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Food and pottery use at ultra-high elevation on the southern Tibetan Plateau revealed by lipid residues

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Ultra-high elevation impacts human subsistence and adaptive strategies, and our understanding of the history of this region has been limited due to the paucity of archaeological materials. In this study, lipids preserved in pottery fragments and animal bones from the archaeological site of Mabu Co (4400–4000 cal. BP) at ultra-high elevation (4446 masl) on the southern Tibetan Plateau were analysed using gas chromatography-mass spectrometry (GC-MS) and gas chromatography-combustion-isotope ratio mass spectrometry (GC-C-IRMS) to explore the food compositions and pottery use. Fatty acids indicative of animal and plant products were detected. The carbon isotopic results of fatty acids indicate the combination of aquatic and terrestrial animal resources. Combining with faunal and botanical evidence, the results on the southern Tibetan Plateau indicate farming in the lower altitude regions and agropastoralism in the higher altitude regions, reflecting different adaptive ways.

With the extremely harsh environment of coldness, hypoxia and high ultraviolet radiation, the adaptive ways of ancient humans on the Tibetan Plateau attract much attention worldwide. Many scholars have discussed the prehistoric human occupations on the Tibetan Plateau from the perspective of chronology, subsistence strategies, ecological background and genetic evidence[1–7]. So far, the earliest evidence of human presence on the Tibetan Plateau can be traced back to the late Middle Pleistocene[8]. Before 6000 BP, the subsistence on the Plateau was dominated by seasonal hunting and gathering. During 6000–4000 BP, millet farming from the Loess Plateau expanded into the low-altitude regions on the northeast and southeast Tibetan Plateau. Since 3600 BP, the introduction of agropastoral economy facilitated the dispersal of population and the establishment of sustained settlement in the high-altitude region on the Plateau[4,9].

The subsistence economy on the Tibetan Plateau has been investigated by archaeobotanical and zooarchaeological studies. Based on the archaeobotanical studies, the development of crop agriculture on the Plateau has been defined as three stages: millet agriculture, mixed millet-barley-wheat agriculture, and barley-wheat agriculture[3,10,11]. Zooarchaeological studies revealed that domestic pigs (*Sus scrofa domesticus*) emerged on the eastern Tibetan Plateau around 5500 BP[12–14] and domesticated cattle (*Bos taurus*), goats (*Capra hircus*) and sheep (*Ovis aries*) were introduced into the northeast Tibetan Plateau and further spread to the central Plateau during 4500-3000 BP. Since 3000 BP afterwards, cattle, goats, sheep, horses (*Equus caballus*) and yaks (*Bos grunniens*) have been the main domestic animals on the Tibetan Plateau[15,16]. In addition, multi-isotope ($\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$, and $\delta^{34}S$) analyses of animal remains including bone collagen and teeth enamel provided evidence of herding strategies and sustained farming systems on the Plateau[17–19].

Ultra-high elevation is defined as exceeding 3500 masl. Abundant modern surveys have revealed that ultra-high elevations influence the environment, human metabolic profiles, and even mental health[20–23]. On the Tibetan Plateau, ultra-high elevations are mostly located in the southern region. Until now, due to the lack of archaeological materials, very few studies have focused on the ancient food and subsistence at ultra-high elevations on the southern Tibetan Plateau.

The analysis of lipid residues preserved in the matrix of pottery has been widely applied in the exploration of ancient resource exploitation and pottery use worldwide[24–27]. Lipid molecular biomarkers can be used to differentiate ruminant and non-ruminant animal fats, dairy fats, marine and freshwater organisms, and plants[28–31]. Based on lipid residue analysis, dairy

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products have been recorded at the European high Alps region and highland Lesotho in Africa, implying the production of highly nutritious food to resist the living risks in the marginal environments[32,33].

So far, pottery lipid residue analysis has been applied in three archaeological sites on the Tibetan Plateau, namely Klu lding (3600–3300 cal. BP, ca. 2900 masl), Khog Gzung (3400-3000 cal. BP, ca. 3900 masl) and Gongtang (around 3000 cal. BP, 3938 masl). Leafy plants and porcine fats were discovered in the pottery residues at Klu lding[34]. Higher proportions of ruminant adipose fats and dairy fats were detected from the sherds at Khog Gzung and Gongtang, associated with early pastoralism in the high-altitude regions on the southern Tibetan Plateau[34,35]. Compared with stable isotope analyses, lipid residues from the pottery fragments provide information on more specific and diversified food compositions and are related to daily activities using cooking utensils.

In this study, we applied the lipid residue analysis of pottery fragments from the archaeological site of Mabu Co on the southern Tibetan Plateau to reveal the food origins and pottery use at ultra-high elevation (4446 masl). Through building the local references using fatty acid carbon isotopic data of animal bones and comparing the local references with pottery lipid data, together with the lipid molecular characterisation, the food compositions were determined. The food contributions were further calculated using Bayesian modelling of carbon isotopic values of fatty acids. Combined with typological evidence, various ways of pottery use were suggested. Through summarising the multiple lines of archaeological evidence on the southern Tibetan Plateau, subsistence strategies and human adaptive ways were discussed.

Methods

The study site

The Mabu Co site (28.31°N, 89.43°E) is located at a lakeshore along the Nyang Qu River, in the middle reaches of the Yarlung Tsangpo River on the southern Tibetan Plateau (Fig. 1). The site was discovered in 2019, and an area of 1100 m^2 was excavated during 2020–2023. A large number of burials were found and pits, stone features and living surfaces were exposed. Artefacts were uncovered from the refuse deposits, including pottery sherds, crystal microliths, ground stone tools, bone tools and ornaments. The site was dated back to 4400-4000 cal. BP based on the radiocarbon dating of mammal bones and carbonised seeds.

Fish bones consist 81.5% of the total number of faunal remains, and large numbers of fishing tools, such as gorge hooks, were recovered. Other identified animals are birds and diverse species of terrestrial mammals such as gazelle (*Procapra przewalskii*), argali (*Ovis ammon*), red deer (*Cervus elaphus*) and Himalayan marmot (*Marmota himalayana*). A very small amount of cereals, including foxtail millet (*Setaria italica*), broomcorn millet (*Panicum miliaceum*), and rice (*Oryza sativa* sp. *japonica*), were identified. The elevated δ^{15}N values and higher δ^{13}C values of human bone collagen evidence that the diets of inhabitants were dominated by fish. It has been concluded that the inhabitants of the Mabu Co site employed a sedentary lifestyle supported by fishing[36].

Sample selection

Due to the highly diverse environments on the Tibetan Plateau, animal bones of the representative faunal species identified at Mabu Co were collected to build the local references, including fish ($n = 3$), Caprinae ($n = 2$), bird ($n = 1$), rabbit ($n = 1$), and unidentified mammals ($n = 2$). Two sediment samples as background control were collected from the layers (Layer 2 and 3) where sherds were uncovered.

In total, 17 sherds were selected for the lipid residue analysis. The pottery is made of clay or tempered with quartzite or feldspar, black, grey and reddish brown in colour. Most fragments are plain-surfaced and a small number of sherds are polished or decorated with additional stacking patterns. Among 17 sherds analysed, 14 can be classified as jar or bowl (Fig. 2, Table 1).

Sample preparation and instrumental analyses

For the ceramic samples, the first layer (1 mm depth) of the inner surface was removed using a modelling drill. After that, about 1 g of ceramic powder was drilled from the internal surface of each sherd to a depth of around 4 mm and the powder was collected. Drill bits were cleaned prior to use and in-between samples with dichloromethane (DCM) and methanol (MeOH).

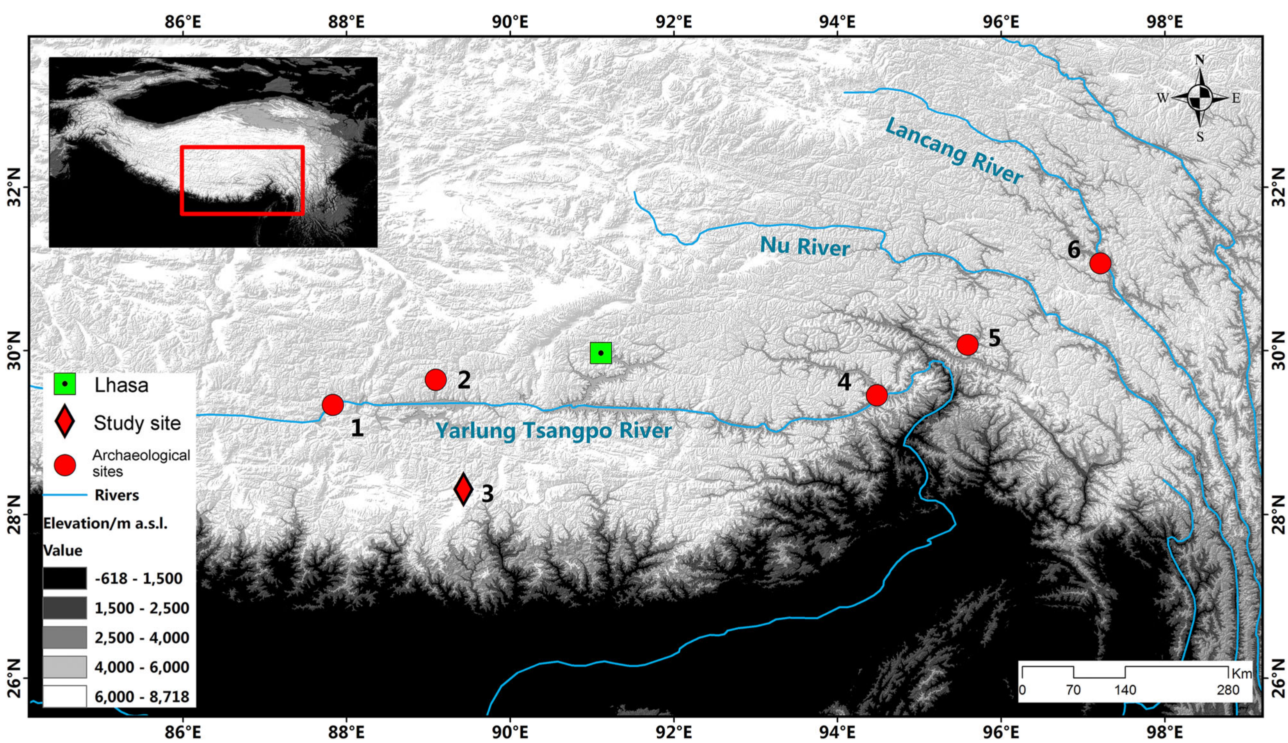


Fig. 1 | The location of the study site and other key archaeological sites mentioned in the text. 1. Khog Gzung (ca. 3400–3000 cal. BP); 2. Gongtang (around 3000 cal. BP); 3. Mabu Co (4400–4000 cal. BP); 4. Klu lding (ca. 3600–3300 cal. BP); 5. La phob (ca. 4800–3800 cal. BP); 6. Karuo (Early phase: ca. 4800–4000 cal. BP).

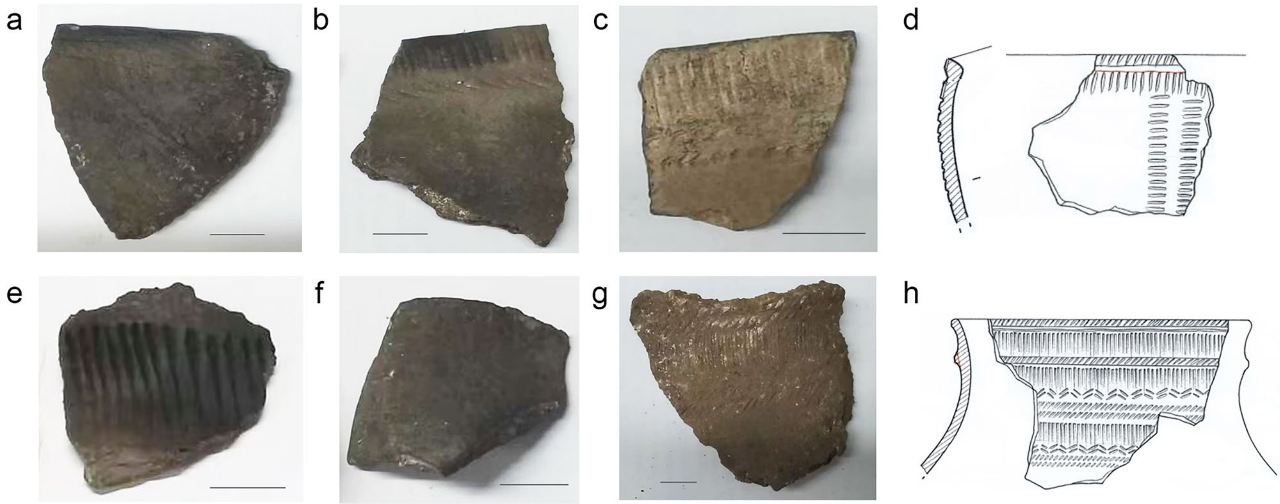


Fig. 2 | Typical sherds at Mabu Co. Bowl. (**a**. MBC-1; **b** MBC-4; **c** MBC-5; **d** illustration of bowl). Jar (**e** MBC-9; **f** MBC-11; **g** MBC-15; **h** illustration of jar) (Scale bar = 1 cm)

The pottery residue and sediment control samples were treated with the acidified methanol technique[37]. 4 ml of methanol was added to the ceramic powder and sonicated for 15 min. Concentrated sulphuric acid (800 μl) was added and the mixture was heated for 4 h at 70 °C. The lipids were extracted with hexane (3 × 2 ml). The lipid extraction was analysed by gas chromatography-mass spectrometry (GC-MS) and gas chromatography-combustion-isotopic ratio mass spectrometry (GC-C-IRMS). Hexamethylbenzene was added as an internal standard prior to analysis. Laboratory blank samples were analysed using the same methods for contamination control.

Ancient animal bones were first cleaned with dichloromethane (DCM): methanol (MeOH) (2:1 vol/vol; 3 × 2 mL) by ultrasonication for 15 min. The supernatant was discarded and the bone sample was completely dried. The acidified methanol method was then applied to the bone powder for lipid extraction[38].

The methylated samples were analysed using a ThermoQuest TraceMS GC-MS equipped with the HP-5MS column (30 m × 0.25 mm × 0.25 μm; Agilent Technologies) at the Institute of Tibetan Plateau Research, Chinese Academy of Sciences. Oven temperature programme was set as: 50 °C for 2 min, rising to 120 °C at 20 °C/min, rising to 315 °C at 4 °C/min, holding 15 min; 40 °C for 2 min, rising to 120 °C at 10 °C/min, rising to 315 °C at 4 °C/min, holding 15 min. The ion source was maintained at 220°C and the interface temperature at 300°C. The ionisation energy was set to 70 eV, carrier gas helium, constant flow 1 ml/min. The analyser was set to scan m/z 50–650. Different compounds were identified based on their mass spectra and retention times.

Carbon isotopic values of $C_{16:0}$ and $C_{18:0}$ fatty acid methyl esters from pottery and references were analysed using an Isolink-Delta V advantage gas isotope ratio mass spectrometer (Thermo Fisher) equipped with the HP-1MS column (60 m × 0.32 mm × 0.25 μm; Agilent Technologies) at the Institute of Earth Environment, Chinese Academy of Sciences. Isotopic values were measured against a calibrated CO_2 reference gas and are reported in per mil (‰) vs Vienna Peedee Belemnite (VPDB). Instrument precision is less than 0.3‰. Isotopic values were further corrected to account for the methylation of the carboxyl group, using the measured carbon isotopic value of the methanol for methylation.

The Bayesian mixing model "food reconstruction using isotopic transferred signals (FRUITS)", was used to calculate food contributions based on $C_{16:0}$ and $C_{18:0}$ fatty acid carbon isotopic data[39] (FRUITS software 3.1). Based on the faunal remains at Mabu Co and the lipid compositions of pottery residues, ruminant animal and fish were selected as potential sources of food groups and the carbon isotopic values of Caprinae and fish at Mabu Co were used as references for calculation. A concentration-dependent Bayesian mixing model was applied. Concentrations of fatty acids for ruminant animals and fish from Admiraal et al.[40] were used for the weighted model. The parameters used for Bayesian modelling were summarised in Supplementary Information Table S5.

Results

Lipid concentration and molecular characterisation

Lipid concentrations of pottery samples at Mabu Co range from 66 to 496 μg/g, with an average of 177 μg/g. All analysed sherds yielded interpretable concentrations of lipid (above 5 μg/g) based on the criterion in Dudd et al.[28] No differences in lipid concentrations of sherds with different texture and colour can be observed (Supplementary Information Fig. S1, S2). However, the lipid concentrations of jars (68–496 μg/g) are generally higher than bowls (75–310 μg/g), and the range of lipid concentrations of jars is wider than that of bowls (Fig. 3, Table 1). Based on an unpaired equal variance student's *t*-test, there are statistically significant differences between the lipid concentration values of jars and bowls ($t = 2.32$, $p = 0.04$).

Lipid profiles from all pottery samples are dominated by $C_{16:0}$ and $C_{18:0}$ fatty acids, characterising degraded animal fats[28]. The palmitic/stearic acid ratios (P/S ratios) of samples range from 0.5 to 2.8, showing the origins of various food items based on the observations in the previous experiments (P/S ratio > 1: aquatic animals or plants[29]; P/S ratio < 1.3: ruminant adipose fats[41], P/S ratio > 4: plant lipids[30]). Other compounds include saturated medium to long-chain fatty acids with an even number of carbons ($C_{14:0}$, $C_{20:0}$, $C_{22:0}$, $C_{24:0}$) and unsaturated fatty acids ($C_{16:1}$, $C_{18:1}$, $C_{22:1}$). Odd-chain fatty acids including $C_{15:0}$ and $C_{17:0}$ related to ruminant fats, are present in about one-third of the samples (Fig. 4, Table 1).

Evidence of plant products can be observed. Very long-chain fatty acids with carbon chain length C_{24} and C_{26}, indicative of plant origins, were detected in four samples (Fig. 4b). Dicarboxylic acids and hydroxy fatty acids with carbon chain lengths C_{12}, $C_{1,4}$ and C_{16} were detected in MBC-9 (Fig. 4c), probably related to different oxidation conditions or different food items. The presence of medium-chain length dicarboxylic acids and hydroxy fatty acids in pottery residues has been considered to originate from plants[42,43].

ω-(o-alkylphenyl) alkanoic acids (APAAs) of carbon length C_{18} (*m/z* 290) can be identified in seven samples. However, concentrations are very low in most samples in the scan mode chromatograms. TMTD (4,8,12-trimethyltridecanoic acid), pristanic acid (2,6,10,14-tetramethylpentadecanoic acid), and phytanic acid (3,7,11,15-tetramethylhexadecanoic acid) could not be identified in the scan mode chromatograms. Therefore, SIM mode was not used. C_{18} APAA can be created during the heating of various foodstuffs, including plant oils, aquatic and terrestrial fats[44], and the established criteria in the literature for identifying aquatic lipids[45,46] cannot be met in this study.

Table 1 | Summary of pottery samples and lipid residue data in this study

Sample Number	Sampling Location	Typology	Texture	Colour	Sherd Type	Lipid Concentration (μg/g)	Palmitic/stearic acid ratios	Molecular Characterisation (Cn:x are fatty acids with carbon length n and number of unsaturations x)	$\delta^{13}C_{16:0}$ (‰)	$\delta^{13}C_{18:0}$ (‰)
MBC-1	20KMITG2 ②b-27	Bowl	Clay	Black	Rim	111.3	0.9	$C_{14:0}$, $C_{16:0}$, $C_{18:0}$, $C_{18:1}$, $C_{22:0}$, $C_{22:1}$	-24.5	-24.9
MBC-2	20KMITN04E01 ③a	Bowl	Tempered with quartzite or feldspar	Reddish brown	Rim	119.4	0.5	$C_{14:0}$, $C_{16:0}$, $C_{18:0}$, $C_{22:1}$	-26.4	-25.3
MBC-3	20KMITG1 ②a-4	Bowl	Clay	Grey	Rim	129.3	0.7	$C_{14:0}$, $C_{16:0}$, $C_{17:0}$, $C_{18:0}$, $C_{18:1}$, $C_{20:0}$, $C_{22:1}$, C_{18} APAA	-24.4	-25.6
MBC-4	20KMITG1 ②b-5	Bowl	Clay	Grey	Rim	104.3	0.8	$C_{14:0}$, $C_{16:0}$, $C_{18:0}$, $C_{18:1}$, $C_{20:0}$, $C_{22:1}$	-24.0	-24.7
MBC-5	20KMITG1 ②b-3	Bowl	Clay	Grey	Rim	75.4	0.6	$C_{14:0}$, $C_{16:0}$, $C_{16:1}$, $C_{18:0}$, $C_{18:1}$, $C_{20:0}$, $C_{22:1}$	-25.7	-25.6
MBC-6	20KMITG1 ③c-28	Bowl	Tempered with quartzite or feldspar	Grey	Rim	118.0	0.8	$C_{14:0}$, $C_{15:0}$, $C_{16:0}$, $C_{17:0}$, $C_{18:0}$, $C_{18:1}$, $C_{22:1}$	-24.1	-25.1
MBC-7	20KMITG1 ③c	Unidentified	Tempered with quartzite or feldspar	Grey	Rim	96.5	1.6	$C_{14:0}$, $C_{15:0}$, $C_{16:0}$, $C_{17:0}$, $C_{18:0}$, $C_{18:1}$, $C_{20:0}$, $C_{22:0}$, $C_{22:1}$, C_{18} APAA	-22.7	-23.7
MBC-8	20KMITG1 ③c-37	Bowl	Clay	Grey	Rim	310.6	0.8	$C_{14:0}$, $C_{16:0}$, $C_{18:0}$, $C_{20:0}$, $C_{22:0}$, $C_{22:1}$	-24.7	-25.6
MBC-9	20KMITG1 ③c-4	Jar	Clay	Black	Rim	329.5	1.3	$C_{12:0}$, $C_{14:0}$, $C_{16:0}$, $C_{18:0}$, $C_{20:0}$, $C_{22:0}$, $C_{22:1}$, $C_{24:0}$, $C_{26:0}$ fatty acids, C_{12}, C_{14}, C_{16} hydroxy fatty acids, C_{12}, C_{14}, C_{16} dicarboxylic acids, C_{18} APAA	-26.0	-26.6
MBC-10	20KMITG1 ③c	Bowl	Tempered with quartzite or feldspar	Black	Rim	109.2	1.0	$C_{14:0}$, $C_{16:0}$, $C_{18:0}$, $C_{20:0}$, $C_{22:1}$, C_{18} APAA	-23.4	-24.7
MBC-11	20KMITG1 ③b	Jar	Clay	Black	Rim	182.9	0.9	$C_{14:0}$, $C_{16:0}$, $C_{18:0}$, $C_{18:1}$, $C_{20:0}$, $C_{22:1}$, C_{18} APAA	-22.1	-24.3
MBC-12	20KMITG1 ③b-17	Jar	Clay	Grey	Rim	68.2	0.6	$C_{14:0}$, $C_{16:0}$, $C_{18:0}$, $C_{22:1}$	-26.7	-25.4
MBC-13	20KMITG1 ②b-7	Jar	Tempered with quartzite or feldspar	Black	Rim	396.8	2.4	$C_{14:0}$, $C_{15:0}$, $C_{16:0}$, $C_{17:0}$, $C_{18:0}$, $C_{20:0}$, $C_{22:0}$, $C_{22:1}$, C_{18} APAA	-23.6	-23.5
MBC-14	20KMITG2 ②b-32	Jar	Tempered with quartzite or feldspar	Black	Rim	203.5	2.8	$C_{14:0}$, $C_{15:0}$, $C_{16:0}$, $C_{17:0}$, $C_{18:0}$, $C_{18:1}$, $C_{20:0}$, $C_{22:1}$, C_{18} APAA	-15.2	-16.4
MBC-15	20KMTN04E01②b:28	Jar	Clay	Black	Rim	496.3	0.9	$C_{14:0}$, $C_{15:0}$, $C_{16:0}$, $C_{17:0}$, $C_{18:0}$, $C_{18:1}$, $C_{19:0}$, $C_{20:0}$, $C_{22:0}$, $C_{24:0}$, $C_{26:0}$	-23.8	-27.0
MBC-16	20KMITN04E01②a: 9	Unidentified	Clay	Grey	Rim	85.6	1.4	$C_{16:0}$, $C_{18:0}$, $C_{18:1}$, $C_{20:0}$, $C_{22:0}$, $C_{24:0}$	-21.3	-24.1
MBC-17	20KMTG1②b: 54	Unidentified	Clay	Black	Rim	66.6	1.7	$C_{14:0}$, $C_{16:0}$, $C_{18:0}$, $C_{18:1}$, $C_{20:0}$, $C_{22:0}$, $C_{24:0}$	-21.0	-20.9

The sediment samples as background control exhibit different lipid profiles from those of the pottery residues, with evidently higher proportions of cholestanol than fatty acids (Fig. 4d, Supplementary Information Table S1). Organic residue compounds were not identified in the laboratory blank samples.

Carbon isotopic values of $C_{16:0}$ and $C_{18:0}$ fatty acids

In local reference samples at Mabu Co, Caprinae bones display $\delta^{13}C_{16:0}$ values of −28.7‰ and −27.1‰, and $\delta^{13}C_{18:0}$ values of −28.1‰ and −27.3‰ (Fig. 5a, Supplementary Information Table S2). The $\Delta^{13}C$ values ($\delta^{13}C_{18:0}$-$\delta^{13}C_{16:0}$) of Caprinae bones at Mabu Co are relatively higher compared with both the modern ruminant adipose fats on the southern Tibetan Plateau ($\Delta^{13}C$ range: −3.2‰ - −2‰)[34] and global references ($\Delta^{13}C < -0.7$‰)[47]. However, they are very similar to the $\Delta^{13}C$ values of ancient Caprinae bone on the southern Tibetan Plateau analysed in the previous study[34] (Supplementary Information Table S3). Rabbit and unidentified mammals were also analysed at Mabu Co. Their bones exhibit $\delta^{13}C_{16:0}$ values ranging from −27.7‰ to −26.8‰ and $\delta^{13}C_{18:0}$ values ranging from −28.6‰ to −27.7‰, similar to the carbon isotopic values of Caprinae bones (Fig. 5a, Supplementary Information Table S2).

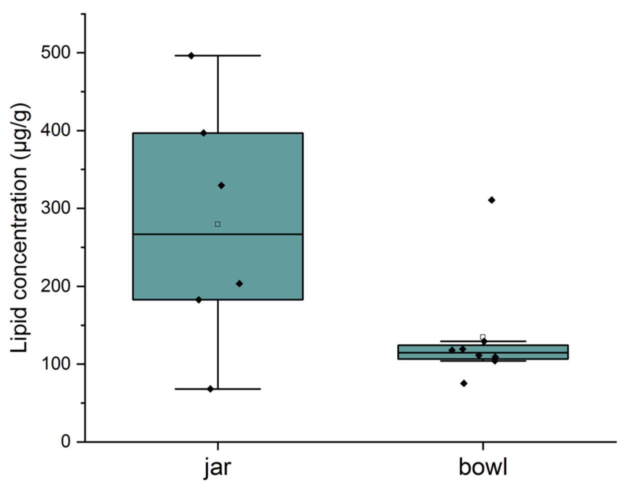


Fig. 3 | Lipid concentrations of jars and bowls at Mabu Co.

Fish bones have higher $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values, ranging from −20.5‰ to −19.1‰ and −20.9‰ to −19.1‰ (Fig. 5a, Supplementary Information Table S2). The enrichment of carbon isotope of fish has been observed from modern fish oils and ancient fish bones analysed on the southern Tibetan Plateau[34] (Supplementary Information Table S3). The carbon isotope of fish bone collagen at Mabu Co also showed enrichment compared with that of the terrestrial animals[36].

In global references, the enrichment of carbon isotope is usually attributed to marine resources[48]. However, the unique aquatic carbon cycle system on the Tibetan Plateau has been reported and discussed. Bulk $\delta^{13}C$ values of macrophytes on the Tibetan Plateau showed considerable variations. The shift towards less negative $\delta^{13}C$ values has been explained as the limited CO_2 availability due to special geographical conditions[49]. Spatial variations of lake reservoir effect have also been emphasised in the radiocarbon dating analysis of sediments on the Plateau[50]. Based on geographical investigations, the lake at Mabu Co is a closed water system[51], and the carbon isotope can be highly influenced by the local reservoir effect. For example, the carbon isotopic values of dissolved inorganic substances of closed lakes on the Tibetan Plateau have been observed to be much higher than those in rivers and freshwater lakes and have been related to the carbonate weathering in the catchment and strong evaporation of lake water[52]. Based on the ecosystem cycling, it can be assumed that the aquatic resources, including fish in the Mabu Co lake, can yield more positive carbon isotopic results. Bird bone analysed in this study has intermediate carbon isotopic value between terrestrial animals and fish, with $\delta^{13}C_{16:0}$ of −25.5‰ and $\delta^{13}C_{18:0}$ of −24.3‰ (Fig. 5a, Supplementary Information Table S2), most likely from waterfowl.

The carbon isotopic data of pottery fragments at Mabu Co show wide ranges, with $\delta^{13}C_{16:0}$ values ranging from −15.2‰ to −26.7‰ and $\delta^{13}C_{18:0}$ values ranging from −16.4‰ to −27.0‰ (Fig. 5b, Table 1). Compared with local terrestrial animals, the enriched carbon isotopic results of pottery fragments most likely indicate the contributions of aquatic resources. Considering the very small amount of cereals and seeds uncovered from the site and the abundant faunal remains, the large contributions of plant oils in the pottery residues are not possible, and most results suggest the mixture of aquatic and terrestrial products in the pottery. The evidently enriched carbon isotopic data of MBC-14 ($\delta^{13}C_{16:0}$ −15.2‰, $\delta^{13}C_{18:0}$ −16.4‰) may

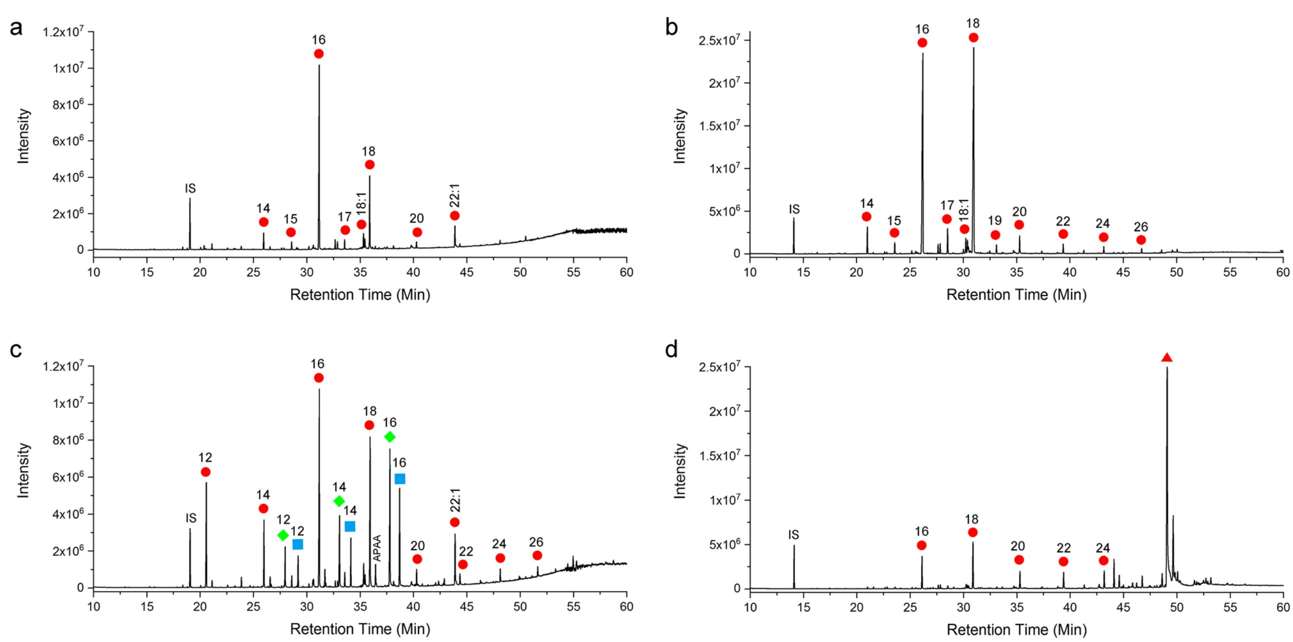


Fig. 4 | Typical lipid profile of pottery residues and soil sample at Mabu Co. a MBC-14. **b** MBC-15. **c** MBC-9. **d**. Lipid profile of soil sample at Mabu Co. (Circles represent fatty acids; squares represent dicarboxylic acid; Diamonds represent hydroxy fatty acids; Triangle represents cholestanol; IS represents internal standard; Numbers are carbon chain lengths).

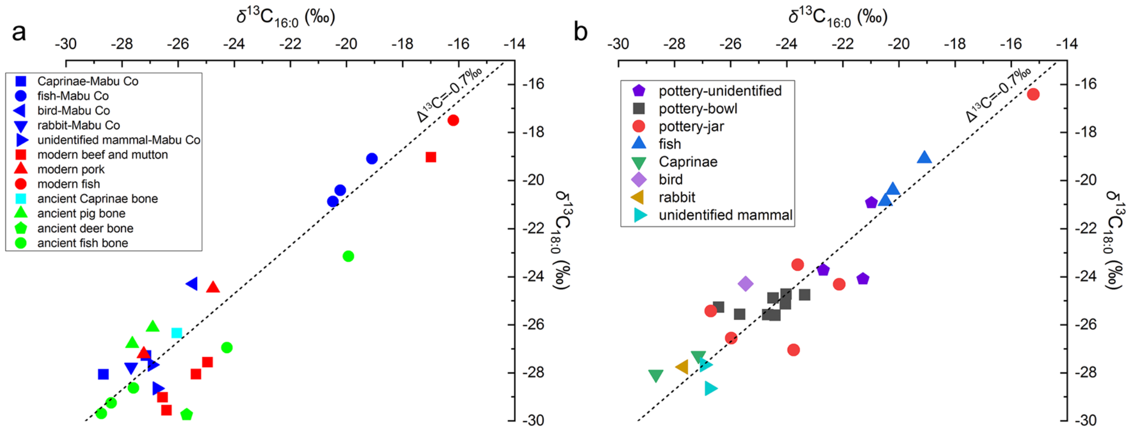
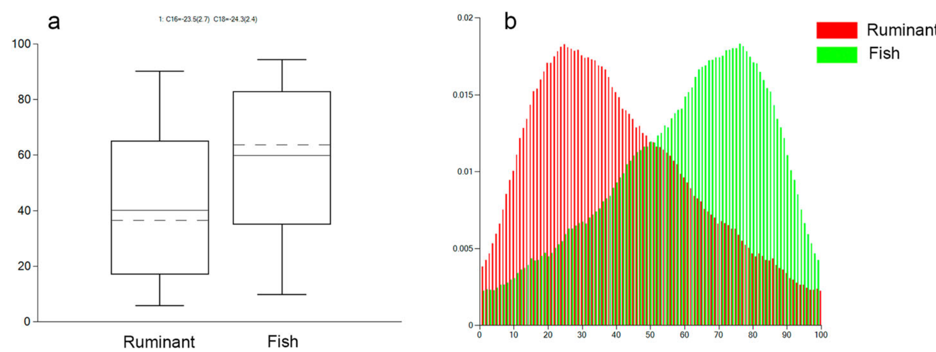


Fig. 5 | Carbon isotopic results of fatty acids. **a** $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values of modern references and ancient animal bones on the southern Tibetan Plateau[34] (Supplementary Information Table S2) and in this study (Supplementary Information Table S3); **b** $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values of pottery residues and local references at Mabu Co. (Dash line refers to global reference range of non-ruminant and ruminant adipose fats, drawn based on Suryanarayan et al.[47]). $\Delta^{13}C = \delta^{13}C_{18:0}$-$\delta^{13}C_{16:0}$.

Fig. 6 | Results of Bayesian modelling of food contributions. **a** Box plots. **b** Posterior probability distributions.



point to the contribution of C_4 cereal millets, which are also present in the archaeobotanical remains at the site. MBC-14 also displays the highest P/S ratio (2.8) in this study.

The $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values of jars and bowls analysed in this study exhibit differences. Bowls show relatively narrower distributions of carbon isotope data ($\delta^{13}C_{16:0}$: −26.4‰- −23.4‰; $\delta^{13}C_{18:0}$: −25.6‰- −24.7‰) and jars have much wider ranges of carbon isotopic values ($\delta^{13}C_{16:0}$: −26.7‰- −15.2‰; $\delta^{13}C_{18:0}$: −27.0‰- −16.4‰). However, based on an unpaired equal variance student's t-test, there are no statistically significant differences in the $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values between jars and bowls ($\delta^{13}C_{16:0}$ values: $t = 1.17$, $p = 0.27$; $\delta^{13}C_{18:0}$ values: $t = 0.96$, $p = 0.36$).

The calculation of food contributions based on $C_{16:0}$ and $C_{18:0}$ fatty acid carbon isotopic data using Bayesian modelling FRUITS indicates a mean value of 40% contribution of ruminant animals and a mean value of 60% contribution of fish (Fig. 6, Supplementary Information Table S6).

Discussion

Recent inter-disciplinary studies on zooarchaeology, archaeobotany, and bone collagen stable isotope revealed that the subsistence strategies at the site of Mabu Co were dominated by fishing, and supplemented by hunting and small-scale exchanges of crops[36]. In this study, pottery residue analysis suggests that, in addition to the aquatic resources provided by fishing, terrestrial animals and plants also played non-negligible roles in the culinary practices at Mabu Co. Mixtures of aquatic resources and terrestrial animals are common in the pottery, either by intentional mixing of food or multiple uses of vessels. Plant signatures can be identified from two samples, suggesting the specialised culinary practices using pottery, or plants were consumed in a single meal. In general, compared with the previous zooarchaeology, archaeobotany, and bone collagen stable isotope studies, the lipid residue analysis in this study emphasised the diverse food compositions and the contributions of terrestrial animal resources in daily diets. Furthermore, in addition to fishing and hunting, the results confirmed the contributions of plants in the diets rather than as rare exchange items such as crops.

Although fish bones dominated the total numbers of recovered faunal remains (81.5%) in the zooarchaeological studies, when comparing their body size and energy supply with that of terrestrial animals, their real contributions in human diets can be reconsidered, and the calculation based on Bayesian modelling in this study suggests a mean value of 60% contribution of fish. Fish may also have been processed without the use of pottery and thus the pottery lipid residue results are more biased towards terrestrial resources. For example, drying fish for long-term storage has been recorded in the ethnographic literature in Tibet[53]. From archaeological evidence of Neolithic sites, studies of the skeletal elements indicated fish gutted, transported, or salted for storage in Israel, Korea, and Sudan, which further facilitated the economic stability and sedentism[54–56].

The limited number of sherds analysed in this study restricts comprehensive interpretations of pottery functions; however, the lipid residues of jars and bowls display differences. In general, jars have higher lipid concentrations and wider ranges of $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values compared with bowls. Combining the typological features and pottery residue results, it is likely that jars were used more intensively for cooking diversified food compositions, dominated by either aquatic resources or terrestrial animals. Bowls may have been used as serving or storing vessels for the mixing of different food items, resulting in the lower lipid concentrations and the intermediate carbon isotopic values. Furthermore, although the large number of burials suggests the ritual importance of the Mabu Co site, the lipid residue results in this study confirm the actual use of pottery and human occupation of the site for daily activities.

At an elevation of 4446 masl, Mabu Co shows the example of early human adaptation in the environment with the scarcity of resources. The pottery residue results, together with the previous zooarchaeological, archaeobotanical, and stable isotope studies, revealed the reliance on aquatic resources in human subsistence and indicated the importance of the lake ecosystem as the ecological niche. The occupation of the best ecological niche by the Mabu Co ancients secured the stable food production for human living at the ultra-high elevation, and the exploitation of diversified resource,s including aquatic and terrestrial animals, and plants, further made full use of the environment.

The Mabu Co site provides evidence of early occupation on the Plateau hinterland by the Neolithic hunter-gatherer-fishers. The discussions of the reasons that the ancients chose to occupy the ultra-high elevation regions would be interesting. The spread of population and the sedentism in the high-altitude regions have been explained by the "pull and push model"[57] and "pull model"[58]. Compared with the "pull and push model" emphasising the "competitive exclusion" which leads to human migration to the high-elevation regions, the case study at Mabu Co is more likely to be explained by the "pull model" that the ancients first discovered the ultra-high regions and then the abundant resources attracted humans for long-time occupation.

Based on DNA analysis, the population at Mabu Co originated from the southern plateau ancestry[36]. During the same period of the Mabu Co site, millet agriculture appeared in the high-altitude region on the Tibetan Plateau, and small-scale exchanges of millet and rice crops were confirmed at Mabu Co[36]. It has been argued that in the high-altitude regions, the ecological barriers to growing crops created a competitive advantage for foragers[59]. The future excavation at Mabu Co with archaeological remains of different time periods will give us more information about the interactions between the ultra-high altitude foragers and nearby farmers and their choices of subsistence strategies.

Generally, lipid residue analysis of pottery fragments from four archaeological sites on the southern Tibetan Plateau, namely Mabu Co (4400–4000 cal. BP), Klu lding (3600–3300 cal. BP), Khog Gzung (3400–3000 cal. BP,) and Gongtang (around 3000 cal. BP), revealed diverse patterns of pottery use (Fig. 7, Supplementary Information Table S4). Lipid residue analysis alone cannot provide conclusive evidence of domestication and resource exploitation. However, through the comparison with the latest zooarchaeological and archaeobotanical studies, more comprehensive scenarios of subsistence strategies on the southern Tibetan Plateau can be discussed.

In the southeast region of the Tibetan Plateau with lower altitudes, porcine fats have been discovered in the pottery residues at Klu lding. The very narrow ranges of the carbon isotopic data of fatty acids implied the presence of pigs intentionally raised by humans at Klu lding[34]. Recently, domestic pig remains were identified at Klu lding by zooarchaeological analysis and comprised 10.5% of the total identifiable specimens[16], confirming the speculation by lipid residue analysis. Domestic pigs were also identified through DNA analysis in the latest studies at the sites of Karuo and La Phob, in the same region as Klu lding and dated back to as early as 4800–4100 BP[17]. Stable isotope analysis in Yang et al.[17]confirmed the existence of a millet-pig agricultural system proposed by d'Alpoim Guedes et al.[3]. Although the lipid biomarker of millets was not detected in the pottery residues at Klu lding, some samples displayed slightly enriched carbon isotopic data, probably indicating the mixture of animal fats and C_4 plant oils. The presence of lipid biomarkers of leafy plants at Klu lding revealed the gathering of local wild plants and also suggests the sedentary subsistence strategies.

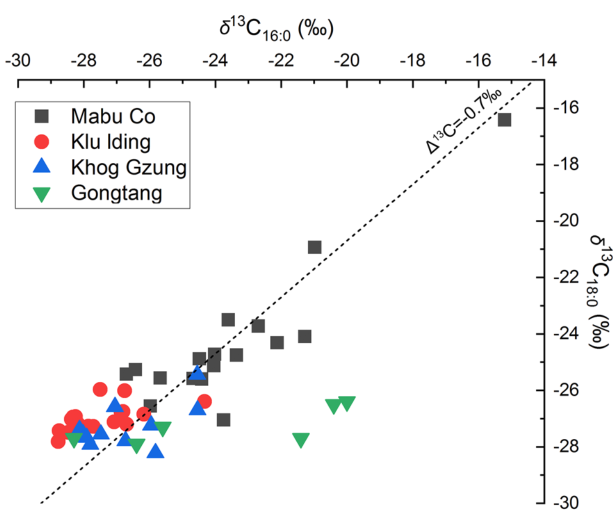


Fig. 7 | Summary of $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values of pottery residues on the southern Tibetan Plateau[34,35] (Supplementary Information Table S4. Dash line refers to the global reference range of non-ruminant and ruminant adipose fats, drawn based on Suryanarayan et al.[47]). $\Delta^{13}C = \delta^{13}C_{18:0}\text{-}\delta^{13}C_{16:0}$.

On the southern Tibetan Plateau with higher altitudes, higher proportions of ruminant fats appeared in the pottery residues at Khog Gzung and Gongtang. The wide ranges of carbon isotopic data of fatty acids were related to the enrichment of carbon isotopes with the increased elevation[34,35]. In the recent zooarchaeological studies at Khog Gzung, domestic ruminant,s including *Bos* sp., sheep, and goats, were confirmed and comprised 23.3% of the total identifiable specimens[16]. The wide moving ranges of the domestic animals with different altitudes may indicate the presence of animal husbandry strategies such as transhumance in the higher altitude regions. Although non-ruminant fats were detected from the pottery samples at Khog Gzung, no non-ruminant animal bones were identified in the faunal assemblages[16]. The hand-picking collection method of faunal remains and the small sample size at Khog Gzung may limit further interpretations. Dairy fats were detected from the pottery residues at Gongtang around 3000 cal. BP[35]. During the same period on the western Tibetan Plateau, milk proteins were recovered from human dental calculus, dated back as early as 3500 BP[60]. Both the dairy lipid and protein evidence are in accordance with the hypothesis of the formation of agropastoralism in the high-altitude regions after 3600 BP[4].

With the paucity of study materials and analytical results on the southern Tibetan Plateau, currently, further interpretations are still limited. Combining the pottery lipid residue results and multiple lines of evidence, it can be seen that the diversified and localised subsistence strategies facilitated human adaptations in the different altitude regions on the southern Tibetan Plateau. The spread of agriculture has been adapted to local geographical conditions. At ultra-high elevation, with the most scarcity of resources in the environment, foraging and the targeted exploitation of lake resources supported human living at Mabu Co. In the high-altitude regions, higher mobility with hunting and pastoralism improved the utilisation ranges of living resources. In the low-altitude regions, with the relatively more abundant local resources, sedentary agriculture spread and was established.

Data availability

The raw datasets generated during the current study are available from the corresponding author on reasonable request.

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Author contributions

Y.Z. conducted experiments, performed data analysis, wrote the manuscript, and acquired funding. X.Y. and S.W. arranged resources. Y.G., J.Y., S.C., Y.T., N.J., Q.S., J.R., and Y.W. participated in the excavation and selected samples. All authors reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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