In this context, the mid-chain \( n \)-alkanes (\( nC_{23} \) and \( nC_{25} \)) (Fig. 6G) are derived from submerged/floating macrophytes, and longer-chain \( n \)-alkanes (\( > nC_{25} \)) are dominated by plants with terrestrial habitats. Resultant \( \delta^{13}C \) ANOVA data demonstrate a statistical difference (\( p \)-value < 0.01) between \( \delta^{13}C_{31} \) as compared to contemporaneous mid-chain and longer-chain \( n \)-alkanes. Our results suggest that \( nC_{31} \) had a discrete source with more \( ^{13}C \)-enriched lipids—such as arid-adapted C4 graminoids—as compared to other \( n \)-alkanes. In contrast, the other mid- and longer-chained homologues do not show statistical differences in average isotopic composition. With this in mind, we suggest that the algae and submerged/floating aquatic plants at AGS incorporated higher amounts of dissolved \( HCO_3^- \) as a source of carbon, resulting in heavier \( \delta^{13}C \) values in mid-chain \( n \)-alkanes. Complementary proxies viz. \( n \)-alkane ratios (Figs. 3A,B, 6A–E) further suggest that AGS functioned like a seasonal-to-permanent freshwater-fed floodplain or river margin dominated by graminoids and C3-like macrophytes with sparse woody plants and limited C4 grasses. This is in accordance with the geological and sedimentological description that suggested a playa lake margin with small rivers with low-energy.

Alkanoic acid \( \delta^{13}C \) values. The ubiquity of \( nC_{16:0} \) and \( nC_{18:0} \) makes their \( \delta^{13}C \) values useful to differentiate organic matter sources. Individual \( \delta^{13}C_{16:0} \) and \( \delta^{13}C_{18:0} \) values range from \(-26.2 \) to \(-28.3\%\) with a \(-2\%\) offset that indicates respective organic matter sources had a dominantly C3 photosynthetic pathway (Fig. 5A). Further, individual \( \delta^{13}C_{16:0} \) and \( \delta^{13}C_{18:0} \) values show similar \( \delta^{13}C \) values as compared to mid-chain (\( nC_{23} \) and \( nC_{25} \)) and longer-chain (\( nC_{27} \) and \( nC_{31} \)) alkanes, suggesting both compound classes share similar organic matter sources. The crossplot of \( \delta^{13}C_{16:0} \) against the offset between \( \delta^{13}C_{16:0} \) and \( \delta^{13}C_{18:0} \) (\( \Delta^{13}C_{18:0-16:0} \)) demonstrates additional differences in \( n \)-alkanoic acid inputs derived from C3 and C4 sources (Fig. 5B). Considered together, molecular isotopic values suggest that AGS was a microhabitat defined by a mixture of C3-graminoids with extensive aquatic plant inputs.

The Zinj Paleolandscape and hominin evolution. At least three hominin taxa—including Homo cf. ergaster, Paranthropus boisei and Homo habilis—have been recovered from the Zinj Paleolandscape. Across this contiguous archaeological horizon, artifacts and fossil bones are embedded within a distinctive silty-clay layer covered by airfall Tuff IC, which suggests that the remains were captured in situ under volcanic ash fallout. Rapid burial fostered the exceptional preservation of fine-sediment features (e.g., root ichnofossils), macrofossils and biomarkers across its surface. Sedimentological features at AGS further reveal that this site was situated at littoral–supralittoral interface, where alluvial fans and floodwater river runoff interposed the
mudflat littoral zone. Altogether, such multidisciplinary proxies reveal that Olduvai, and the Zinj Paleland-scape especially, presented hominins with a variegated landscape of heterogeneous resource distributions, and thus impacted hominin diets and behaviour.

Diet is considered to serve as a major selective force amid hominin encephalization, and the intake of ‘essential’ lipids (e.g., polyunsaturated fatty acids), which are uniquely prevalent in wetland flora, is critical to cerebral development in modern infant humans. Aquatic macrophytes proliferate in wetlands today in East Africa and likely provided hominins with high-quality provision, rootstocks and leaves all year long. Contemporary pan-African macrophytes rarely use dedicated C4 photosynthesis; but, these (semi)aquatic plants can incorporate bicarbonate when in alkaline waters and, in doing so, create C4-like δ13C isotopic signature. Mid-chain n-alkanes from AGS reveal δ13C-enriched biomass (Fig. 4), and that their source vegetation (i.e., macrophytes) can account for high δ13C signatures in hominin diets, as reflected through bioapatite isotopes and dentition analyses.

Our molecular and isotope data (Figs. 3A, Fig. 6A,C) suggest there was a intermittently-waterlogged floodplain environment at AGS, which is consistent with earlier mineralogical descriptions at the vicinal DS site (Fig. 1C). We suggest there was a notably perennial large stream or river near AGS that flowed from south-to-north into nearby paleolake Olduvai, and brought with it the allochthonous plant lipid from nearby grasslands and forest patches. Given overall low relief in the immediate area around AGS, which likely produced lower-energy paludal flow, entrainment of allochthonous materials most likely peaked through seasonal flooding pulses. In any case, associated freshwater fluvial input must have attracted both hominins and large carnivores alike to AGS.

Biomarkers at AGS build upon earlier reconstructions at Olduvai and the Zinj Palelandscape that imply plants and freshwater distribution exerted direct influence on hominin behaviour. However, in contrast to earlier reconstructions among penecontemporaneous sites at Olduvai Gorge, our data at AGS indicates hominins took strategic advantage of low- or unvegetated locations in addition to dense woodland thickets, low-visibility

Figure 5. Stable carbon isotope composition (δ13C values) of individual fatty acids in sediments excavated from at AGS. (A) δ13C16:0 and δ13C18:0 values are shown as medians with their median absolute deviation (± MAD) and ANOVA test distributions. Boxplots depict distributional differences between individual homologue δ13C values. (B) Qualitative isotopic source allocation of dominant fatty acids extracted from sediments at AGS. Graphical framework modified from Evershed and colleagues.
Figure 6. Key proxies measured for sediments excavated from AGS. (A) API: alcohol preservation index uses only n-hexacosanol and n-nonacosane. Higher values indicate more hypoxic conditions. C\textsubscript{33}/C\textsubscript{31}: ratio of nC\textsubscript{33} to nC\textsubscript{31}. Higher values indicate more grasses. P\textsubscript{alg}: ratio of algal lipids (nC\textsubscript{17} + nC\textsubscript{19}) relative to algal and terrestrial plant lipids (nC\textsubscript{17} + nC\textsubscript{19} + nC\textsubscript{29} + nC\textsubscript{31}). Higher values indicate more algal input. ACL = average chain length of individual n-alkane abundances. CPI = (Σodd(C\textsubscript{21–33}) + Σodd(C\textsubscript{23–35}))/ (2Σeven C\textsubscript{22–34}): carbon preference index, which is indicative of the abundance of odd over even carbon chain lengths. In general, lower CPIs indicate microbial inputs or maturation of the sample. TAR\textsubscript{FA}: terrigenous to aquatic n-alkanoic acids ratio reflecting the importance of terrigenous as compared to aquatic sources (C\textsubscript{24} + C\textsubscript{26} + C\textsubscript{28})/(C\textsubscript{14} + C\textsubscript{16} + C\textsubscript{18}). Higher values indicate more terrestrial input. (G, H) Plant-lipid δ\textsuperscript{13}C values for n-alkane C\textsubscript{25} and C\textsubscript{31}. Higher values indicate more C4 plant dominated environment.
papyrus stands, and tall grassland. AGS itself likely harboured occasional large woody plants such as Hyphaene palms, but the abundance of this vegetation would have been nominal.

The occurrence of discrete plants on otherwise unvegetated fluviolacustrine surfaces might be one explanation for differing paleoecologic reconstructions with biomarkers, which integrate immediate and upstream organic matter inputs, as compared to, e.g., phytoliths, which capture only productive in situ vegetation and do not transport downstream. Regardless, vicinal (over)bank deposits and levee ridges would be dominated by generally groundcover vegetation such as macrophytes, pteridophytes (e.g., ferns) and low woody plants, meaning that hominins at AGS would have an unencumbered view of the surrounding landscape, including precious refuge about 400 m away at FLK Zinj itself (Fig. 1C). Biomarkers across the Zinj Paleolandscape and from the AGS site show distributions of plants that suggests critical resources had a direct implication on hominin behaviour at Olduvai Gorge.

The AGS archaeological site contains one of the highest densities of faunal remains on the Zinj Paleolandscape after DS, which to date is the biggest window into an Early Pleistocene anthropogenic site. This suggests that the area at AGS must have been occupied for repeated instances of large carcass consumption. To boot, AGS was dominated by (semi)aquatic plants, minimal trees or shrubs, although in all likelihood hominins were occupying the site especially for its vicinity to flowing water. In contrast, FLK NN (500 m west from AGS) contained limited faunal remains and lithics within an environment that featured floating and submerged aquatic plants located nearby freshwater carbonates (tufa). If AGS was not a terrestrial plant-dominated habitat, because of its barren vegetation, and hominin and carnivore visibility were similar, as in open grasslands, this poses the question of how hominins efficiently avoided carnivore hazards for the prolonged occupation(s) inferred from the intensity of ungulate carcass butchery documented at the site (Fig. 7). This is mostly notable, especially given the paucity of taphonomic evidence signalling carnivore modification of carcass remains. The evidence is suggestive of hominins having carved a competitive niche against other predators by efficiently fending off their hazard.

By comparing our results at AGS to previously published data about biomarker distributions amid the Zinj Paleolandscape, we suggest that AGS functioned as a seasonally waterlogged, low-vegetation environment characterised by dense accumulations of butchery-process debris within a wider mosaic environment that harboured both open and dense, closed ecotones, such as at DS. FLK Zinj, DS and PTK are the other three anthropogenic sites occupying the same thin clay stratum as AGS on the Zinj Paleolandscape. These three sites were created in a wooded to forested alluvial environment. The close spatial association between stone tools and fossil bones indicates a functional relationship resulting from butchery. This is further supported by the abundant cut-marked and percussed bones retrieved in the archaeofaunal assemblage, which is currently under analysis. Given that in the other anthropogenic sites, with areas sampled similar to the size of the area sampled at AGS, the paleobotanical signal is of closed vegetation, we assume that the area sampled at AGS is equally representative of the main vegetational characteristics of the setting. In this case, the signal retrieved, in contrast with the other anthropogenic middle Bed I sites is of a fairly open environment. The butchery patterns documented in those sites are identical to those observed at AGS (work in progress), with a similar number of animals and taxa represented and a similar single-round cluster site structure. This latter feature is clearly showing a carcass butchery and consumption pattern and a distinctive use of the space that contains crucial socio-reproductive information. To conclude, we suggest the spatial landscape ecology patterns...
defined by macro- and molecular fossils reveal hominin engagement in social transport of large resources, such as bringing animal carcasses and freshwater-sourced food to AGS from the surrounding grasslands and lakeside environments.

Conclusions
Our multi-proxy geochemical interpretations of the new site called AGS at Olduvai Gorge ca. 1.84 Ma reveal that it was a sparsely vegetated, high-visibility paludal location on a riverbank within a wider mosaic environment defined by the Zinj Paleolandscape. Standing plant biomass at AGS was dominated by aquatic vegetation viz. macrophytes and C4 graminoids, consistent with its riparian and lake margin setting. Comparison with literature data for coeval localities at Olduvai Gorge suggest that this ancient landscape was rich in ecotones with abrupt transitions between disparate vegetation communities, as is often observed today in East African wetlands. Given the markedly patchy paleoenvironment that defined the vicinal Zinj Paleolandscape and the unique (sub)seasonal floodplain at AGS, we conclude early hominins at Olduvai Gorge selected locations for cooperative resource processing—such as animal butchery—as related to water resources rather than refuge (i.e., closed thickets). This conclusion diversifies the environments in which vertically discrete anthropogenic sites occur and furthermore insinuates that hominins felt equally at ease in such environments. Considered together, new and old data at Olduvai reveal that hominins had reached an adaptive carnivore status by 1.84 Ma that enabled them to cope with terrestrial predation risks and fend off other carnivore competitors.

Materials and methods
Sampling. Samples were collected from sediment 0–2 cm below Tuff IC that is isochronous with Zinj level 22A, in a silty-clay layer where bones and lithic tools occurred in situ (Fig. 1C). Representative sediment samples (~50 g; n = 24) from individual 1 m² gridding quadrats (Fig. 1D) were collected between fossil remains and stone tools with a clean aluminium spoon.

Biomarker extraction and isolation. Sediments were freeze-dried and powdered with a clean agate mortar and pestle. Lipids were extracted from sediments via an accelerated solvent extractor (Dionex ASE 350 system) with dichloromethane (DCM) and methanol (MeOH) (9:1 vol/vol) in 3 cycles at 100 °C (10.3 MPa) with static time of 5 min. Resultant total lipid extracts (TLE) were dried beneath a gentle stream of nitrogen, and then derivatized through acid methanolysis (0.5 M HCl in MeOH diluted with ultrapure water) before subsequent liquid–liquid isolation into hexane:DCM (4:1 vol/vol) [17]. Derivatized TLEs were concentrated and chromatographically partitioned into three fractions using deactivated silica gel (2% H₂O by weight) by elution in methanol) were made via δ¹³C for esterified benzene-1,2-dicarboxylic acid (phthalic acid [Schimmelmann = 1152), to 0.3‰ (FAMEs, -alkanes, (Mixture F8-3 [Schimmelmann Standards]). Standard deviation of the calibration standards is 0.2‰ (n = 24) from individual 1 m² gridding quadrats (Fig. 1D) were collected between fossil remains and stone tools with a clean aluminium spoon.

Molecular analysis. Lipid biomarkers were characterized by gas chromatography-mass spectrometry (GC–MS; Thermo Scientific TRACE 1310 [GC] with coupled ISQ LT [MS]) by splitless injection of 1 μL aliquots of individual lipid fractions onto a 60-m VF1 fused-silica column (0.25 mm × 0.25 μm) before combustion over copper, nickel, and platinum wire with oxygen and helium at 1000 °C. Isotopic values were normalized and corrected using a mixture of n-alkanes (nC₁₄ to nC₃₀) of known isotopic composition (Mixture B4 [Schimmelmann Standards]) or a mixture of fatty acid methyl esters (FAMEs [C₁₂:0, C₁₆:0, C₁₈:0, C₂₀:0]) of known composition (Mixture F8-3 [Schimmelmann Standards]). Standard deviation of the calibration standards is 0.2‰ (n-alkanes, n = 1152), to 0.3‰ (FAMEs, n = 288). Isotopic corrections for carbon added through esterification (0.5 M HCl in methanol) were made via δ¹³C for esterified benzene-1,2-dicarboxylic acid (phthalic acid [Schimmelmann Standards]) that then was used to correct for isotopic mass-balance of derivative carbon.

Data availability
All data generated or analysed during this study are included in this published article or in the accompanying Supplementary Information file.

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Author contributions
L.M.S., M.D.R., and C.R.M. conceived the study. L.M.S., C.R.M. and A.S. conducted the investigation and methodology. L.M.S., D.U., J.A., M.D.R. and C.R.M. conducted fieldwork excavations. All authors wrote, reviewed, and edited the manuscript.

Competing interests
The authors declare no competing interests.

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