

**Direct chemical evidence of dairying by hunter-gatherers in the highlands of  
Lesotho in the late first millennium AD**

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## **Abstract**

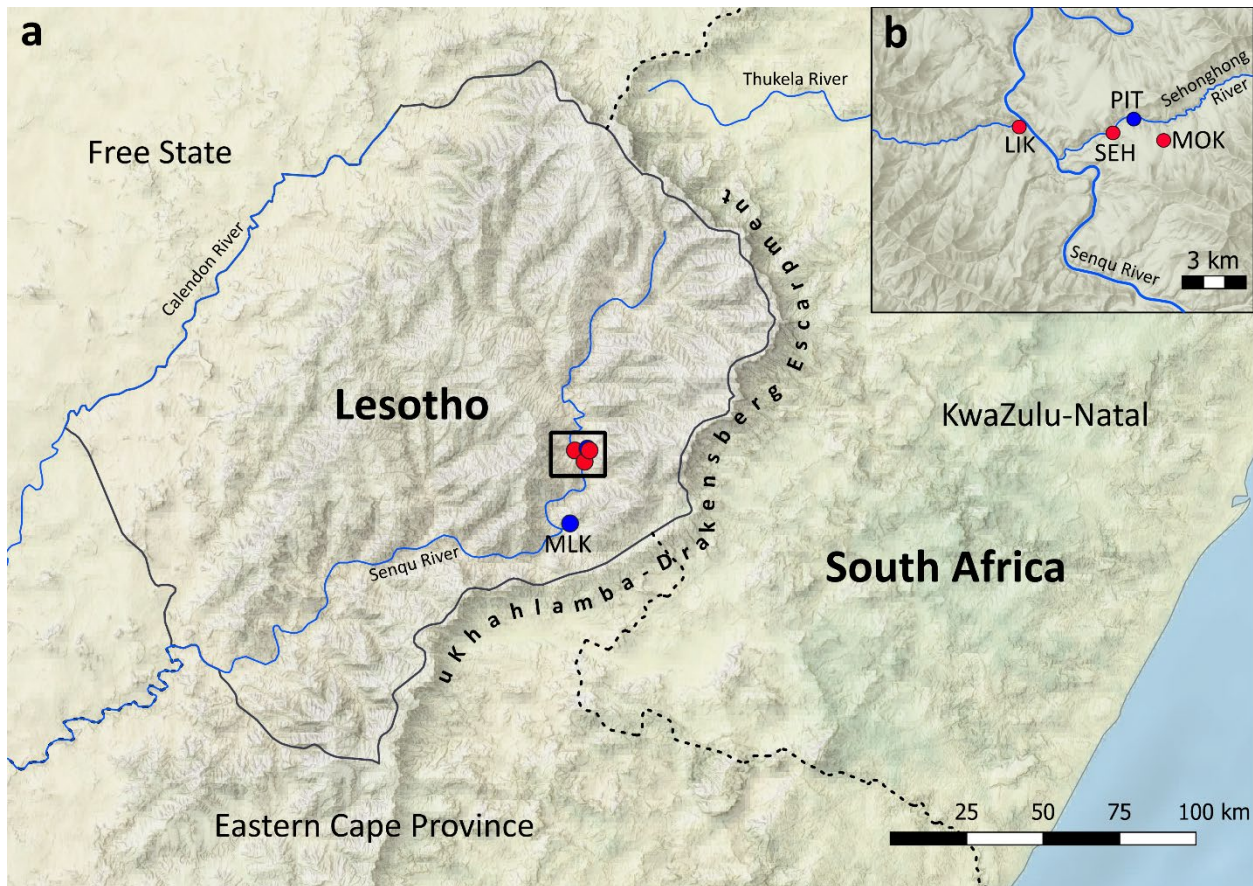
The recovery of Early Iron Age (EIA) artefacts and domestic animal remains from hunter-gatherer contexts at Likoaeng, Lesotho, has been argued to indicate contact between highland hunter-gatherers and EIA agropastoralist communities settled in lowland areas of south-eastern Africa during the second half of the first millennium AD. However, disagreement between archaeozoological studies and ancient DNA means that the possibility that those hunter-gatherers kept livestock themselves remains controversial. Here we report analyses of pottery-absorbed organic residues from two hunter-gatherer and one agriculturalist sites in highland Lesotho to reconstruct prehistoric subsistence practices. Our results demonstrate the exploitation of secondary products from domestic livestock by hunter-gatherers in Lesotho, directly dated to the seventh century AD at Likoaeng and the tenth century AD at the nearby site of Sehonghong. The data provide compelling evidence for the keeping of livestock by hunter-gatherer groups and their likely incorporation as ancillary resources into their subsistence strategies. These findings support previous osteoarchaeological identifications of domestic livestock at both archaeological sites, notwithstanding contrary results from ancient DNA obtained at Sehonghong.

## Introduction

Early Iron Age (EIA) populations who combined cereal and legume cultivation with livestock-keeping and almost certainly spoke Bantu languages began settling in southernmost Africa from the third century AD, initially focusing on the Woodland Savanna Biome of the region's summer rainfall zone<sup>1-3</sup>. Only in the early centuries of the second millennium AD did they begin to penetrate the grassland areas of Gauteng or northern KwaZulu-Natal, and effective occupation of the Highveld of the Free State and western Lesotho was not established until the seventeenth century. In contrast, the Maloti-Drakensberg Mountains of the remainder of Lesotho and the upland areas to its east along the uKhahlamba-Drakensberg Escarpment remained the domain of hunter-gatherer groups until the nineteenth century and the earliest farming villages along the upper portions of Lesotho's Senqu River (Fig. 1a) were not established until 1878<sup>4</sup>. Despite their geographical separation, rock art and historical accounts have long been cited as evidence of prolonged contact between Maloti-Drakensberg hunter-gatherers and agricultural populations in neighbouring areas<sup>5-10</sup>. On the farmer side of this equation, linguistic and cultural borrowings among both Nguni and South Sotho speakers attest to such contacts<sup>11-13</sup>, as do more recent genetic studies that point to considerable admixture between hunter-gatherers and Bantu-speaking agropastoralist groups in south-eastern Africa<sup>14-17</sup>.

At Likoaeng in the highlands of Lesotho (Fig. 1), excavations in the 1990s uncovered remains in Layer 1 (Supplementary Figs. 1; 2) of domestic sheep and cattle, a few fragments of iron and a single decorated EIA potsherd from a context securely radiocarbon dated (on bone, charcoal and iron) to the second half of the first millennium AD (Table 1)<sup>18</sup>. Other aspects of the assemblage suggest that this was otherwise an exclusively hunter-gatherer site, comparable to others known in the region. The rest of the pottery, for example, falls into a class of thin-walled (mean thickness ~6–8 mm), almost invariably grey to black, grit-tempered and undecorated ceramics found in multiple hunter-gatherer contexts elsewhere in highland Lesotho and across the uKhahlamba-Drakensberg Escarpment in KwaZulu-Natal and the Eastern Cape Province<sup>19,20</sup>. Associated stone and bone artefacts, which include scrapers, adzes and arrowpoint/linkshaft fragments, are also typical of such sites and fall within the well-known Final Later Stone Age (post-classic Wilton) complex<sup>21-24</sup>. Contemporary EIA pottery, on the other hand, is thick-walled (mean thickness >10 mm), often decorated, and generally oxidised, rather than reduced, characteristics only matched by the one EIA sherd already mentioned<sup>3</sup>. Collectively, this evidence suggested contact between highland hunter-gatherers and agropastoralists in the lowlands of KwaZulu-Natal on a scale sufficient to account for the presence of domestic livestock within the Senqu Valley, a

millennium or more before they are otherwise attested there. Isolated events such as raiding, trade or even hunter-gatherer care for agropastoralists' livestock were deemed unlikely given the distance to the nearest known EIA village (>150 km over rugged terrain), the ready availability of pasture within KwaZulu-Natal and the 3000-m high barrier of the uKhahlamba-Drakensberg Escarpment that intervenes between it and Likoaeng (Fig. 1a)<sup>21,23</sup>. It was therefore suggested that the Layer 1 assemblage might support the 'hunters-with-sheep' hypothesis previously proposed by Sadr<sup>25,26</sup> with respect to the Western Cape Province of southern Africa whereby some hunter-gatherer groups successfully acquired livestock from food-producers and incorporated them as ancillary resources into their own subsistence strategies.



**Figure 1. a)** Location of sites included in the study (red) and mentioned in the text (blue) within Lesotho, including Melikane (MLK). **b)** Close-up of the locality of Likoaeng (LIK), Sehonghong (SEH), Pitsaneng (PIT) and Mokatlapi (MOK). (Base map downloaded from Natural Earth, free vector and raster maps available at [naturalearthdata.com](http://naturalearthdata.com)).

Site	Layer	Laboratory number	Material	<sup>14</sup> C age (BP)	Calibrated age range (2σ)	Notes	Reference
Likoaeng	1	GrA-23237	Bone - sheep/goat ulna	1285 ± 40	AD 681–884		Mitchell, et al. <sup>21</sup>
Likoaeng	1	GrA-26831	Iron	1290 ± 30	AD 682–879		Mitchell, et al. <sup>21</sup>
Likoaeng	1	Pta-7877	Charcoal	1310 ± 80	AD 641–969		Mitchell, et al. <sup>21</sup>
Sehonghong	DC	Wk-34786	Bone – distal metapodial fragment (SHH_7355)	1130 ± 30	AD 892–1018	Morphological ID: <i>Ovis aries</i> (sheep) aDNA ID: <i>Redunca fulvorufula</i> (reedbuck)	Horsburgh, et al. <sup>27</sup>
Sehonghong	DC	Wk-34785	Bone – tarsal fragment (SHH_7449)	1130 ± 30	AD 892–1018	Morphological ID: <i>Bos taurus</i> (cattle) aDNA ID: <i>Tragelaphus oryx</i> (oryx)	Horsburgh, et al. <sup>27</sup>
Sehonghong	DC	Wk-34784	Bone – distal first phalanx fragment (SHH_7356)	1200 ± 30	AD 775–983	Morphological ID: <i>Bos taurus</i> (cattle) aDNA ID: <i>Tragelaphus oryx</i> (oryx)	Horsburgh, et al. <sup>27</sup>
Sehonghong	DC	Pta-6084	Charcoal	1240 ± 50	AD 685–971	This sample was published and previously attributed to Layer GAP. The new Horsburgh et al. <sup>23</sup> dates from Layer DC and re-assessment of the sample's stratigraphic provenance suggest that it in fact comes from DC.	Mitchell <sup>28</sup>
Sehonghong	DC	Wk-34787	Bone – proximal radius (SHH_7459)	5870 ± 30	4787–4581 BC	Morphological ID: <i>Ovis aries</i> (sheep). No DNA recovered. The date indicates that this cannot be from a domestic animal and that the bone must have moved upward from the underlying mid-Holocene Layer GWA.	Horsburgh, et al. <sup>27</sup>
Sehonghong	GAP	Pta-885	Charcoal	1400 ± 50	AD 594–771	From the original 1971 excavation of the site.	Carter, et al. <sup>29</sup>
Sehonghong	GAP	Pta-6063	Charcoal	1710 ± 50	AD 247–520	Associated with pressure-flaked stone projectile points.	Mitchell <sup>28</sup>

**Table 1.** Published radiocarbon dates from pottery-containing horizons at Likoaeng and Sehonghong, Lesotho. BP = radiocarbon years before 1950. All dates have been recalibrated using the 2013 southern hemisphere calibration curve<sup>30</sup> in OxCal 4.3<sup>31</sup>.

Likoaeng is not alone in its evidence for contact between Maloti-Drakensberg hunter-gatherers and agropastoralists. A domestic sheep mandible excavated from Melikane, 40 km south of Likoaeng (Fig. 1a), is stratigraphically associated with a date of cal AD 545 – 656 (95.4% probability: Pta-1364: 1450 ± 40 BP)<sup>32</sup>. Much closer to Likoaeng, two rockshelters — Sehonghong<sup>33</sup> and the nearby site of Pitsaneng<sup>34</sup> (Fig. 1b) — have both produced faunal remains identified as domestic sheep and cattle in layers dating to the first and second millennia AD, implying that hunter-gatherer possession of livestock may have been a recurrent, rather than a temporally isolated, phenomenon<sup>35</sup>. The story remains contentious however, with recently published archaeogenetic studies arguing that the presence of domestic species in hunter-gatherer contexts in southern Africa has been over-estimated<sup>27,36,37</sup>. At both Blydefontein in South Africa's Eastern Cape Province and at Sehonghong in Lesotho, analysis of the ancient DNA of faunal remains morphologically identified as domestic species has instead identified the genetic signatures of wild species, leading to the conclusion that previous morphological analyses are incorrect<sup>27,36,37</sup>. Although these claims have been refuted by the zooarchaeologist involved in the original analysis<sup>38</sup>, debate over the relative merits of morphological analysis *versus* molecular analysis continues<sup>39-42</sup>. Thus far, however, there has been no biochemical evidence to support the long-term exploitation of domestic species by hunter-gatherer groups in the Lesotho highlands.

In recent decades, lipid residue analysis of archaeological pottery has become a core tool for exploring ancient diet. Gas chromatography (GC), GC-mass spectrometry (GC-MS) and compound-specific stable carbon isotope analysis allow differentiation between ruminant (e.g. cattle, sheep and goats) and non-ruminant (e.g. pigs) adipose fats. Crucially, using this approach, ruminant dairy fats can be distinguished from the carcass fats due to biosynthetic differences between the major fatty acids<sup>43-47</sup>. This technique has proven pivotal for tracing the spread of dairying practices across Europe<sup>44,48-55</sup>, the Levant<sup>56,57</sup>, Central Asia<sup>58</sup> and northern<sup>59,60</sup> and eastern<sup>61,62</sup> Africa. Increasingly high sensitivity mass spectrometry has further allowed the identification of a suite of diagnostic aquatic biomarkers which may be preserved in absorbed lipid residues, including dihydroxy acids (DHYA),  $\omega$ -(*o*-alkylphenyl)alkanoic acids (APAAs) and isoprenoid fatty acids (IFAs)<sup>63</sup>. Recent advances in the direct radiocarbon dating of individual lipid compounds extracted from archaeological pottery now provide the potential to gain crucial chronological context for the interpretation of ancient diet<sup>62,64,65</sup>.

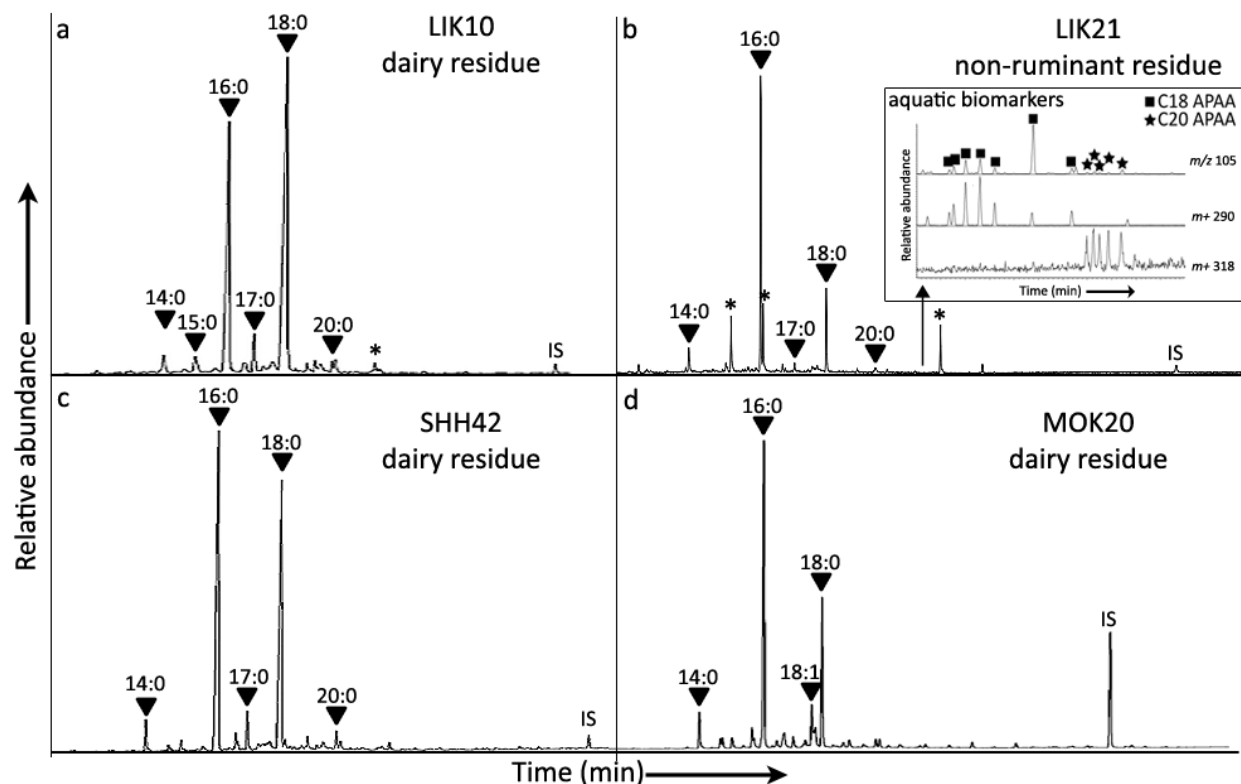
Lipid residue analysis of hunter-gatherer pottery excavated from Likoaeng and Sehonghong and agropastoralist ceramics from the surface of a nearby abandoned Basotho village was undertaken to explore the diet of these groups after the arrival of agropastoralists in adjacent parts of southern Africa

from the early centuries AD. The specific aim was to determine if there was any evidence for contact with agropastoralist groups through the subsistence strategies of highland hunter-gatherers. The results hold important implications for understanding the interactions between, and practices of, indigenous and incoming groups since the arrival of agriculture in south-eastern Africa in the first millennium AD.

## Results

### *Lipid preservation and distribution*

Thirty potsherds from Likoaeng (Layer 1), 17 from Sehonghong (eight from Layer GAP, nine from Layer DC) and 27 from the Basotho village Mokatlpoli were analysed in the study. Lipid preservation was excellent at all three sites. Likoaeng had an average yield of 0.4 mg lipid per gram of potsherd ( $\text{g}^{-1}$ ) with 87% of sherds ( $n=27$ ) yielding sufficiently high lipid concentrations for analysis via gas chromatography – combustion – isotope ratio mass spectrometry (GC-C-IRMS) (Supplementary Table 1). The high rate of preservation at Likoaeng is comparable with sites in the hyper-arid conditions of North Africa<sup>59</sup>. At Sehonghong, 41% of potsherds ( $n=7$ ) contained sufficient lipids for isotopic analysis (five from Layer DC, two from Layer GAP; Supplementary Table 2), while at Mokatlpoli 41% ( $n=11$ ) did so (Supplementary Table 3). One exceptional sherd from Sehonghong Layer DC contained  $> 10\text{mg g}^{-1}$ . Excluding this outlier, the average lipid yield from Sehonghong was  $0.5 \text{ mg g}^{-1}$ , whereas that from Mokatlpoli was  $0.3 \text{ mg g}^{-1}$ . The composition of the majority of lipid extracts resembled degraded animal fats (Fig. 2), dominated by  $\text{C}_{16:0}$  and  $\text{C}_{18:0}$  fatty acids although five residues from the historic site of Mokatlpoli and one from Layer GAP at Sehonghong contained high intensities of unsaturated fatty acids, possibly deriving from plant-based oils<sup>62</sup>. Only the animal-derived fats are considered further here.



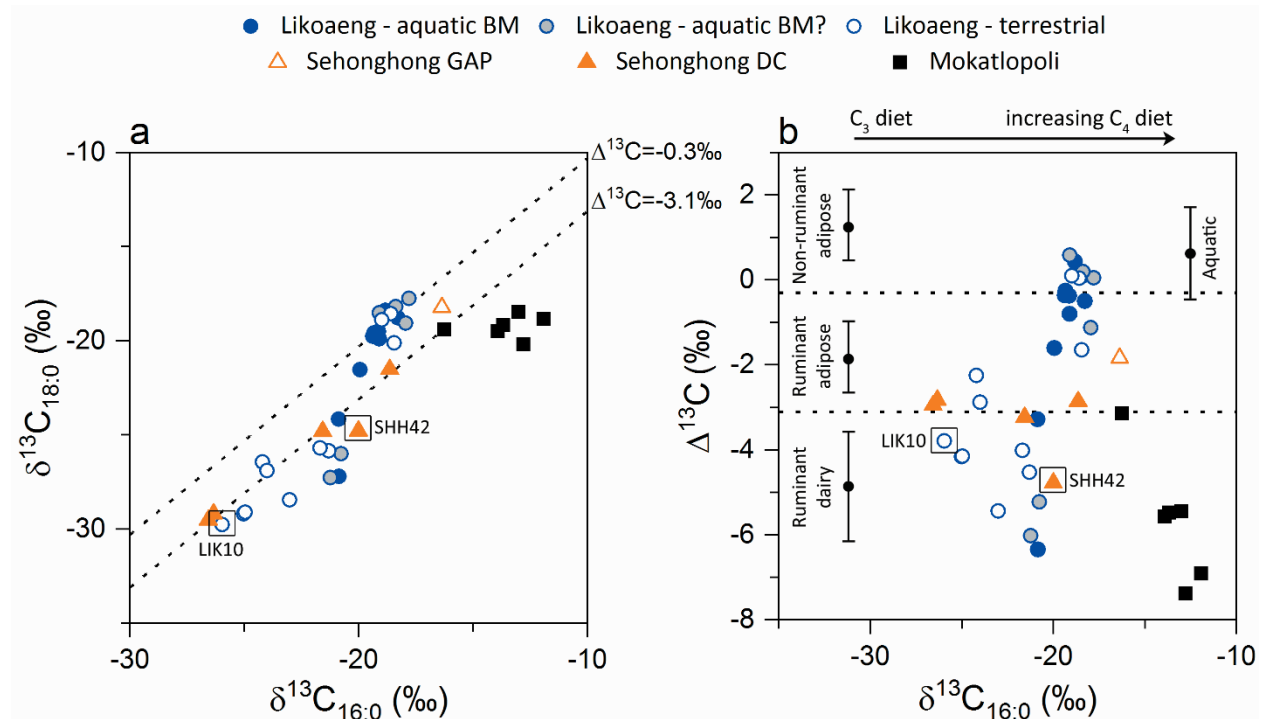
**Figure 2.** Partial gas chromatograms from four extracted lipid residues with compositions characteristic of degraded animal fats: **a)** dairy residue from Likoaeng which was directly radiocarbon dated; **b)** non-ruminant adipose residue from Likoaeng; inset shows mass chromatogram from same residue run in SIM mode ( $M/z$  105,  $M+ 290$ ,  $M+ 318$ ) identifying aquatic biomarkers  $C_{18:0}$  and  $C_{20:0}$  APAAs; **c)** dairy residue from Layer DC at Sehonghong rock shelter which was also directly radiocarbon dated and **d)** dairy residue from Mokatlapi. Peaks marked with black triangles represent individual fatty acids labelled (x:y) with carbon chain length x and degree of unsaturation y. IS is the internal standard (*n*-tetratriacontane). Asterisks mark phthalate peaks.

### Compound specific stable isotopic values

The compound-specific stable carbon isotope values of lipid residues extracted from pottery from Likoaeng, Sehonghong and Mokatlapi are shown in Fig. 3 (Supplementary Tables 1-3). The  $C_{16:0}$  and  $C_{18:0}$  fatty acids exhibited a wide range of  $\delta^{13}C$  values, from -30‰ to -13‰ (Fig. 3a). To allow comparison of lipid residues derived from mixed  $C_3/C_4$  sources the results are compared using the globally applicable  $\Delta^{13}C$  proxy ( $\delta^{13}C_{18:0} - \delta^{13}C_{16:0}$  plotted against  $\delta^{13}C_{16:0}$ ; Fig. 3b), which emphasises metabolic origins of fats over environmental variability<sup>48,59,67,68</sup>. From Layer 1 at Likoaeng, 10 of the lipid extracts exhibited  $\delta^{13}C_{18:0}$  and  $\delta^{13}C_{16:0}$  values characteristic of ruminant dairy fats, 10 those of ruminant adipose fats and seven those of non-ruminant adipose fats. The single animal fat residue from Layer GAP at Sehonghong had an isotopic composition characteristic of ruminant adipose fat whereas two of the lipid extracts from Layer DC had  $\delta^{13}C_{18:0}$  and  $\delta^{13}C_{16:0}$  values characteristic of dairy fats and three of ruminant adipose fats. At



Mokatlapoli, five of the degraded animal fats derived from dairy products and one sits on the border between dairy and ruminant adipose fat. Due to the low content of  $C_{18:0}$  fatty acids in aquatic fats, the mixing of these with terrestrial adipose fats can lead to more negative  $\Delta^{13}C$  values (Cramp et al, 2014, Proc R Soc B). A theoretical mixing model based on the data obtained in this study indicates that such mixtures would not produce  $\Delta^{13}C$  values reaching the range of ruminant dairy fats and would be far removed from the very negative  $\Delta^{13}C$  values obtained for the dairy residues at all three sites (Supplementary Fig. S6).

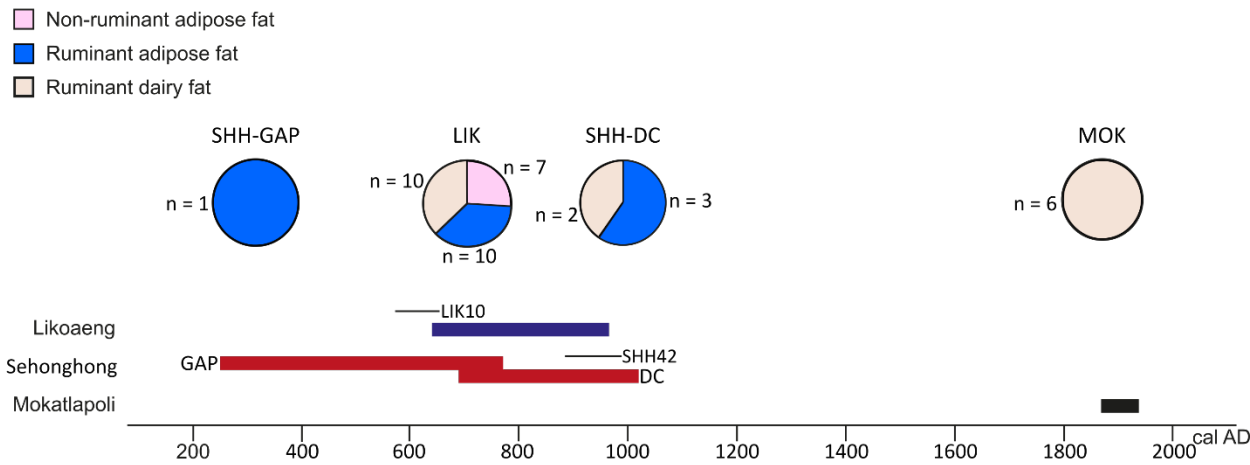


**Figure 3. a)**  $\delta^{13}C_{18:0}$  values plotted against  $\delta^{13}C_{16:0}$  values and **b)**  $\delta^{13}C_{18:0} - \delta^{13}C_{16:0}$  ( $\Delta^{13}C$ ) values plotted against the  $\delta^{13}C_{16:0}$  values obtained from pottery organic residues with biomolecular compositions characteristic of degraded animal fats from Likoaeng Layer 1, Sehonghong rock shelter from Layer GAP and Layer DC and from the late nineteenth-/early twentieth-century agricultural village Mokatlapoli. The dashed lines delimit the  $\Delta^{13}C$  values ranges typical of dairy ( $\Delta^{13}C < -3.1\text{‰}$ ), ruminant adipose ( $\Delta^{13}C = -3.1\text{‰} - -0.3\text{‰}$ ) and non-ruminant adipose ( $\Delta^{13}C > -0.3\text{‰}$ ) products. Dairy residues LIK10 and SHH42 (boxed) were directly dated. Residues with evidence for aquatic biomarkers (BM) are indicated. The ranges in **b** show the mean  $\pm 1$  s.d. from a database of modern terrestrial reference values published in <sup>59</sup> and aquatic reference values published in <sup>48,58,63,69</sup>. The modern reference ranges have been corrected for post-industrial carbon contribution +1.3‰; <sup>66</sup> Analytical precision is  $\pm 0.4\text{‰}$ .

### Aquatic biomarkers

An aquatic contribution was determined in 10 potsherds from Likoaeng, based upon the presence of long chain ( $C_{20:0}$  and  $C_{22:0}$ ) APAAs (Fig. 2b) and two or more isoprenoid fatty acids (IFAs; Fig. 3;

Supplementary Table 1). In a further six residues, the identification of only C<sub>18:0</sub>–C<sub>20:0</sub> APAAs and one IFA means that an aquatic contribution is likely but not certain (Table S1; marked as ‘Likoaeng - aquatic?’ in Fig. 3). The aquatic biomarkers were identified in residues characterised isotopically as deriving predominantly from ruminant adipose products (n = 6), as well as non-ruminants (which would include fish) (n = 2) and dairy (n = 2), implying that the pots were used for processing both aquatic and terrestrial fats. The relatively low proportion of C<sub>18:0</sub> fatty acid in aquatic fats means that the stable isotopic values obtained from such mixtures will be strongly biased towards the terrestrial species<sup>69</sup>. In contrast, at Sehonghong aquatic biomarkers were recovered from possibly only one residue (SHH41), classified as predominantly of dairy origin, and no aquatic biomarkers at all were recovered from residues from Mokatlapioli (Supplementary Tables 2; 3).



**Figure 4.** Timeline showing span of the layers that were analysed at the two Later Stone Age sites, Likoaeng Layer 1, Sehonghong Layer GAP and Layer DC (95.4% calibrated ranges of dates shown in Table 1) and the possible range of the late nineteenth-/early twentieth-century agricultural village, Mokatlapioli (see ‘Sites and samples’ for details). The calibrated (95%) date ranges for the combined compound-specific radiocarbon dating of fatty acids from two terrestrial dairy fats LIK10 and SHH42 are shown as black lines. The pie charts show the proportions of different animal-derived products identified from each assemblage through compound-specific stable isotope analysis.

#### *Direct dating of dairy residues in pottery*

To confirm the antiquity of the pottery and its dairy contents, we conducted compound-specific radiocarbon dating of the absorbed fatty acids from two sherds<sup>62,64,65,71,72</sup>. Sherds LIK10 and SHH42

(Supplementary Fig. 5), containing high concentrations of saturated C<sub>16:0</sub> and C<sub>18:0</sub> fatty acids and shown through compound-specific stable carbon isotope analysis to derive from a dairy origin, were selected and individual fatty acids collected using preparative-GC and radiocarbon dated (Supplementary Table 4). The radiocarbon dates from these residues calibrate to cal AD 579 – 654 (95% probability; BRAMS-2613: 1481 ± 27 BP) for LIK10 (combined date) and cal AD 885 – 990 (95% probability; BRAMS-2612: 1161 ± 28 BP) for SHH42 (combined date). They confirm that the dairy residues, and thus the pottery vessels from which they derive, date to the mid- and late-first millennium AD at Likoaeng and Sehonghong respectively (Fig. 4).

## Discussion

The biomolecular analysis of residues extracted from potsherds from Likoaeng and Sehonghong, which include two directly dated examples, provides strong evidence for the exploitation of domesticated secondary products by hunter-gatherer groups in the highlands of Lesotho in the mid-/late-first millennium AD, with dairy residues comprising *ca.* 35% of residues characterised (n=12). The direct date from the dairy residue LIK10 from Likoaeng (cal AD 579-654 at 95.4% probability; BRAMS-2613: 1481 ± 27 BP) is within 2σ of the dated charcoal from the same layer (cal AD 641–969 at 95.4% probability; Pta-7877: 1310 ± 80 BP) although the precision of the charcoal date is rather low. The dairy residue dates slightly older than the bone (cal AD 681–884 at 95.4% probability; GrA-23237: 1285 ± 40 BP) and iron (cal AD 682–879 at 95.4% probability; GrA-26831: 1290 ± 30 BP) dates from Layer 1, possibly indicating a longer span of occupation represented in the layer than the existing dates suggested. Based upon archaeological interpretation and five existing radiocarbon dates (Table 1), Layer DC at Sehonghong was thought to have accumulated during occupation of the site during both the first and second millennia AD, but the clustering of radiocarbon dates indicates that the bulk of material originates from the late first millennium AD. The direct date we obtained from the dairy residue SHH42 (cal AD 885-990 at 95.4% probability; BRAMS-2612: 1161 ± 28 BP) is consistent with this earlier cluster, confirming that dairying was practised here from the earliest phase of this occupation layer. In the late nineteenth/early twentieth centuries at nearby Mokatlapoli nearly all of the animal-derived pottery lipid residues derive from dairy products ( $\Delta C_{18}-C_{16} \leq -3.1\text{‰}$ ; one is on the border between ruminant dairy and ruminant adipose indicating mixing). This indicates that dairy products formed an important part of the subsistence strategies of both precolonial hunter-gatherers and nineteenth-/twentieth-century Basotho agriculturalists (Fig. 4). When taken in conjunction with the osteoarchaeological identification of domestic livestock in the faunal assemblages at Likoaeng<sup>22</sup> and Sehonghong<sup>73</sup>, the evidence for

224 maintenance and exploitation of domestic animals and their secondary products in the Lesotho  
225 highlands by hunter-gatherer groups is compelling.

226 The exploitation of dairy products confers an important adaptive advantage on humans, providing a  
227 predictable source of carbohydrate, fat, protein and calcium, as well as liquid during times of drought,  
228 and greatly increases the degree of nutrition represented by one animal. The distinct advantages of milk  
229 consumption led to a rapid increase in the frequency of adult humans able to digest lactose (lactase  
230 persistence), representing one of the strongest signals of positive selection observed in recent *Homo*  
231 *sapiens* populations, and one that occurs at highest frequencies in traditionally pastoralist populations<sup>74-</sup>  
232 <sup>77</sup>. Lactase persistence was likely present only in low frequencies in the hunter-gatherer groups  
233 inhabiting Likoaeng and Sehonghong in the mid-late first millennium AD. However, fermented dairy  
234 products, facilitated by the use of pottery, retain their nutritional value<sup>78</sup> and are much more palatable  
235 for lactose intolerant individuals compared to fresh milk, largely due to the hydrolysis of lactose to  
236 its component sugars during the fermentation process<sup>79</sup>. It is probable that the dairy residues recovered  
237 during this study originate from fermented milk products, which permit the consumption of secondary  
238 products by lactose intolerant individuals without detrimental health effects. Fermented milk is still  
239 widely consumed in Lesotho ('mafi') and South Africa ('amasi') today<sup>80</sup>.

240 The high variety of animal taxa present at Likoaeng and Sehonghong indicates that a wide range of  
241 resources was exploited by the hunter-gatherer groups who occupied these sites in the first and second  
242 millennia AD<sup>22,33,73</sup>. Whereas dairy residues most likely derive from domestic species, such as sheep,  
243 goats or cattle, the ruminant carcass fats could originate from either domesticates or hunted antelope  
244 including common duiker (*Sylvicapra grimmia*), grey rhebuck (*Pelea capreolus*), mountain reedbuck  
245 (*Redunca fulvorofula*), red hartebeest (*Alcelaphus buselaphus*) and eland (*Taurotragus oryx*). The non-  
246 ruminant carcass residues, on the other hand, most likely derive from fish (at both sites), or, at  
247 Sehonghong in particular, mammals such as rock hyrax (*Procavia capensis*), scrub hare (*Lepus saxatilis*),  
248 warthog (*Phacochoerus africanus*) and baboon (*Papio hamadryas*).

249 Whilst the stable carbon isotopic composition of wild animals reflects their preferred pasture, that of  
250 domestic species will reflect an average of the different pastures they are exposed to by the groups  
251 managing them. Although the environmental composition of Layer 1 at Likoaeng predominantly  
252 consisted of C<sub>4</sub> grassland (ca. 70%)<sup>81</sup>, both aspect and elevation significantly affect the C<sub>3</sub>/C<sub>4</sub>  
253 composition. Only relatively short-distance movements of no more than 5–15 km from both Likoaeng

and Sehonghong (readily achieved by following rivers upstream from these sites) would reach elevations where the vegetation cover becomes predominantly  $C_3$  (2100–2700 m a.s.l. depending on aspect)<sup>82</sup>.

The  $\delta^{13}C_{16:0}$  and  $\delta^{13}C_{18:0}$  values of the dairy residues from Likoaeng are lower than the ruminant/non-ruminant carcass fats from the same site (Fig. 3), indicating a greater  $C_3$  contribution to the dairy fats. This could reflect the preferential grazing of domesticates (predominantly exploited for milk) at elevated  $C_3$  pastures whereas the mixed  $C_3/C_4$  signal of the carcass fats could represent the preferred pastures of hunted wild game or be a reflection of the integrated signature of carcass tissues from domestic animals moved seasonally between  $C_3$  and  $C_4$  pastures. The practice of vertical transhumance is well attested in Lesotho historically<sup>83</sup> and continues today. Traditionally, livestock would be kept in the village environs throughout winter and moved to better grazing at higher elevations for the summer months<sup>84</sup>, a period when milk production is highest. The isotopic patterning of the dairy residues observed at Likoaeng, directly dated to the first millennium AD, suggests that a mobile system of animal management was also practised by the population occupying that site during that time.

A striking isotopic separation (*ca.* 5 - 6‰) can also be observed in the dairy residues between the late first-millennium hunter-gatherer sites and the historic Basotho agropastoralist village (Fig. 3), which is located in close proximity to the site of Sehonghong. The dairy residues from Mokatlapi have a clear  $C_4$  isotopic signal. Considering the 1000 year time gap between these observations, the wide isotopic separation in the dairy residues likely reflects differences in animal husbandry practices. Historically and today, cattle are grazed on maize stubble after crops are harvested<sup>84</sup> (P. Mitchell, pers. obs.), which would increase the  $C_4$  signal in the diet of domesticates after its introduction in the nineteenth century and explain the shift in the isotopic composition of domesticated tissues.

Fish remains represent just under 20% of the faunal collection of Layer 1 at Likoaeng<sup>22</sup>. Due to the site's location on the bank of the Senqu River, the presence of aquatic fats in potsherds from Likoaeng is unsurprising. Indeed, a rock art scene immediately adjacent to the site depicts the use of what are probably basket traps and fences to catch fish migrating up the Senqu, although its age is unknown<sup>85</sup>. The Sehonghong sequence likewise documents a long history of exploitation of fish, with fish forming a large portion of the faunal assemblage from Layers GAP and DC<sup>73</sup>. The presence of partial suites of aquatic biomarkers in potsherds from Likoaeng further attests to the exploitation of aquatic resources by people inhabiting the sites. Consistent with the fact that Basotho largely ignored fish as a source of food in precolonial times<sup>86,87</sup>, aquatic biomarkers are absent from the potsherds from Mokatlapi.

284 The decoration on the single EIA potsherd from Likoaeng indicates that it belongs to either the Msuluzi  
285 (AD 650–750), or Ndondonwane (AD 750–950), phase of the Kalundu Tradition of the Early Iron Age<sup>21</sup>,  
286 both of which are well-represented at farming villages in KwaZulu-Natal<sup>3</sup>. Work by Maggs<sup>88</sup> and Mazel<sup>89</sup>  
287 in KwaZulu-Natal's Thukela Basin region immediately northeast of the uKhahlamba-Drakensberg  
288 Escarpment has uncovered extensive evidence for contact between hunter-gatherers and incoming  
289 agricultural populations in the first millennium AD. The agricultural settlement of Msuluzi Confluence,  
290 for example, appears to have produced iron in excess of local demand, leading Maggs<sup>88</sup> to suggest that  
291 this was likely for exchange with non-iron-producing hunter-gatherer groups. The iron fragments  
292 recovered at Likoaeng must also come from this kind of source.

293 Existing networks of exchange between hunter-gatherer groups living on both sides of the uKhahlamba-  
294 Drakensberg Escarpment may have facilitated the easy spread of such commodities, but the presence of  
295 dairy residues in potsherds at both Likoaeng and Sehonghong suggests that those making and using the  
296 ceramics from which they came had sufficient knowledge of animal husbandry to exploit the secondary  
297 products of cattle and/or caprines. Moreover, the fact that – except for the single decorated EIA sherd  
298 from Likoaeng – all the pottery analysed there and from Layers DC and GAP at Sehonghong is of hunter-  
299 gatherer type<sup>19,20</sup> strongly suggests that those dairy residues derive from livestock living in or very close  
300 to the Senqu Valley. Although these animals, or their ancestors, must originally have been obtained  
301 from an agropastoralist source, there is absolutely no archaeological or historical evidence to indicate  
302 that agropastoralists were living in highland Lesotho prior to 1878. Had they been, they would, for  
303 example, undoubtedly have been recognised when Joseph Orpen and James Murray Grant led a British  
304 military expedition through the region, stopping off at Sehonghong, in 1873<sup>90,91</sup>. The absence of  
305 agropastoralists and the otherwise entirely Later Stone Age context of the pottery from both Likoaeng  
306 and Sehonghong reinforces the argument that the ceramics we have analysed are indeed of hunter-  
307 gatherer origin.

308 Although the numbers of livestock identified as being present at Sehonghong<sup>73</sup> have been questioned,  
309 Horsburgh, et al.<sup>27</sup> confirmed the presence of one *Bos taurus* specimen (SHH-7358) in Layer DC at  
310 Sehonghong. Unfortunately, pretreatment of this particular bone yielded insufficient collagen for direct  
311 radiocarbon dating. The bone came from the same square and context as a distal phalanx (SHH-7356)  
312 that Horsburgh, et al.<sup>27</sup> identified as eland (rather than cattle) and directly dated to cal AD 775–983 (95%  
313 probability; Wk-34784: 1200 ± 30 BP). This may indicate that it is of similar age but associated dates  
314 must be treated with caution. Although this result does provide molecular support for the small-scale

presence of domestic livestock at Sehonghong, the presence of a single donkey (*Equus asinus*) specimen in Layer GAP and of several pig (*Sus scrofa*) and chicken (*Gallus gallus*) specimens in Layer DC shows that some disturbance of the uppermost levels of Sehonghong's stratigraphy has taken place; none of these species can have been available locally before the onset of Basotho settlement in 1878<sup>73</sup>. However, the direct dating of a dairy residue from Sehonghong does now confirm the antiquity of domesticates at this site.

Although molecular analysis of the Likoaeng domestic assemblage has not yet been undertaken, the reliability of the identification of sheep remains at Likoaeng has specifically been questioned based on the aDNA results obtained at Sehonghong<sup>37</sup>. From the faunal collection at Likoaeng, nine specimens were morphologically attributed to sheep/goat, two to sheep (*Ovis aries*) and eight to cattle (*Bos taurus*)<sup>23</sup>. Most of these were recovered from Layer 1, with just a few small elements displaced downwards below this<sup>23</sup>. Although collagen from the cattle bones was insufficiently preserved for dating, direct AMS dating of one sheep/goat bone confirms the antiquity of this specimen and produced a result (cal AD 681–884 at 95% probability; GrA-23237: 1285 ± 40 BP) consistent with the remainder of the chronological evidence for Layer 1<sup>23</sup>. The directly dated dairy residue from Likoaeng (cal AD 600–644 at 95% probability; BRAMS-2613: 1481 ± 27 BP) clearly attests to the presence of domestic livestock at the site in the first millennium AD. It does not, however, tell us the number of animals that were present. The high calorific value of milk means that dairy products could have formed an important supplement to the diet even at very low numbers of livestock or in situations where few such animals were killed and the rest kept as socio-political capital and/or for dairy production<sup>92</sup>.

## Conclusion

The results reported here provide further evidence that by the late first millennium AD hunter-gatherer communities living in the highlands of eastern Lesotho had established contact with agropastoralist communities, most likely ones located in lowland areas of KwaZulu-Natal over 150 km away. The presence of dairy residues in otherwise Later Stone Age contexts at both Sehonghong and, more compellingly, Likoaeng supports the notion of hunter-gatherer people practising a 'hunters-with-sheep' form of subsistence<sup>25</sup>. This directly-dated evidence lends support to the argument that such contacts, and the incorporation of caprines and cattle, were a feature of people living in highland Lesotho during the late first millennium AD. This suggests that only a few centuries after the establishment of EIA agropastoralist communities in KwaZulu-Natal, such contacts were sufficiently close to allow for the successful transfer to Maloti-Drakensberg hunter-gatherers of both domestic livestock and of the

knowledge required to look after them. Patterning in the isotopic values of the residues reveals likely differences in animal management strategies between then and recent times, as evidenced by the  $C_4$  animal signatures from the late nineteenth-/early twentieth-century agropastoralist settlement at Mokatlapoli, likely deriving from foddering on more recently-introduced crops including maize and sorghum.

The ongoing debate surrounding the relative merits of osteoarchaeological versus molecular analyses for correctly identifying the presence of domestic livestock in faunal assemblages from archaeological sites<sup>27,36-41</sup> attests to the importance of investigating such wide-reaching questions via multiple lines of enquiry. Considering the high level of lipid residue preservation at these southern African sites, this type of analysis has an important part to play in the ongoing debate surrounding the introduction of livestock-keeping into the region. Since direct dating of faunal remains from the area has been hampered by poor collagen preservation<sup>23,27</sup>, the direct dating of fatty acids of dairy origin extracted from the potsherds provides an important alternative approach<sup>62,64,65</sup>. Osteoarchaeological identification is clearly a practice that may at times deliver faulty results (for example, the proximal radius from Sehonghong morphologically identified as sheep<sup>73</sup>, but directly dated to 5870±30 BP (Wk-34787), several millennia before any domestic livestock were present in southern Africa<sup>27</sup>). However, it cannot be assumed that ancient DNA identifications are without difficulties of their own, especially where, as in highland Lesotho<sup>27</sup>, organic preservation is poor. Both approaches would likely benefit from blind-testing and comparative analysis by more than a single specialist or laboratory, following the examples of radiocarbon dating or microwear and residue analyses of stone tools. In the meantime, our biomolecular analysis and direct dating of fatty acid residues from hunter-gatherer ceramics at Sehonghong and Likoaeng not only provide an independent line of evidence to address this debate, but also suggest that, on the whole, the osteoarchaeological identifications previously reported there<sup>22,73</sup> are likely to be correct.

## Materials and methods

### *Sites and samples*

Likoaeng (29°44"S, 28°45"E; 1725 metres above sea level (m a.s.l.)) is located in the Senqu Valley in the Thaba Tseka District of Lesotho. It is an open-air campsite on the southern side of the confluence of a stream (of the same name) with the western bank of the Senqu (Orange) River (Fig. 1b; Supplementary Fig. 1). Eighteen radiocarbon dates set the duration of human activity from 3700–1100 BP. The uppermost occupation horizon (Layer 1) (located under approximately 0.2–1.5 m of culturally sterile



sediment; Supplementary Fig. 2) is dated by three radiocarbon determinations to cal AD 641–969 (Table 1), consistent with the age of the one decorated sherd recovered which belongs to the Msuluzi or, more likely, Ndondonwane phase of the Early Iron Age<sup>3</sup>. Layer 1 was the only excavated context at Likoaeng to contain pottery. In their thin walls (mean =  $7.6 \pm 9.5$  mm thick,  $n=80$ ), grit temper, largely grey colour and lack of decoration, 77 of the remaining 79 potsherds recovered are typical of the ceramics found at other hunter-gatherer sites in highland Lesotho<sup>28,32,34</sup>, KwaZulu-Natal<sup>19</sup> and the Eastern Cape Province<sup>93</sup>. Such pottery continued to be made locally into the late nineteenth century<sup>94-96</sup>, while sources of clay were exploited by Basotho residents of the area into the early 1900s (Chris Wingfield, pers. comm.). Thirty of these sherds, along with the decorated EIA sherd, were selected for analysis (Supplementary Fig. 5). Two conjoining red-coloured sherds with exceptionally thin walls and highly burnished exteriors complete the ceramic assemblage from Likoaeng Layer 1, but cannot readily be paralleled elsewhere in the region, except perhaps at Good Hope Shelter in the uKhahlamba-Drakensberg Escarpment of KwaZulu-Natal<sup>97</sup>. Neither was analysed in this study.

Sehonghong rockshelter (29°46"S, 28°47"E, 1750 m a.s.l.; Supplementary Fig. 3) lies 3 km south-east of Likoaeng, on the south-eastern bank of the Sehonghong River, which meets the Senqu River 3 km further downstream (Fig. 1b). Sehonghong was first occupied in the Middle Stone Age and preserves a series of occupation pulses across Marine Isotope Stages 3 and 2 as well as the Holocene<sup>98,99</sup>. Oral histories indicate that it was an important hunter-gatherer base as late as *ca.* 1870 and that the last San individuals to live there did so as recently as *ca.* 1902<sup>96,100</sup>. Pottery attributable to Maloti-Drakensberg hunter-gatherers by virtue of its thin walls (mean thickness =  $7.8 \pm 1.6$  mm,  $n=268$ ), overwhelmingly reduced condition (grey/black colour), grit temper and lack of decoration (except for rare instances of burnishing) was recovered from the uppermost three layers (Supplementary Fig. 4)<sup>28</sup>. Layer SS (Surface Scrapings) is a loose grey brown dust that forms the modern surface of the site. Underneath this, Layer DC (Dung Crust) is a hard friable layer rich in bovine and equine dung that becomes finer and ashier towards the bottom. This layer includes the material culture of the hunter-gatherers who made use of the site in the late first and second millennia AD<sup>28</sup>, but the consistency of radiocarbon dates from it recently obtained by Horsburgh et al.<sup>27</sup> raises the possibility that much of its content dates to the late first millennium AD and might therefore be close in age to Layer 1 at Likoaeng. Underlying DC, Layer GAP accumulated in the first half of the first millennium AD and is a soft, loose, grey charcoal-rich ashy layer. In total, eight sherds were analysed from GAP and nine from DC.

During field survey of the area around Sehonghong in 1992 an open-air stone artefact scatter (2928DB38) was identified 2 km upstream of the site close to a small cluster of abandoned stone-walled houses with adjacent stock enclosures (29°44"S, 28°48"E). Although no enquiries were made at the time regarding the history of this site or of the nearby village of Masakoane, a settlement by the name of Mokatlapudi (Mokatlapoli in correct Sesotho spelling) appears just to the west of Masakoane on the map of Lesotho prepared by Captain M.C. Dobson<sup>101</sup> between 1904 and 1909. This village was described as "now stated in ruins" in 1950 in Webb's<sup>102</sup> *Gazetteer of Basutoland*. It seems very plausible that the ruins near 2928DB38 therefore belong to Mokatlapoli (Fig. 1b). Webb's observation, coupled with the fact that there was no Basotho settlement anywhere in the Sehonghong or broader Upper Senqu region before 1878, narrows the age of the ceramics retrieved from the surface of Mokatlapoli to the last two decades of the nineteenth and first four decades of the twentieth centuries. This pottery differs from that recovered from Likoaeng and Sehonghong in being thicker (mean thickness =  $10.5 \pm 3.7$  mm,  $n=69$ ), predominantly orange or buff (rather than grey to black) in colour and not infrequently burnished<sup>28</sup>. Twenty-seven of these sherds were analysed in order to obtain a set of residue results for comparison with the hunter-gatherer pottery from Sehonghong and Likoaeng.

#### *Lipid extraction*

Potsherds were cleaned of exogenous lipids by removing the outer surface (*ca.* 2 mm) using a Dremel drill. 1-3 g of potsherd was sampled and ground to a fine powder in a solvent-washed glass mortar and pestle. Lipids were simultaneously extracted and methylated using established methods (4% v/v H<sub>2</sub>SO<sub>4</sub>/MeOH, 5 mL, 70 °C, 1h)<sup>103</sup>. Analytical blanks were prepared alongside each batch of 10 sherds to monitor laboratory-based contamination. The same extraction method repeated three times on new powdered clay (up to 5 g) was followed for the radiocarbon analyses of lipid residues.

#### *Instrumental analysis*

Samples were analysed on an Agilent 7890A GC fitted with an on-column injector, flame ionisation detector and a non-polar high temperature DB1-HT column (stationary phase 100% dimethylpolysiloxane, 0.32 mm internal diameter, 0.1 µm film thickness) using helium as a carrier gas (1 µl injection volume). The temperature program consisted of a 1 min isothermal at 50 °C, increasing to 350 °C (5 min isothermal) at 25 °C min<sup>-1</sup>.

For analysis via GC-MS, fatty acid methyl esters (FAMES) were initially analysed using a ThermoFinnigan Trace mass spectrometer fitted with a non-polar column (100% dimethylpolysiloxane, length 50 m,

437 internal diameter of 0.32 mm and film thickness of 0.17  $\mu\text{m}$ ) in EI mode, scanning from  $m/z$  50 – 650  
438 (electron energy 70 eV, scan time of 0.6 s). The temperature program commenced at 50  $^{\circ}\text{C}$  (1 min)  
439 increasing at 10  $^{\circ}\text{C min}^{-1}$  until 300 $^{\circ}\text{C}$  (10 min isothermal). The FAMEs were re-analysed using a  
440 ThermoFinnigan single quadrupole TraceMS in EI mode (electron energy 70 eV) fitted with a fused silica  
441 capillary column with a high cyano-modified cyanopropyl polysilphenylenesiloxane stationary phase  
442 (Agilent J & W, VF-23ms, 60 m x 0.32 mm i.d., 0.15  $\mu\text{m}$  film thickness). The oven temperature  
443 programme comprised an isothermal at 70  $^{\circ}\text{C}$ , ramping to 100  $^{\circ}\text{C}$  at 10  $^{\circ}\text{C min}^{-1}$  and a second ramp to  
444 250  $^{\circ}\text{C}$  at 4  $^{\circ}\text{C min}^{-1}$ . The GC/MS was operated in both full scan ( $m/z$  50 – 650) and selected ion  
445 monitoring ( $m/z$  105, 262, 290, 318 and 346) mode for the identification of aquatic biomarkers (APAAs  
446 and IFAs). Data were collected and analysed using Xcalibur software (v. 2.0) and a NIST spectral  
447 database.

448 The  $\delta^{13}\text{C}$  values of the  $\text{C}_{16:0}$  and  $\text{C}_{18:0}$  fatty acids were obtained using an Agilent 7890A GC fitted to an  
449 Isoprime isotope ratio mass spectrometer (IRMS). The temperature program began at 40  $^{\circ}\text{C}$  (2 min),  
450 increasing by 10  $^{\circ}\text{C min}^{-1}$  to reach 300  $^{\circ}\text{C}$  (10 min isothermal). Samples were run in duplicate; final  
451 results are an average taken of the two values. Analytical reproducibility was  $\pm 0.4\text{‰}$ . Instrumental error  
452 was  $\pm 0.2\text{‰}$ . The isotopic values were corrected to account for the carbon atoms added during the  
453 methanolic extraction according to Rieley<sup>104</sup>. The  $\delta^{13}\text{C}$  values were derived according to the equation:  
454  $\delta^{13}\text{C}\text{‰} = ((R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}) \times 1000$  (relative to the international standard Pee Dee Belemnite  
455 (PDB) and where  $R = {}^{13}\text{C}/{}^{12}\text{C}$ ).

456 For  $^{14}\text{C}$  dating, the  $\text{C}_{16:0}$  and  $\text{C}_{18:0}$  fatty acids were isolated by preparative capillary GC (pcGC) on an  
457 Hewlett-Packard 5890 series II GC coupled to a Gerstel preparative fraction collector (PFC) following  
458 recently established procedures<sup>64,65,105</sup>. Total lipid extracts (TLEs) concentrated at *ca.* 5  $\mu\text{g} \cdot \mu\text{L}^{-1}$  were  
459 injected 40 times into a Rxi-1ms (DB1, 30mx 0.53 mm i.d., 1.5  $\mu\text{m}$  film thickness) column and the fatty  
460 acids were collected in a solvent-less trapping system (STS). He (10 psi) was used as carrier gas. The GC  
461 oven started with an isothermal hold at 50  $^{\circ}\text{C}$  for 2 min, increased to 200  $^{\circ}\text{C}$  at 40  $^{\circ}\text{C} \cdot \text{min}^{-1}$ , then  
462 increased to 270  $^{\circ}\text{C}$  at 10  $^{\circ}\text{C} \cdot \text{min}^{-1}$  and finally increased to 300  $^{\circ}\text{C}$  at 20  $^{\circ}\text{C} \cdot \text{min}^{-1}$  and held for 8.75 min.  
463 Procedural blanks and standard consisted of trapping sequences of *n*-hexane mirroring the one of  
464 FAMEs, then addition of the radiocarbon standards (IAEA C7, Phtalic anhydride) to the traps content.  
465 The isolated compounds were combusted and graphitised in a Vario Microcube Elemental Analyser  
466 coupled with an Automated Graphitization Equipment (EA-AGE3)<sup>106</sup>. Graphite targets were pressed  
467 using a Pneumatic Sample Press and analysed on the BRIS-MICADAS accelerator mass spectrometer of

the Bristol Radiocarbon Accelerator Mass Spectrometry (BRAMS) facility alongside radiocarbon and processed standards (OXA II, IAEA C7, phthalic anhydride). Correction of the measurements for the methyl group added during the derivatization was performed using a mass balance<sup>71</sup>. Combination of the measurements was performed as described in Casanova, et al.<sup>65</sup>. Radiocarbon ages were calibrated in OxCal 4.3<sup>31</sup> against the southern hemisphere, SHCal13, calibration curve<sup>30</sup>.

## Data availability

All data generated or analysed during this study are included in this published article and its supplementary information files.

## References

- 1 Mitchell, P. J. *The Archaeology of Southern Africa*. (Cambridge University Press, 2002).
- 2 Mitchell, P. J. & Whitelaw, G. The archaeology of southernmost Africa from c. 2000 BP to the early 1800s: a review of recent research. *Journal of African History* **46**, 209-241, doi:10.1017/S0021853705000770 (2005).
- 3 Huffman, T. N. *Handbook to the Iron Age: the Archaeology of Pre-colonial Farming Societies in Southern Africa*. (University of KwaZulu-Natal Press, 2007).
- 4 Gill, S. *A Short History of Lesotho*. (Morija Museum and Archives, 1993).
- 5 Vinnicombe, P. V. *People of the Eland: Rock Paintings of the Drakensberg Bushmen as a Reflection of their Life and Thought*. (University of Natal Press, 1976).
- 6 Manhire, A. H., Parkington, J. E., Mazel, A. D. & Maggs, T. M. O. C. Cattle, sheep and horses: a review of domestic animals in the rock art of southern Africa. *South African Archaeological Society Goodwin Series* **5**, 22-30, doi:10.2307/3858142 (1986).
- 7 Jolly, P. Melikane and Upper Mangolong revisited: the possible effects on San art of symbiotic contact between south-eastern San and southern Sotho and Nguni communities. *South African Archaeological Bulletin*, 68-80 (1995).
- 8 Jolly, P. Interaction between south-eastern San and southern Nguni and Sotho communities c.1400 to c.1880. *South African Historical Journal* **35**, 30-61, doi:10.1080/02582479608671246 (1996).
- 9 Jolly, P. The San rock painting from "The Upper Cave At Mangolong", Lesotho. *South African Archaeological Bulletin* **61**, 68-75 (1996).
- 10 Jolly, P. Before farming? Cattle kept and painted by the southeastern San. *Before Farming* **4**, 1-29 (2007).
- 11 Louw, T. A. A preliminary survey of Khoi and San influence in Zulu. *Khoisan Linguistic Studies*, 8-21 (1979).
- 12 Tesele, F. T. *Symbols of power: beads and flywhisks in traditional healing in Lesotho*, University of Cape Town (1994).
- 13 Hammond-Tooke, W. D. Selective borrowing? The possibility of San shamanistic influence on Southern Bantu divination and healing practices. *South African Archaeological Bulletin* **53**, 9-15 (1998).

508 14 González-Santos, M. *et al.* Genome-wide SNP analysis of southern African populations provides  
509 new insights into the dispersal of Bantu-speaking groups. *Genome Biology and Evolution* **7**,  
510 2560-2568, doi:10.1093/gbe/evv164 (2015).

511 15 Marks, S. J. *et al.* Static and moving frontiers: the genetic landscape of southern African Bantu-  
512 speaking populations. *Molecular Biology and Evolution* **32**, 29-43, doi:10.1093/molbev/msu263  
513 (2015).

514 16 Schlebusch, C. M., Prins, F., Lombard, M., Jakobsson, M. & Soodyall, H. The disappearing San of  
515 southeastern Africa and their genetic affinities. *Human Genetics* **135**, 1365-1373,  
516 doi:10.1007/s00439-016-1729-8 (2016).

517 17 Bajić, V. *et al.* Genetic structure and sex-biased gene flow in the history of southern African  
518 populations. *American journal of physical anthropology* **167**, 656-671, doi:10.1002/ajpa.23694  
519 (2018).

520 18 Mitchell, P. J., Plug, I. & Bailey, G. N. Spatial patterning at Likoaeng, an open-air hunter-gatherer  
521 campsite in the Lesotho Highlands, southern Africa. *Archaeological Papers of the American*  
522 *Anthropological Association* **16**, 81-94, doi:10.1525/ap3a.2006.16.1.81 (2008).

523 19 Mazel, A. D. Early pottery from the eastern part of southern Africa. *South African Archaeological*  
524 *Bulletin* **47**, 3-7 (1992).

525 20 Sadr, K. & Sampson, C. G. Through thick and thin: early pottery in southern Africa. *Journal of*  
526 *African Archaeology* **4**, 235-252 (2006).

527 21 Mitchell, P. J., Plug, I., Bailey, G. N. & Woodborne, S. Bringing the Kalahari debate to the  
528 mountains: late first millennium AD hunter-gatherer/farmer interaction in highland Lesotho.  
529 *Before Farming* **3**, 1-22 (2008).

530 22 Plug, I., Mitchell, P. J. & Bailey, G. N. Animal remains from Likoaeng, an open-air river site, and  
531 its place in the post-classic Wilton of Lesotho and eastern Free State, South Africa. *South African*  
532 *Journal of Science* **99**, 143-152 (2003).

533 23 Mitchell, P. J. *et al.* Beyond the drip-line: a high-resolution open-air Holocene hunter-gatherer  
534 sequence from highland Lesotho. *Antiquity* **85**, 1225-1242, doi:10.1017/S0003598X00062025  
535 (2011).

536 24 Lombard, M. *et al.* South African and Lesotho Stone Age sequence updated (I). *South African*  
537 *Archaeological Bulletin* **67**, 123-144 (2012).

538 25 Sadr, K. The Neolithic of southern Africa. *Journal of African History* **44**, 195-209,  
539 doi:10.1017/S0021853702008393 (2003).

540 26 Sadr, K. Invisible herders? The archaeology of Khoekhoe pastoralists. *Southern African*  
541 *Humanities* **20**, 179-203 (2008).

542 27 Horsburgh, K. A., Moreno-Mayar, J. V. & Gosling, A. L. Revisiting the Kalahari debate in the  
543 highlands: ancient DNA provides new faunal identifications at Sehonghong, Lesotho. *Azania:*  
544 *Archaeological Research in Africa* **51**, 295-306, doi:10.1080/0067270X.2016.1169041 (2016).

545 28 Mitchell, P. J. Sehonghong: the late Holocene assemblages with pottery. *South African*  
546 *Archaeological Bulletin* **51**, 17-25, doi:10.2307/3888928 (1996).

547 29 Carter, P. L., Mitchell, P. J. & Vinnicombe, P. V. *Sehonghong: the Middle and Later Stone Age*  
548 *industrial sequence at a Lesotho rockshelter*. (British Archaeological Reports, 1988).

549 30 Hogg, A. G. *et al.* SHCal13 Southern Hemisphere calibration, 0–50,000 years cal BP. *Radiocarbon*  
550 **55**, 1889-1903, doi:10.2458/azu\_js\_rc.55.16783 (2013).

551 31 Bronk Ramsey, C. Bayesian analysis of radiocarbon dates. *Radiocarbon* **51**, 337-360 (2009).

552 32 Carter, P. L. *The prehistory of eastern Lesotho*, University of Cambridge, (1978).

553 33 Plug, I. & Mitchell, P. J. Fishing in the Lesotho highlands: 26,000 years of fish exploitation, with  
554 special reference to Sehonghong Shelter. *Journal of African Archaeology* **6**, 33-55,  
555 doi:10.3213/1612-1651-10102 (2008).

556 34 Hobart, J. H. Pitsaneng: evidence for a neolithic Lesotho? *Before Farming*, 1-10,  
557 doi:10.3828/bfarm.2004.4.4 (2004).

558 35 Mitchell, P. J. Hunter-gatherers and farmers: some implications of 1,800 years of interaction in  
559 the Maloti-Drakensberg region of Southern Africa. *Senri Ethnological Studies*, 15-46 (2009).

560 36 Horsburgh, K. A. & Moreno-Mayar, J. V. Molecular identification of sheep at Blydefontein Rock  
561 Shelter, South Africa. *Southern African Humanities* **27**, 65-80 (2015).

562 37 Horsburgh, K. A., Orton, J. & Klein, R. G. Beware the springbok in sheep's clothing: how secure  
563 are the faunal identifications upon which we build our models? *African Archaeological Review*  
564 **33**, 353-361, doi:10.1007/s10437-016-9231-1 (2016).

565 38 Scott, K. & Plug, I. Osteomorphology and osteometry versus aDNA in taxonomic identification of  
566 fragmentary sheep and sheep/goat bones from archaeological deposits: Blydefontein Shelter,  
567 Karoo, South Africa. *Southern African Humanities* **28**, 61-79 (2016).

568 39 Bousman, B. C. *et al.* The quest for evidence of domestic stock at Blydefontein Rock Shelter.  
569 *Southern African Humanities* **28**, 39-60 (2016).

570 40 Plug, I. Reply to Horsburgh *et al.* 2016: 'Revisiting the Kalahari debate in the highlands'. *Azania: Archaeological Research in Africa* **53**, 98-113, doi:10.1080/0067270X.2017.1377957 (2018).

571 41 Horsburgh, K., Moreno-Mayar, J. V. & Klein, R. G. Counting and miscounting sheep: genetic  
572 evidence for pervasive misclassification of wild fauna as domestic stock. *Southern African*  
573 *Humanities* **30**, 53-69 (2017).

574 42 Horsburgh, K. A. A reply to Plug: science requires self-correction. *Azania: Archaeological*  
575 *Research in Africa* **53**, 114-118, doi:10.1080/0067270x.2017.1387430 (2018).

576 43 Evershed, R. P. *et al.* New criteria for the identification of animal fats preserved in archaeological  
577 pottery. *Naturwissenschaften* **84**, 402-406 (1997).

578 44 Dudd, S. N. & Evershed, R. P. Direct demonstration of milk as an element of archaeological  
579 economies. *Science* **282**, 1478-1481 (1998).

580 45 Evershed, R. P. *et al.* Chemistry of archaeological animal fats. *Accounts of Chemical Research* **35**,  
581 660-668, doi:10.1021/ar000200f (2002).

582 46 Evershed, R. P. Organic residue analysis in archaeology: the archaeological biomarker revolution  
583 *Archaeometry* **50**, 895-924, doi:10.1111/j.1475-4754.2008.00446.x (2008).

584 47 Roffet-Salque, M. *et al.* From the inside out: upscaling organic residue analyses of archaeological  
585 ceramics. *Journal of Archaeological Science: Reports* **16**, 627-640,  
586 doi:10.1016/j.jasrep.2016.04.005 (2017).

587 48 Copley, M. S. *et al.* Direct chemical evidence for widespread dairying in prehistoric Britain.  
588 *Proceedings of the National Academy of Sciences* **100**, 1524-1529,  
589 doi:10.1073/pnas.0335955100 (2003).

590 49 Copley, M. S., Berstan, R., Straker, V., Payne, S. & Evershed, R. P. Dairying in antiquity. II.  
591 Evidence from absorbed lipid residues dating to the British Bronze Age. *Journal of*  
592 *Archaeological Science* **32**, 505-521, doi:10.1016/j.jas.2004.07.005 (2005).

593 50 Spangenberg, J. E., Jacomet, S. & Schibler, J. Chemical analyses of organic residues in  
594 archaeological pottery from Arbon Bleiche 3, Switzerland – evidence for dairying in the late  
595 Neolithic. *Journal of Archaeological Science* **33**, 1-13, doi:10.1016/j.jas.2005.05.013 (2006).

596 51 Craig, O. E. *et al.* Ancient lipids reveal continuity in culinary practices across the transition to  
597 agriculture in northern Europe. *Proceedings of the National Academy of Sciences* **108**, 17910-  
598 17915, doi:10.1073/pnas.1107202108 (2011).

599 52 Salque, M. *et al.* Earliest evidence for cheese making in the sixth millennium BC in northern  
600 Europe. *Nature* **493**, 522-525, doi:10.1038/nature11698 (2013).

601

- 53 Cramp, L. J. E. *et al.* Immediate replacement of fishing with dairying by the earliest farmers of the Northeast Atlantic archipelagos. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20132372, doi:10.1098/rspb.2013.2372 (2014).
- 54 Cramp, L. J. E. *et al.* Neolithic dairy farming at the extreme of agriculture in northern Europe. *Proceedings of the Royal Society B: Biological Sciences* **281**, doi:10.1098/rspb.2014.0819 (2014).
- 55 Craig, O. E. *et al.* Did the first farmers of central and eastern Europe produce dairy foods? *Antiquity* **79**, 882-894, doi:10.1017/S0003598X00115017 (2015).
- 56 Evershed, R. P. *et al.* Earliest date for milk use in the Near East and southeastern Europe linked to cattle herding. *Nature* **455**, 528-531, doi:10.1038/nature07180 (2008).
- 57 Gregg, M. W., Banning, E. B., Gibbs, K. & Slater, G. F. Subsistence practices and pottery use in Neolithic Jordan: molecular and isotopic evidence. *Journal of Archaeological Science* **36**, 937-946, doi:10.1016/j.jas.2008.09.009 (2009).
- 58 Outram, A. K. *et al.* The earliest horse harnessing and milking. *Science* **323**, 1332-1335, doi:10.1126/science.1168594 (2009).
- 59 Dunne, J. *et al.* First dairying in green Saharan Africa in the fifth millennium BC. *Nature* **486**, 390-394, doi:10.1038/nature11186 (2012).
- 60 Dunne, J., di Lernia, S., Chłodnicki, M., Kherbouche, F. & Evershed, R. P. Timing and pace of dairying inception and animal husbandry practices across Holocene North Africa. *Quaternary International* **471**, 147-159, doi:10.1016/j.quaint.2017.06.062 (2018).
- 61 Keute, J. Chemical analysis of fatty acid residues on archaeological pottery of pastoralist communities in northern Tanzania.in *The 81st Annual Meeting of the Society for American Archaeology*. (2016).
- 62 Dunne, J., Grillo, K. M., Casanova, E., Whelton, H. L. & Evershed, R. P. Pastoralist foodways recorded in organic residues from pottery vessels of modern communities in Samburu, Kenya. *Journal of Archaeological Method and Theory*, doi:10.1007/s10816-018-9384-0 (2018).
- 63 Cramp, L. J. E. & Evershed, R. P. in *Treatise on Geochemistry: Archaeology and Anthropology* Vol. 12 (eds H.D. Holland & K.K. Turekian) 319-339 (Elsevier, 2014).
- 64 Casanova, E., Knowles, T. D. J., Williams, C., Crump, M. P. & Evershed, R. P. Practical considerations in high-precision compound-specific radiocarbon analyses: eliminating the effects of solvent and sample cross-contamination on accuracy and precision. *Analytical Chemistry* **90**, 11025-11032, doi:10.1021/acs.analchem.8b02713 (2018).
- 65 Casanova, E. *et al.* Accurate compound-specific radiocarbon dating of archaeological pottery vessels. *Nature* (In review).
- 66 Woodbury, S. E., Evershed, R. P. & J., B. R. Purity assessments of major vegetable oils based on  $\delta^{13}\text{C}$  values of individual fatty acids. *Journal of the American Oil Chemists' Society* **75**, 371-379, doi:10.1007/s11746-998-0055-2 (1998).
- 67 Evershed, R. P., Dudd, S. N., Copley, M. S. & Mutherjee, A. Identification of animal fats via compound specific  $\delta^{13}\text{C}$  values of individual fatty acids: assessments of results for reference fats and lipid extracts of archaeological pottery vessels. *Documenta Praehistorica* **29**, 73-96 (2002).
- 68 Roffet-Salque, M., Lee, M. R. F., Timpson, A. & Evershed, R. P. Impact of modern cattle feeding practices on milk fatty acid stable carbon isotope compositions emphasise the need for caution in selecting reference animal tissues and products for archaeological investigations. *Archaeological and Anthropological Sciences* **9**, 1343-1348, doi:10.1007/s12520-016-0357-5 (2016).
- 69 Cramp, L. J. E. *et al.* Regional diversity in subsistence among early farmers in Southeast Europe revealed by archaeological organic residues. *Proceedings of the Royal Society B: Biological Sciences* **286**, 20182347, doi:10.1098/rspb.2018.2347 (2019).

649 70 Friedli, H., Lotscher, H., Oeschger, H., Siegenthaler, U. & Stauffer, B. Ice core record of the  
650  $^{13}\text{C}/^{12}\text{C}$  ratio of atmospheric  $\text{CO}_2$  in the past two centuries. *Nature* **324**, 237-238 (1986).

651 71 Stott, A. W. *et al.* Direct dating of archaeological pottery by compound-specific  $^{14}\text{C}$  analysis of  
652 preserved lipids. *Analytical Chemistry* **75**, 5037-5045, doi:10.1021/ac020743y (2003).

653 72 Berstan, R. *et al.* Direct dating of pottery from its organic residues: new precision using  
654 compound-specific carbon isotopes. *Antiquity* **82**, 702-713, doi:10.1017/S0003598X00097325  
655 (2008).

656 73 Plug, I. & Mitchell, P. J. Sehonghong: hunter-gatherer utilization of animal resources in the  
657 highlands of Lesotho. *Annals of the Transvaal Museum* **45**, 31-53 (2008).

658 74 Leonardi, M., Gerbault, P., Thomas, M. G. & Burger, J. The evolution of lactase persistence in  
659 Europe. A synthesis of archaeological and genetic evidence. *International Dairy Journal* **22**, 88-  
660 97, doi:10.1016/j.idairyj.2011.10.010 (2012).

661 75 Gerbault, P., Roffet-Salque, M., Evershed, R. P. & Thomas, M. G. How long have adult humans  
662 been consuming milk? *IUBMB Life* **65**, 983-990, doi:10.1002/iub.1227 (2013).

663 76 Ranciaro, A. *et al.* Genetic Origins of Lactase Persistence and the Spread of Pastoralism in Africa.  
664 *The American Journal of Human Genetics* **94**, 496-510, doi:10.1016/j.ajhg.2014.02.009 (2014).

665 77 Macholdt, E., Slatkin, M., Pakendorf, B. & Stoneking, M. New insights into the history of the  
666 C-14010 lactase persistence variant in Eastern and Southern Africa. *American Journal of Physical*  
667 *Anthropology* **156**, 661-664 (2015).

668 78 Buttriss, J. Nutritional properties of fermented milk products. *International Journal of Dairy*  
669 *Technology* **50**, 21-27, doi:10.1111/j.1471-0307.1997.tb01731.x (1997).

670 79 Lomer, M. C. E., Parkes, G. C. & Sanderson, J. D. Review article: lactose intolerance in clinical  
671 practice - myths and realities. *Alimentary Pharmacology and Therapeutics* **27**, 93-103,  
672 doi:10.1111/j.1365-2036.2007.03557.x (2008).

673 80 Gadaga, T. H., Lehohla, M. & Ntuli, V. Traditional fermented foods of Lesotho. *The Journal of*  
674 *Microbiology, Biotechnology and Food Sciences* **2**, 2387-2391 (2013).

675 81 Parker, A. G., Lee-Thorp, J. & Mitchell, P. J. Late Holocene Neoglacial conditions from the  
676 Lesotho highlands, southern Africa: phytolith and stable carbon isotope evidence from the  
677 archaeological site of Likoaeng. *Proceedings of the Geologists' Association* **122**, 201-211,  
678 doi:10.1016/j.pgeola.2010.09.005 (2011).

679 82 Morris, C. Historical vegetation-environment patterns for assessing the impact of climatic  
680 change in the mountains of Lesotho. *African Journal of Range & Forage Science* **34**, 45-51,  
681 doi:10.2989/10220119.2017.1333150 (2017).

682 83 Ashton, H. *The Basuto*. (Oxford University Press, 1952).

683 84 Quinlan, T. & Morris, C. Implications of changes to the transhumance system for conservation of  
684 the mountain catchments in eastern Lesotho. *African Journal of Range & Forage Science* **11**, 76-  
685 81, doi:10.1080/10220119.1994.9647851 (1994).

686 85 Challis, S., Mitchell, P. J. & Orton, J. Fishing in the rain: control of rain-making and aquatic  
687 resources at a previously undescribed rock art site in Highland Lesotho. *Journal of African*  
688 *Archaeology* **6**, 203-218, doi:10.3213/1612-1651-10111 (2008).

689 86 Jacobs, N. Environment, production and social difference in the Kalahari Thornveld, c.1750-  
690 1830. *Journal of Southern African Studies* **25**, 347-373 (1999).

691 87 Whitelaw, G. An Iron Age fishing tale. *Southern African Humanities* **21**, 195-212 (2009).

692 88 Maggs, T. M. O. C. Msuluzi Confluence: a seventh century Early Iron Age site on the Tugela River.  
693 *Annals of the Natal Museum* **24**, 111-145 (1980).

694 89 Mazel, A. D. People making history: the last ten thousand years of hunter-gatherer communities  
695 in the Thukela Basin. *Natal Museum Journal of Humanities* **1**, 132-150 (1989).



- 696 90 Orpen, J. M. A glimpse into the mythology of the Maluti Bushmen. *Cape Monthly Magazine* **9**, 1-  
697 13 (1874).
- 698 91 Mitchell, P. J. & Challis, W. A 'first' glimpse into the Maloti Mountains: the diary of James Murray  
699 Grant's expedition of 1873-74. *Southern African Humanities* **20**, 399-461 (2008).
- 700 92 Russell, T. & Lander, F. 'What is consumed is wasted': from foraging to herding in the southern  
701 African Later Stone Age. *Azania* **50**, 267-317, doi:10.1080/0067270X.2015.1079082 (2015).
- 702 93 Opperman, H. *The Later Stone Age of the Drakensberg Range and its foothills*. (British  
703 Archaeological Reports, 1987).
- 704 94 Ellenberger, V. *La fin tragique des Bushmen*. (Amiot Dumont, 1953).
- 705 95 Mitchell, P. J. Remembering the Mountain Bushmen: observations of nineteenth century  
706 hunter-gatherers in Lesotho as recorded by Victor Ellenberger. *Southern African Field*  
707 *Archaeology* **15/16**, 3-11 (2006/07).
- 708 96 Vinnicombe, P. V. in *The eland's people: new perspectives in the rock art of the Maloti-*  
709 *Drakensberg Bushmen. Essays in memory of Patricia Vinnicombe* (eds P.J. Mitchell & B.W. Smith)  
710 165-191 (Witwatersrand University Press, 2009).
- 711 97 Cable, J. H. C., Scott, K. & Carter, P. L. Excavations at Good Hope Shelter, Underberg District,  
712 Natal. *Annals of the Natal Museum* **24** (1980).
- 713 98 Mitchell, P. J. The late Quaternary of the Lesotho highlands, southern Africa: preliminary results  
714 and future potential of ongoing research at Sehonghong Shelter. *Quaternary International* **33**,  
715 35-43 (1996).
- 716 99 Jacobs, Z. *et al.* Ages for the Middle Stone Age of southern Africa: implications for human  
717 behavior and dispersal. *Science* **322**, 733 (2008).
- 718 100 Mitchell, P. J. Making history at Sehonghong: Soai and the last Bushman occupants of his  
719 shelter. *Southern African Humanities* **22**, 147-168 (2010).
- 720 101 Dobson, M. C. Military report on Basutoland. (The War Office, London, 1910).
- 721 102 Webb, R. S. *Gazetteer for Basutoland*. (privately published, 1950).
- 722 103 Correa-Ascencio, M. & Evershed, R. P. High throughput screening of organic residues in  
723 archaeological potsherds using direct acidified methanol extraction. *Analytical Methods* **6**, 1330,  
724 doi:10.1039/c3ay41678j (2014).
- 725 104 Rieley, G. Derivatization of organic compounds prior to gas chromatographic-combustion-  
726 isotope ratio mass spectrometric analysis: identification of isotope fractionation processes. *The*  
727 *Analyst* **119**, 915-919, doi:10.1039/an9941900915 (1994).
- 728 105 Casanova, E., Knowles, T. D. J., Williams, C., Crump, M. P. & Evershed, R. P. Use of a 700 MHz  
729 NMR microcryoprobe for the identification and quantification of exogenous carbon in  
730 compounds purified by preparative capillary gas chromatography for radiocarbon  
731 determinations. *Analytical Chemistry* **89**, 7090-7098, doi:10.1021/acs.analchem.7b00987 (2017).
- 732 106 Wacker, L., Němec, M. & Bourquin, J. A revolutionary graphitisation system: fully automated,  
733 compact and simple. *Nuclear Instruments and Methods in Physics Research Section B: Beam*  
734 *Interactions with Materials and Atoms* **268**, 931-934, doi:10.1016/j.nimb.2009.10.067 (2010).

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## 745 **Author contributions**

746 LJE and PM devised the study. HF carried out lipid extraction and GC, GC-MS and GC-C-IRMS analyses  
747 under the supervision of LJE. EC carried out compound specific  $^{14}\text{C}$  dating. HF wrote the manuscript  
748 with input from all authors.

## 749 **Competing interests**

750 The authors declare no competing interests.

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## 752 **Figure legends**

## 753 **Tables**

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