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The use of early pottery by hunter-gatherers of the Eastern European forest-steppe

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A B S T R A C T

The Eastern European steppe and forest-steppe is a key region for understanding the emergence of pottery in Europe. The vast region encompasses the basins of two major waterways, the Don and the Volga rivers, and was occupied by hunter-gatherer-fisher communities attracted to highly productive forest/aquatic ecotones. The precise dates for the inception of pottery production in this region and the function of pottery is unknown, but such information is vital for charting the pan-Eurasian dispersal of pottery technology and whether there were common motivations for its adoption. To investigate, we conducted AMS dating, including a re-evaluation of legacy radiocarbon dates together with organic residue analysis and microscopy. The dating programme was able to clarify the sequence and show that hunter-gatherer pottery production was unlikely in this region before the 6th millennium BC. Regarding use, stable isotope and molecular analysis of 160 pottery samples from 35 sites across the region shows that terrestrial animal carcass fats were preferentially processed in pots at Middle Volga sites whereas aquatic resources dominate the residues in pottery from the Middle and Upper Don basin. This is supported by fragments of fish, legumes and grasses in the available charred deposits adhering to the inside of pottery from the Don basin. Since the sites from both river basins had similar environmental settings and were broadly contemporaneous, it is posited that pottery use was under strong cultural control, recognisable as separate sub-regional culinary traditions. The 'aquatic hypothesis', previously suggested to explain the emergence of Eurasian pottery, cannot be substantiated in this context.

1. Introduction

The origin of pottery containers in Europe is often associated with the emergence of agriculture in the south-east of the continent. However, some of the earliest ceramics in Europe were produced by hunter-gatherers living in the temperate forest steppe covering the north-east of the continent (Fig. 1), with an occupation sequence suggested to date between the end of the 7th and first half of the 6th millennium cal BC (Dolukhanov et al., 2009; Piezonka, 2012; Vybornov et al., 2017). There is no adequate explanation of why forager groups adopted pottery at this time and whether, as is evident in early farming communities, this marked a major shift in sedentism, social complexity and/or subsistence economy. The existence of ceramic containers before farming is a

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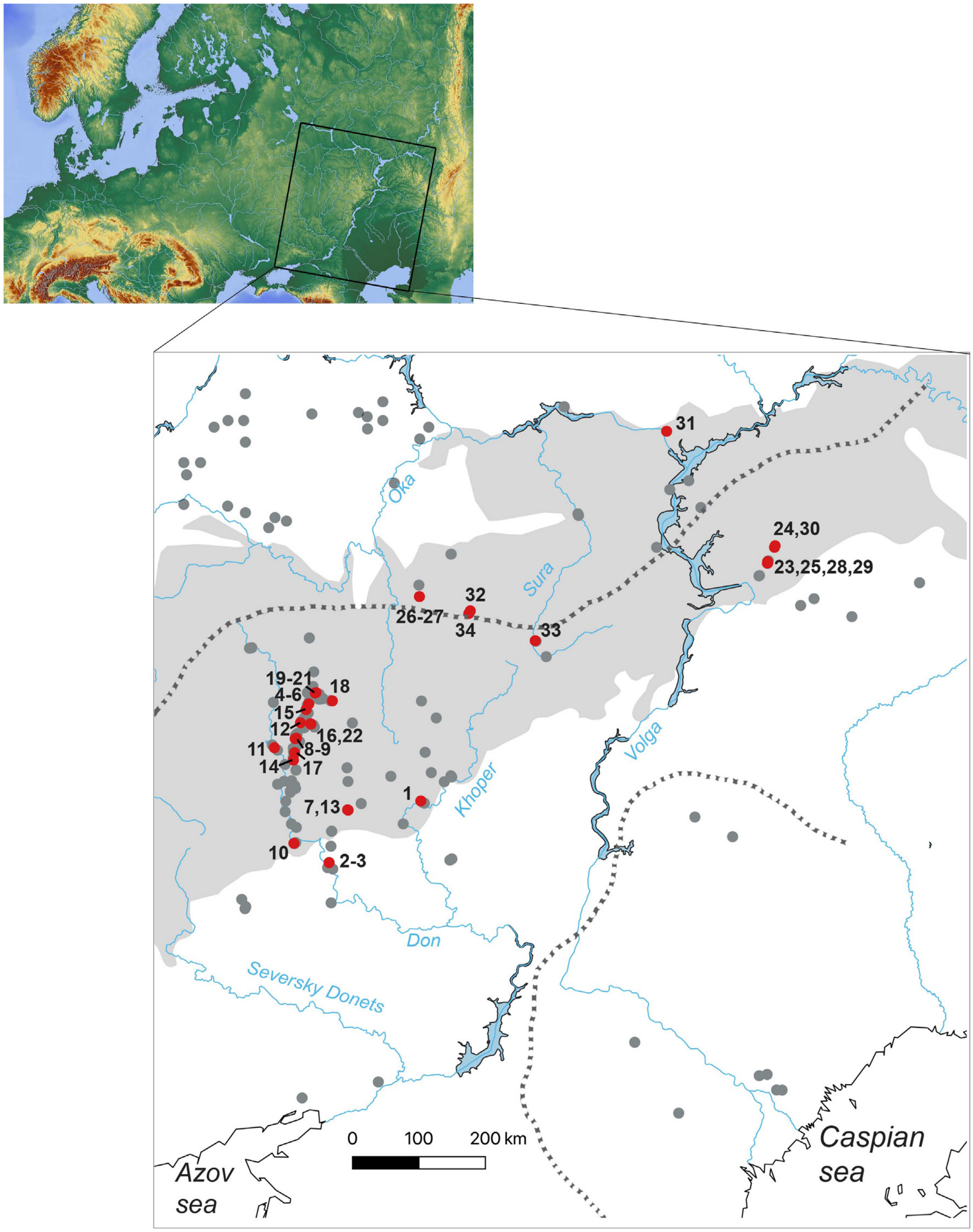

Fig. 1. Map showing the location of Early Neolithic sites in the Don and Volga. Red points indicate the sites where pottery vessels investigated in this study were sampled (other hunter-gatherer sites are in grey). Middle/Upper Don sites are 1: Borisoglebskaya 1, 2: Cherkasskaya 3, 3: Cherkasskaya 5, 4: Dobroe 4, 5: Dobroe 7, 6: Dobroe 9, 7: Dronikha, 8: Karamyshevo 19, 9: Karamyshevo 9, 10: Kopanische, 11: Ksizovo 6, 12: Lipetskoe ozero, site 377, 13: Monastyrskaya 1, 14: mouth of Izlegoschi River 2, 15: Nº380, 16: Rybnoe ozero 2, site 202, 17: Savitskoe, 18: Staroe Torbeevo 11, 19: Vasilievsky kordon 3, 20: Vasilievsky kordon 5, 21: Vasilievsky kordon 7, 22: Yarlukovskaya protoka,p. 222; Middle Volga sites are 23: Bolshaya Rakovka 2, 24: Chekalino IV, 25: Ilyinka, 26: Imerka 7, 27: Imerka 8, 28: Krasny gorodok, 29: Lebyzhinka, 30: Nizhnyaya Orlianka II, 31: Otarskaya 6, 32: Ozimenki 2, 33: Podlesnoe III, 34: Potodeevo. The modern forest-steppe region, as defined in (Olson et al., 2001), is shown in grey and the open steppe at the beginning of the Atlantic period is delineated by the dotted lines (Andreev and Vybornov, 2017; Gerasimov, 1982).

much wider issue across Eurasia (Jordan and Zvelebil, 2009) and beyond. In the circum-Baltic region, the debate has recently benefited from identification of organic residues as indicators of pottery vessel use (Bondetti et al., 2019; Courel et al., 2020; Oras et al., 2017). Oras et al. proposed that pottery served as a tool for processing seasonally abundant aquatic resources, and was an intrinsic technology for processing the surplus created by semi-sedentary foragers, who inhabited resource rich aquatic/forest ecotones during the Holocene climate optimum (Oras et al., 2017). As pottery spread westwards around the Baltic over the following millennium (i.e. from 5500–4500 cal BC) it seems to have had a more diverse range of uses, largely influenced by existing cultural practices and traditions at the sub-regional level rather than the environment context (Courel et al., 2020; Oras et al., 2017; Papakosta et al., 2019).

Although organic residue analysis is increasingly being applied to northeastern European hunter-gatherer pottery, to date there has been no systematic sub-regional study of early pottery use from the vast eastern European forest and open steppe. The inception of pottery defines the start of the Neolithic period in this region. With radiocarbon dates spanning the 7th and 6th millennia cal BC, it appears to predate the earliest pottery in the circum-Baltic, but many sites are poorly dated and it is not yet possible to accurately reconstruct the spatio-temporal dispersal of pottery through this region with any certainty or to understand how different pottery producing traditions may be related. It is also uncertain whether ceramic production and use in this region was associated with the processing of aquatic foods, as in the Eastern Baltic, or had quite separate uses perhaps reflecting the local environment, landscape and/or cultural setting. The region is characterised by rich aquatic/forest ecotones, environments that lend themselves well to surplus-producing hunter-gatherers. Pottery is abundant and structures are recorded on several sites suggesting long-term habitation.

Here we consider some of the best known early ceramic traditions in this region, located in the Middle Volga basin - synonymous with the Middle Volga and Elshanskaya cultures (Dolukhanov et al., 2005; Vasilieva, 2011; Vybornov et al., 2013, 2017) and the Middle and Upper Don basin - synonymous with the Middle Don, Karamyshevo and Cherkassky 5 cultures (Smolyaninov, 2020; Smolyaninov et al., 2017). The aims were (i) to carry out organic residue analysis of pottery vessels across the study area and evaluate the results according to the palaeoenvironmental and cultural setting, (ii) undertake microscopic analysis of charred surface deposits to complement the organic residue analysis, and (iii) to refine the chronology of early pottery assemblages through direct dating, by AMS, of charred surface deposits or ‘foodcrusts’, associated animal bones and reconsidering ‘legacy’ dates from previous studies in the region.

2. Study areas and materials

2.1. Environmental settings

Only a general environmental description of the 6th and 5th millennia cal BC can be made due to the lack of micro-regional paleoecological studies. The territory of the Upper and Middle Don basin is located within an elevated hilly plain separated by a dense network of river valleys, balkas and ravines, with forests covering both river valleys and watersheds (Mil'kov, 1977). Similarly, the Middle Volga basin has a complex and branched hydrological system, with both meridional and latitudinal directions. During the Atlantic period (from ca. 6000 cal BC), forested areas were primarily concentrated along river valleys in the southern part of the forest-steppe Volga (Samara River) basin (Spiridonova and Lavrushin, 1997) while the steppe could have reached the basin of the Sok river and the Upper Don area (Spiridonova, 1991; Vybornov, 2011); Fig. 1). This macro-regional picture is supplemented by occasional site-specific palynological studies, for example, the importance of Chenopodiaceae and wormwood (*Artemisia* spp.) at the site of Ivanovskaja (Vybornov, 2011).

Waterways surrounded by forest are attractive habitats for hunter-gatherers, providing essential natural resources. Most of the Early Neolithic sites of the Upper and Middle Don area are concentrated either on the bars, at the higher level of the first terrace above the floodplain, on floodplains, on lake shores or, occasionally, on the slopes of river valleys. The sites are mostly located along different tributaries of the Don River (e.g. Bityug, Voronezh, Matyra rivers) beside oxbows which are frequently flooded in spring. Likewise, in the Middle Volga, most of the sites are located on the floodplain and first terrace of the Volga tributaries (including Sura, Sok, Moksha rivers). It is suggested that these interconnected waterways facilitated the penetration and the uptake of the pottery in the early Atlantic period (Gapochka, 2001; Sinûk, 1986).

2.2. Faunal remains

Archaeological layers with the earliest pottery usually occur in sandy sediments, resulting in the recovery of asynchronous finds from the same lithological layer, complicating differentiation between occupation phases. The exceptions are several sites located in more humid areas. The poor preservation of organic remains in sandy sediments, including animal bone, allows only partial reconstruction of the subsistence economy. The recovery of faunal assemblages in the Don sub-region, notably at Cherkasskaya 5 and Dobroe 9 (Dataset 1), indicates the presence of wild mammals including elk (*Alces alces*), wild boar (*Sus scrofa*), wild horse (*Equus ferus*), beaver (*Castor fiber*), wild goat/tur (*Capra* spp.), lynx (*Lynx lynx*), pine marten (*Martes martes*), fox (*Vulpes vulpes*), birds such as mallard (*Anas platyrhynchos*) and fish including pike (*Esox lucius*), wels catfish (*Silurus glanis*) and common carp *(Cyprinus carpio)* (Skorobogatov et al., 2018; Yanish et al., 2019). Similarly, in the Middle Volga basin, bones of wild goat, saiga (*Saiga tatarica*), deer (Cervidae), beaver and marten were found at Chekalino IV (Vybornov, 2011). Beaver and elk predominate at the Ivanovka and Vilovatovskaya sites (Andreev and Vybornov, 2017). Additionally, fish bones and turtle remains are documented at the majority of sites. Sinkers found on many sites suggest net fishing. Unionidae (freshwater mussel) shell piles are found at larger sites (Andreev and Vybornov, 2017). There is no clear evidence for substantial differences in the faunal assemblages between the Don and Volga basins, although poor preservation prevents comprehensive comparative assessment.

2.3. Archaeological features

With a few exceptions, evidence of structures is mostly absent at sites located in the Middle Volga, Upper and Middle Don basins, but this might be due to poor preservation. In the Don sub-region, a 22 × 9 m rectangular platform covered with a 10–20 cm layer of crushed mollusc shell was found at Dronikha (Sinûk, 1986) and Shuchie II (Gapochka, 2001). Similar platforms were found at Yarlukovskaya protoka in the Upper Don area (Voronina et al., 1969). Larger pits were also identified on some of the sites, such as at Bukhovoe 10, where a pit (3 × 2.4 m) with fragments of two ceramic vessels lying upright was recorded (Ivashov et al., 2018). An oval dwelling (5.6 × 3.85 m) with a fireplace and a broken vessel on the floor of the dwelling was found at Rybnoe Ozero 2 (site 202), and a subterranean construction of oval form, 18 m^2, attributed to the Karamyshevo culture, was found at Vasilievsky kordon 3. In the Middle Volga, remains of five dwellings have been found, and pits along with fireplaces were recorded (Andreev and Vybornov, 2017).

2.4. Pottery assemblages and sampling

We focused on vessels showing stylistic characteristics (technological, morphological and decorative traits) typical of the earliest ceramic phases; namely Cherkassky 5 type, Middle Don, Karamyshevo, Elshanskaya and Middle Volga cultures. Technological, morphological and decorative features characterising each of these pottery traditions are summarised in Table S1 (Sinûk, 1986; Smolyaninov, 2020; Vasilieva, 2011) and examples of reconstructed vessels are shown in Figs. S1 and S2 (Supplementary Data). The assemblage is highly fragmented and, in many cases, the whole "chaîne opératoire" could not be reconstructed. Decorative elements show some interconnections between Middle Volga, Middle Don, Cherkassky 5 and Karamyshevo group pottery and can be regarded as a commonly spread style (Smolyaninov et al., 2017).

A low percentage of ceramic vessels were associated with charred surface deposits (foodcrusts), crudely estimated to be ca. 0.3 %–1 % of the total potsherds found in the Middle and Upper Don and ca. 0.1 %–1 % of the Elshanskaya sherds. Foodcrusts are absent on Middle Volga pottery. An exception is the Cherkasskaya 5 site in the Middle Don, where up to 80–90 % of vessel fragments are associated with foodcrusts. It is not clear whether the differences in the inter-site prevalence of these deposits on pottery reflect different patterns of pottery use or site-specific preservation conditions.

3. Methods

3.1. AMS dating and Bayesian chronological modelling

Seventy samples of foodcrusts or animal bones, including 3 replicates, so 67 unique samples, were selected for AMS ^{14}C dating (Dataset 2). Samples were dated at the Scottish Universities Environmental Research Centre, East Kilbride, Scotland (SUERC-), the Oxford Radiocarbon Accelerator Unit, Oxford, England (OxA-), and the Hertelendi Laboratory of Environmental Studies (HEKAL), Debrecen, Hungary (DeA-), following routine chemical pretreatment and AMS measurement (Brock et al., 2010; Dunbar et al., 2016; Molnár et al., 2013a, b). Two of the dated samples are foodcrusts from Nizhnyaya Orlianka II and Podlesnoe III, in the Middle Volga basin (Fig. 1). The other 65 samples were from sites in the Upper and Middle Don. Thirty-three were dated, and 32 (including all 27 bones from Dobroe 9) failed. Of the dated samples, 25 were from Cherkasskaya 3 or 5, where most bones had adequate collagen and many pots had foodcrusts. The other new dates were foodcrust samples from Kopanische, Rybnoe ozero 2, site 202, Lipetskoe ozero (4 samples), site №380 and Staroe Torbeevo 11.

As new samples suitable for ^{14}C dating were not available for much of the study region, published ('legacy') ^{14}C data were collated (Dataset 2) and assessed (see Section 3 in Supplementary Data). Bayesian chronological modelling (Bronk Ramsey, 2009) was used to interpret the combined data sets. Although this model incorporates a site chronology for Cherkasskaya 5, it focuses on providing realistic estimates of date ranges for the production of the principal Neolithic pottery types in the study region.

3.2. Organic residue analysis

Early Neolithic ceramic vessels from 23 hunter-gatherer sites in the Upper/Middle Don and 12 sites in the Middle Volga areas (Fig. 1, Table S2 and S3) were identified for study. In total, 81 potsherd samples and 20 foodcrusts from Middle and Upper Don sites and 59 ceramic samples from the Middle Volga basin were sampled. Due to the amounts available, four additional foodcrusts samples (3 from the Middle and Upper Don, 1 from the Middle Volga) were reserved for AMS ^{14}C dating only. Sampling was undertaken with the aim of obtaining a representative sample of the wider assemblage, and not biased with regards to shape, diameter, size, technological traits (e.g., temper and thickness) and the presence or absence of foodcrusts.

Charred deposits were gently dislodged from the ceramic surface using a clean scalpel and the surface layer of each potsherd was removed by light drilling to minimise any contamination from the burial environment or due to the handling post-excavation. Each potsherd was crushed in an agate mortar. The samples were prepared using the acidified methanol extraction method applied to 1 g of ceramic powder and ca. 20 mg of charred surface deposit (Courel et al., 2020; Craig et al., 2013). The acidified methanol extracts were analysed by GC-MS in total ion current mode for general screening purposes, in selected ion monitoring (SIM) mode to target specific markers of aquatic resources and by GC-c-IRMS to obtain the carbon isotope values of the most abundant fatty acids ($C_{16:0}$ and $C_{18:0}$) precisely following published methods (Courel et al., 2020). In addition, 23 potsherds (ca. 1 g) were solvent extracted using established protocols (Evershed et al., 1999) and analysed by GC-FID and GC-MS to investigate either the presence and distribution of triacylglycerols (TAGs) or the presence of other intact lipids (e.g. wax esters).

3.3. Microscopic analysis of fooodcrusts

Initial observation of the selected foodcrusts was carried out using a Leica MZ APO binocular microscope at magnifications between 8× to 50×. Then, pictures were recorded using a VHX-5000 Keyence digital microscope at magnifications from 20× to 200×. Subsequently, SEM analysis, using a Hitachi S–3700 N Scanning Electron Microscope, was undertaken on 13 selected foodcrust samples that appeared to contain potential inclusions including putative animal or plant tissues. Samples were cleaned from adhered materials such as clay residue and sediments with a brush and sputter coated with ca. 1 μm of gold when necessary for image quality purposes.

3.4. Palaeoenvironmental data

Hydrological data were sourced from the EU Joint Research Centre's Catchment and Characterisation Modelling activity (https://ccm.jrc.ec.europa.eu/). Straight-line distance between each site and the closest river was calculated using standard tools in GIS, and the upstream area draining through the corresponding river segment at this point was read from the database. The significance of the geostatistical patterns obtained in this way were assessed through comparison with a cloud of 1000 random points placed within a 10 km buffer enveloping the river paths. For additional comparison, early farming sites in Central Europe (Jordan et al., 2016) were used as an out-group in this analysis.

4. Results

4.1. Absolute chronology

4.1.1. New AMS dates

Cherkassky 5-type pottery: The dates of eight herbivore bones from Cherkasskaya 5, and a plant fibre attached to a stone artefact, cluster in the early 6th millennium cal BC. This is the first coherent set of AMS ^{14}C dates associated with Early Neolithic pottery in the Middle or Upper Don.[2] There are 10 new dates and three legacy dates on foodcrusts from Cherkasskaya 5, three new dates and two

[2] A bone from the top of the Early Neolithic layer at Cherkasskaya 5, identified morphometrically as goat, was dated to the Bronze Age (SUERC-86152, 3855 ± 28 BP, 2460–2200 cal BC).

legacy dates on foodcrusts from Cherkasskaya 3, and one new foodcrust date from Lipetskoe Ozero. Altogether, these 19 foodcrust ^{14}C ages on Cherkassky 5-type pottery span c. 8700-6500 BP, compared to c. 7000-6900 BP for the bones and plant fibre. Foodcrust ^{14}C ages over 7000 BP may be due to reservoir effects (which would imply that some local fish had reservoir effects of at least c. 1700 ^{14}C years; Supplementary Data, Section 3), but the younger foodcrust ^{14}C ages imply that Cherkasskaya 5-type pottery continued to be made well into the mid-6th millennium cal BC.

Middle Don-type pottery: Four new foodcrust ^{14}C dates were obtained on Middle Don pottery, two from Cherkasskaya 3, complementing one legacy foodcrust date, and one each from Lipetskoe Ozero and Kopanische. There are no relevant ^{14}C dates on bones or plant material (27 bones from Dobroe 9 all failed, due to poor collagen preservation).

Karamyshevo-culture pottery: Three new foodcrust ^{14}C dates have been obtained for Karamyshevo-culture sherds (at №380, Staroe Torbeevo 11, and Rybnoe Ozero 2). There are no ^{14}C dates for terrestrial samples associated with Karamyshevo-culture pottery.

Dnepr-Donets pottery: two foodcrust ^{14}C ages were obtained on sherds from Lipetskoe Ozero, the first such dates for this pottery type in the Middle-Upper Don basin. There are no ^{14}C dates for terrestrial samples associated with Dnepr-Donets pottery in this region.

Elshanskaya pottery: One new foodcrust ^{14}C age (DeA-20752, 7440 ± 49 BP) was obtained from Nizhnya Orlyanka II. EA-IRMS results (δ^{13}C −27.2‰, δ^{15}N 4.6‰, C/N 13.3) give little indication of aquatic ingredients, but the foodcrust had an extremely low organic content (10.6 % C, compared to 40–50 % C in the other foodcrusts dated), and its ^{14}C age may therefore be less reliable. There are also no ^{14}C dates for terrestrial samples associated with Early Neolithic pottery types in the Middle Volga basin (Elshanskaya or Middle Volga pottery).

4.1.2. Chronological modelling

The chronological model includes the new AMS dates and over 250 ^{14}C legacy dates. Most of the latter have very large uncertainties once potential ^{14}C age offsets are taken into account, with individual calibrated dates usually spanning more than a millennium. Nevertheless, some broad patterns emerge (Fig. 2) and the vessels subjected to organic residue analysis can be separated into two phases:

1. c. 6000-5200 cal BC, comprising most Elshanskaya pottery from the Middle Volga basin and Cherkassky 5 type from the Don basin
2. c. 5200-4500 cal BC, comprising some late Elshanskaya pottery from the Middle Volga basin, Middle Volga pottery, western-variant Elshanskaya pottery, and Middle Don and Karamyshevo culture from the Don basin.

Early Neolithic pottery types therefore span much of the 6th and 5th millennia cal BC. Dates before 6000 cal BC are possible, but unlikely: wherever there are potential 7th-millennium TOCC ^{14}C ages for pottery, results from the same pottery type are scattered, so the model down-weights them. Where total organic carbon content (TOCC) ^{14}C ages for a particular pottery type are more consistent, and are given more weight by the model, they cannot date earlier than the 6th millennium (e.g. Elshanskaya pottery at Il'inka and Staraya Elshanka II). In the Don basin, the earliest reliable date (7135 ± 20 BP [6055-5985 cal BC]) is the weighted mean ^{14}C age of a horse tooth from Cherkasskaya 5, which is significantly older than the other nine terrestrial samples from the Early Neolithic layer. In the model, the horse tooth result was omitted, as it appears to be a stratigraphic misfit in the Early Neolithic layer (A<60; Bronk Ramsey, 1995).

Elshanskaya pottery has a wide overall date range, but most TOCC ^{14}C dates appear to fall in the early-mid 6th millennium. Where possible, the typological attribution to groups 1 and 2 of Elshanskaya pottery sampled for organic residue analysis was also applied to TOCC-dated Elshanskaya pottery, but although the earliest dates may be associated with group 1, the two groups seem to have coexisted for much of the 6th millennium (Fig. 2). As all the sherds sampled for residue analysis were attributed to either group 1 or group 2, the Elshanskaya residue data should only date to the 6th millennium. Middle Volga culture pottery appears to only date to the early-mid 5th millennium.

Cherkassky-5 type pottery from the Middle Don dates to the early-mid 6th millennium. Although the latest examples of this type, from Cherkasskaya 3 and Lipetskoe Ozero, are not tightly dated, most sherds sampled for organic residue analysis were from Cherkasskaya 5 itself and should date to the first quarter of the 6th millennium. Middle Don pottery is only dated by TOCC, but regardless of the precise parameterisation of the TOCC ^{14}C offset correction model, it always appears to date to the late 6th and earlier 5th millennium. Karamyshevo-type pottery, also dated mainly by TOCC, apparently dates to the early-mid-5th millennium, again regardless of the exact parameters used for ^{14}C offset correction. Thus Cherkassky-5 pottery appears to predate both the Middle Don and Karamyshevo types, and to be contemporaneous with Elshanskaya pottery in the Middle Volga basin; Middle Don, Karamyshevo and Middle Volga pottery were all used during the earlier 5th millennium.

4.2. Biomolecular, isotopic and microscopic analyses

Appreciable quantities of lipids were extracted from foodcrusts (18/20 samples with concentration > 100 μg/g) and potsherds (134/140 samples with >5 μg/g of lipids) (Evershed, 2008). The lipid concentration in potsherds from the two basins are significantly different with median Middle Volga lipid concentrations 23 μg/g higher than those observed for potsherds from the Don basin (Mann-Whitney *U* test: $z = 4.9166$, $p < 0.05$; Fig. S5). This could be due to differences in use (Charters et al., 1997), vessel porosity (Drieu et al., 2019) or the burial environment (Aillaud, 2002).

4.2.1. Pottery use in the Middle and Upper Don

The presence of foodcrusts, especially at Cherkasskaya sites, suggests that high-temperature processing (cooking, rendering etc) was at least one mode of hunter-gatherer pottery use in the Don sub-region. Foodcrusts typically occur in the form of thin deposits (1–2 mm) with no clear layering. The majority of the foodcrusts have semi-compacted microstructures with cracks and channel voids or semi-porous microstructures with visible closed voids (Tables S4 and S5 (González Carretero, 2020; González Carretero et al., 2017);). This, together with the presence of ω-(*o*-alkylphenyl)alkanoic acids (hereafter APAAs, in 56/101 of the samples analysed) supports the fact that a majority of pottery and its contents were exposed to high temperatures (≥200 °C; Bondetti et al., 2021b; Cramp and Evershed, 2014). Two additional foodcrusts showed an almost solid appearance with a high degree of glossiness on the surface that is likely to be the result of extremely high temperature burning or repetitive burning events which led to the vitrification of the contents (González Carretero, 2020; Valamoti et al., 2008).

Lipid residues from Middle and Upper Don pottery show clear evidence for the processing of 'aquatic' products (i.e., freshwater fish, aquatic birds, aquatic molluscs) as revealed by (i) the presence of APAAs composed of 16–20 and/or 22 carbon atoms alongside

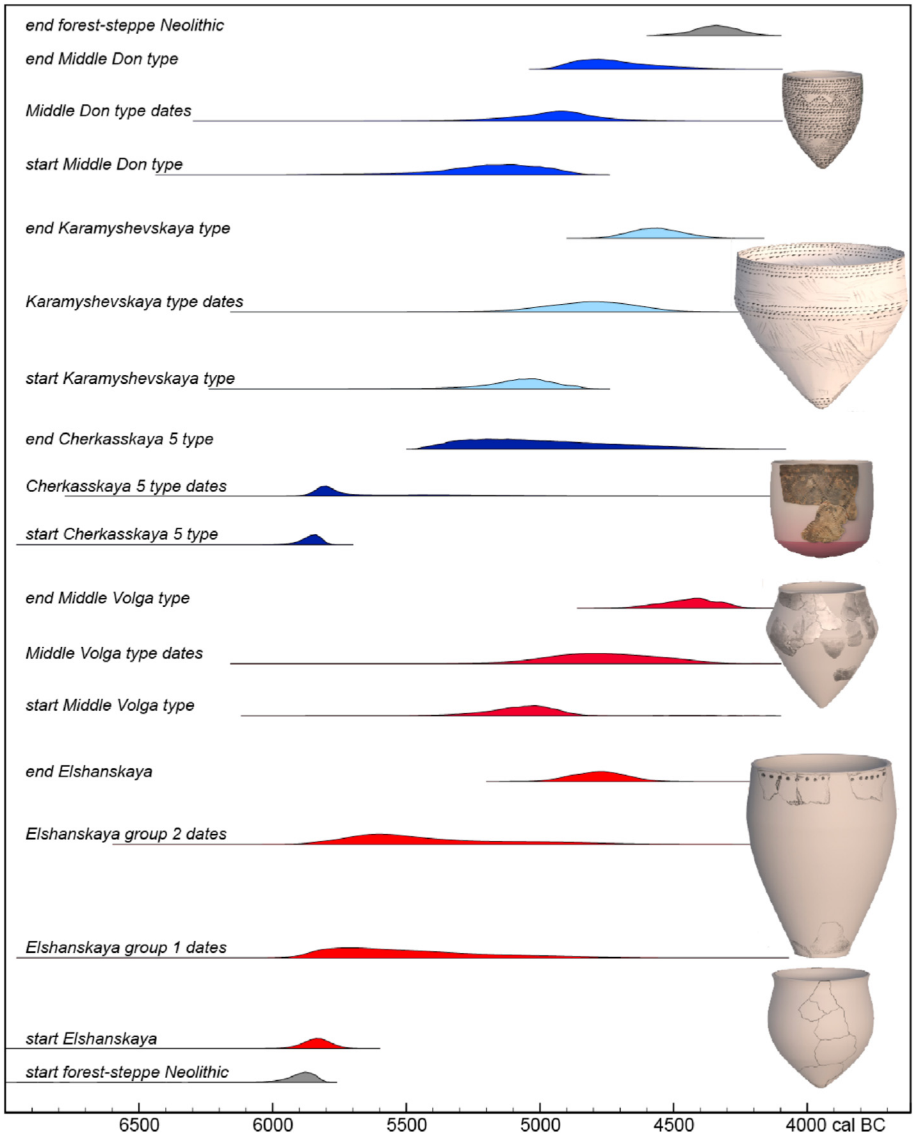

Fig. 2. Details of the Bayesian chronological model output, and reconstructed typical vessels for the corresponding pottery types. The 'start' and 'end' distributions are probability density estimates of when the production of each pottery type began and ended (OxCal function Boundary). The 'dates' distributions are estimated temporal distributions of the dated samples of each pottery type (OxCal function KDE_Plot; (Bronk Ramsey, 2017). The OxCal CQL code used to generate these estimates is given in the Supplementary Data.

isoprenoid acids (4,8,12-TMTD, pristanic acid, phytanic acid) (Cramp and Evershed, 2014), (ii) APAA C_{20}/APAA C_{18} ratios above 0.06 (Bondetti et al., 2021b) and (iii) the predominance of the SRR-isomer of phytanic acid over the RRR-isomer (>75 %; Lucquin et al., 2016a). Freshwater resources dominate in Cherkassky 5 type pottery (90 % of the vessels) and in the Middle Don culture pottery (88 % of the vessels), while only 43 % vessels of the Karamyshevo culture had the full suite of attributes for freshwater resources or a %SRR>75 %.

Within the Don basin, the distribution of isotopic values of fatty acids from shell-tempered vessels (n = 36; median $\delta^{13}C_{16:0} = -31.1$ ‰) was different to those with other tempers (sand, grog, organic; n = 52; median $\delta^{13}C_{16:0} = -29.5$ ‰), indicating a greater tendency for processing of freshwater resources (Mann-Whitney; U = 691.5, z = 2.1, p = 0.04). Similarly, a greater proportion of shell-tempered vessels had C_{20} APAAs (26/31) compared to vessels tempered with other materials (24/61). It is highly unlikely that these lipids are derived from the temper itself (Admiraal et al., 2020). Rather the observed difference more likely reflects a technical choice relating to cooking performance and intended use. Shell tempers were not used by hunter-gatherer-potters in the Middle Volga region.

For the potsherds associated with charred deposits, more than 90 % yielded APAAs, including the C_{20} APAAs, while only 25 % of the potsherds without charred deposits contained C_{20} APAAs, suggesting a possible correlation between the formation of foodcrusts and the processing of aquatic commodities or that these molecules preserve better in foodcrusts. The microscopic identification of a range of fish tissues in the foodcrusts such as cycloid fish scales and laminated bony structures (similar to sturgeon bone) with long fish bones confirm the presence of aquatic resources in, at least, six charred surface samples (Table S5). Such commodities could have been valuable food resources but could also have served to produce non-edible products, for example, fish glue, as has been suggested for hunter-gatherer pottery from the Lower Don (Bondetti et al., 2021a).

Compelling evidence for the processing of plant resources in early Middle and Upper Don pottery is derived from two different strands of evidence. Firstly, organic molecules consistent with plant tissues, such as oleanene, amyrenone and/or amyrin, and β-sitosterol (Courel, 2016), were detected in trace amounts in, at least, 17 % of the Middle Don ceramic vessels studied (14/81; Dataset 3). Secondly, microscopic investigations (SEM) of foodcrusts provide clear evidence of plant processing. Six foodcrusts from the Cherkasskaya sites contained plant tissues which include whole and fragmented seeds, epidermal seed layers and parenchyma cell-tissues among others (Table S6). Among them, wild legume seeds (Fig. 3), tentatively identified as clover-like seeds (cf. *Trifolium* spp) were identified in abundant concentration. Furthermore, tissues from grasses of the cereal family (Poaceae) were found, in particular pericarp tissues such as transverse and longitudinal cells (bran) and aleurone layers, and parenchyma cell tissue in combination with vascular bundles, likely to be derived from rhizomes or tuber-like structures.

4.2.2. Pottery use in the Middle Volga

The near absence of foodcrusts on Elshanskaya and Middle Volga culture vessels and the absence, with few exceptions, of lipid markers indicating heat treatment (i.e., APAAs, mid-chain ketones) may suggest that pottery use did not involve exposure to high temperature (storage, display, etc). However, their use for cooking cannot be completely excluded as several of the Elshanskaya pots showed visible evidence of exposure to fire during their use. Unlike hunter-gatherer pottery used in the Don basin, Elshanskaya and Middle Volga vessels were not primarily used to cook aquatic resources. Only three samples, corresponding to vessels from the early phase of the Elshanskaya culture, yielded the full suite of markers typical of freshwater products including the presence of APAA C_{20} (see Dataset 3). Even when vessels without foodcrusts are compared, aquatic resources were far more prevalent on those from the Don basin (12/58) compared with those from the Volga basin (3/58).

Instead, the processing of ruminant animal fats, such as saiga and wild tur, is more likely, as shown by the difference in ^{13}C values of palmitic acid and stearic acid ($\delta^{13}C_{18:0}-\ \delta^{13}C_{16:0}$ or $\Delta^{13}C$ values < -1 ‰; Fig. 4; 34/59 samples) and the relatively low (<70 %) SRR-isomer ratio (Copley et al., 2003; Craig et al., 2012; Lucquin et al., 2016a). The relatively high $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values (>-30 ‰) obtained in many samples of the Middle Volga basin could be related to the consumption of wild ruminants that grazed on steppe vegetation in which C_4 grasses make a significant contribution. Other molecular proxies, such as monounsaturated carboxylic acids (especially $C_{16:1}$ and $C_{18:1}$), long mid-chain ketones (C_{29}, C_{31}, C_{33}; in only two samples) along with mono- (MAGs), di- (DAGs) and, possibly triacylglycerols (TAGs, Dataset 3) corroborate the presence of terrestrial animal adipose fats in these residues (Evershed et al., 1995).

Wild terrestrial non-ruminants are likely to represent another source of the residues encountered. Such resources can be challenging to identify in part because of an overlap between the carbon isotopic values of the C_{16} and C_{18} carboxylic acids of wild non-ruminant animals and freshwater organisms (Fig. 4). Wild boar are an unlikely source as the $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values fall outside the range of modern reference fat from Eastern Europe specimens ($\delta^{13}C_{16:0} = -26.9 \pm 0.5$ ‰ and $\delta^{13}C_{18:0} = -25.8 \pm 0.7$ ‰; (Courel et al., 2020; Pääkkönen et al., 2018), Table S6) and wild boar have not been found in archaeological assemblages from this region. Other possible non-ruminant animals include beaver, hare, marten and equids.

5. Discussion

The origins of ceramic technology among eastern European hunter-gatherers remains an open question. The major river systems and open steppe may have facilitated long-distance movement, serving as a catalyst for the rapid adoption of innovations, such as pottery manufacture. Connections and exchange between hunter-gatherers occupying the Don and Volga basins are, in part, evidenced by the shared set of decorative features that characterise the respective pottery assemblages (Smolyaninov et al., 2017) although elucidation of the nature, direction and tempo of cultural transmission requires further work. By providing new AMS dates and re-evaluating legacy dates, we show that these groups are likely to have existed concurrently but that two phases can be distinguished in both sub-regions, corresponding to the early-mid 6th and late 6th-mid-5th millennia cal BC. By analysing the contents of pottery belonging to these geographically dispersed hunter-gatherer communities, we can explore whether pottery served common patterns of use and whether the motivations for its adoption were similar to those of other Northern European hunter-gatherers.

Interestingly, the residue analysis shows distinct differences between the two groups. In the Middle and Upper Don, pottery was primarily used for cooking aquatic resources (fish, possibly waterfowl) together with wild plants, perhaps to make stews or soups. This is supported by the presence of numerous charred deposits on the upper parts of the internal surface. The sequential use of the pottery for different commodities instead of intentional mixing is equally possible. Pots from the Middle Volga sites are characterised by the near absence of foodcrusts and were used for cooking, storage and/or serving terrestrial animal resources rather than aquatic foods. Within sites and sub-regions, pottery was used for a wide range of resources and there is no statistical difference in use with regard to the different shape and volume of the vessels.

The results raise a further set of questions. Why is it that hunter-gatherers living, potentially contemporaneously, and in similar environmental settings had such different patterns of pottery use? Why was pottery use apparently constrained within the different river basins? And how variable was pottery use through time? In order to address these questions, the following sections explore the geographical, environmental and cultural factors that might explain the observed patterns in hunter-gatherer pottery use.

5.1. Does proximity to water courses influence the foods processed in pottery?

The location of the sites in the two sub-regions is expected to follow the availability of abundant resources, such as proximity to rivers for aquatic organisms. Sites in both the Don and Volga basins are distributed along major tributaries. More than half of them, including the sites studied here and other contemporary sites with pottery, are located at a very short distance (<0.5 km) from the nearest modern water course. Additionally, the vast majority are near river segments that drain upstream catchments over 5000 km^2. The sites seem to be clustered along particular parts of the rivers - within oxbow lacustrine environments that provided a wider range of resources. This pattern is significantly different from random locations (Wilcoxson rank-sum test, $W = 6015$ for the Volga; $W = 24378$ for the Don; in both cases $p < 10^{-11}$) and remarkably consistent between the two sub-regions ($W = 2241$, $p = 0.85$). By contrast, the proximity of early farmer sites in Central

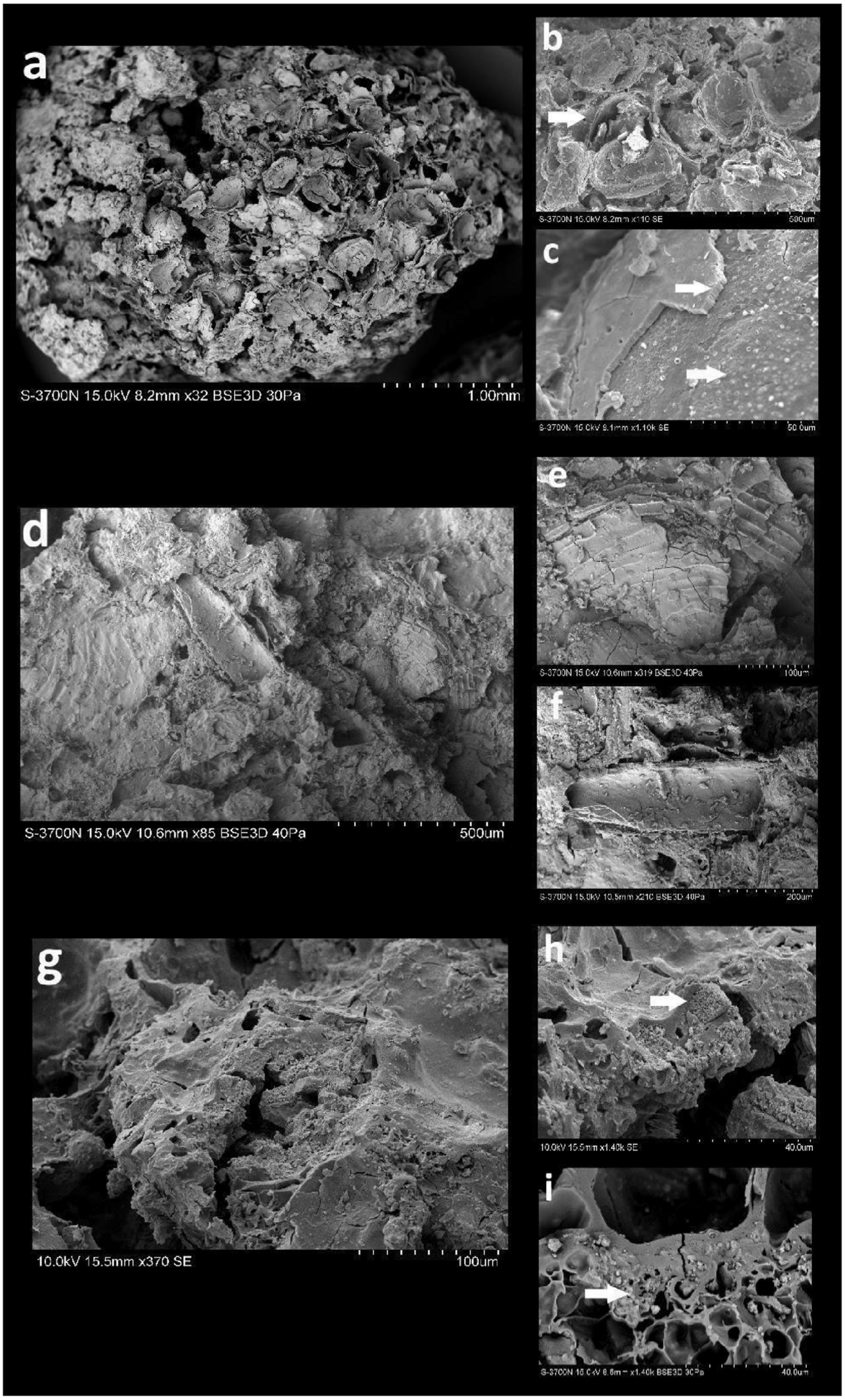

Fig. 3. SEM micrographs showing examples of plant and animal components identified in foodcrusts: (a) CHKA3-680.F. Concentration of small legume seeds (cf. *Trifolium* spp.) embedded in the foodcrust's matrix; (b) CHKA3-680.F. Detail of legume seeds embedded in foodcrust; (c) CHKA3-680.F. Detail of small legume seeds' *testa* pattern and visible palisade layer (marked by arrows); (d) CHKA5-666.F. Fish remains embedded in foodcrust; (e) CHKA5-666.F. Detail of a cycloid fish scale in the foodcrust; (f) CHKA5-666.F. Detail of a fish bone embedded in the foodcrust; (g) CHKA3-680.F. Remains of pericarp and endosperm tissues from grasses (cf. Poaceae); (h) CHKA3-680.F. Detail of single aleurone layer with visible protein-containing aleurone cells (marked by arrow); (i) CHKA3-680.F. Detail of aleurone layer and endosperm cells (marked by arrow).

Europe to watercourses is not significantly different to that of random locations (W = 2637; p = 0.25). Although we cannot exclude the possibility that this finding reflects biases in research, such as site visibility, it is highly likely that proximity to rivers was a major factor influencing site location in the steppe and forest-steppe zone. However, the proximity to large water catchments, in both sub-regions, does not explain the different patterns of pottery use.

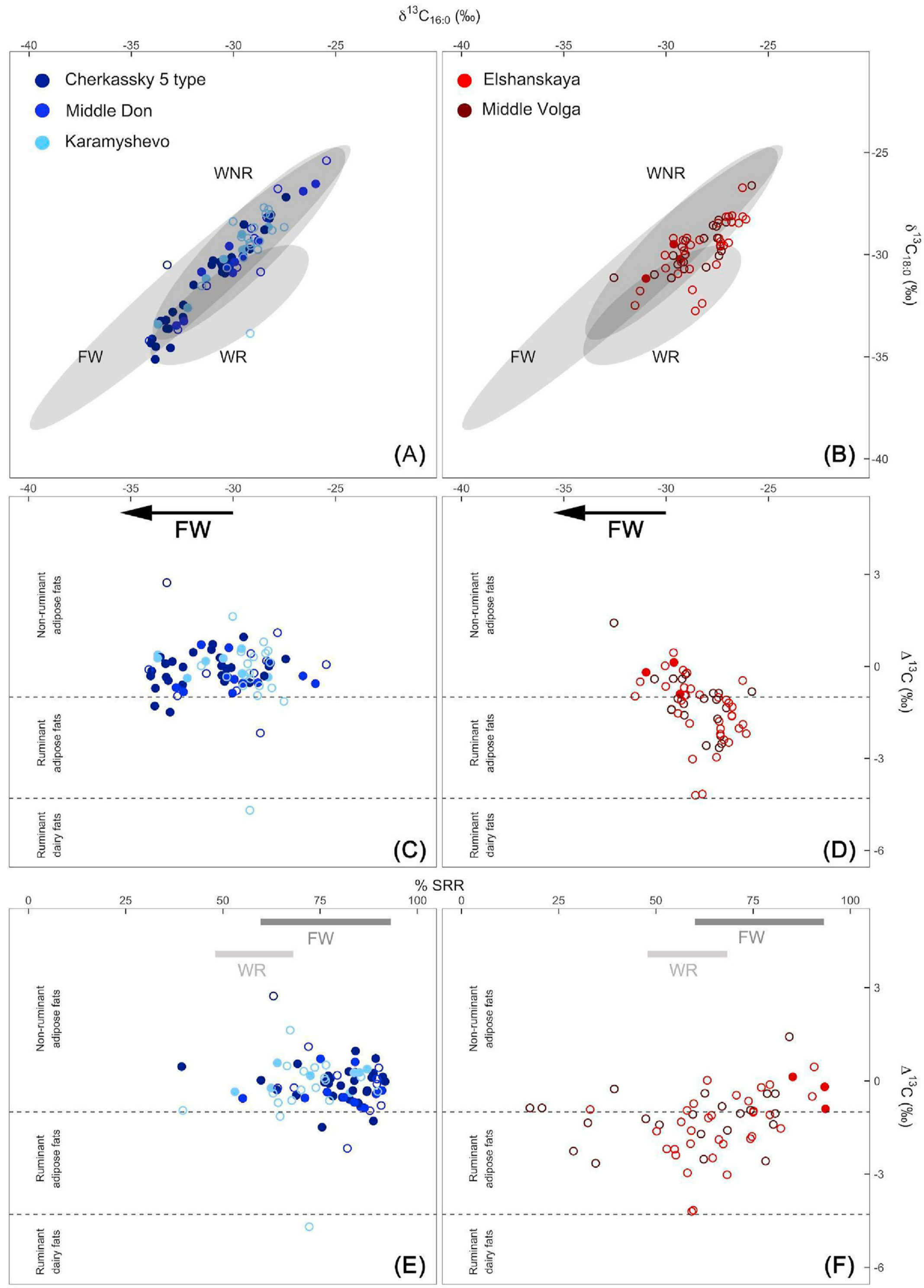

Fig. 4. $\delta^{13}C_{18:0}$ vs. $\delta^{13}C_{16:0}$ values of the main carboxylic acids identified in hunter-gatherer pottery in the forest-steppe area of (A) the Middle and Upper Don basin and (B) the Middle Volga. The 95 % confidence ellipses for aquatic organisms (FW), wild non-ruminants (WNR) and wild ruminants (WR) are determined by authentic reference fats, mostly originating from Russia ((Bondetti et al., 2021a) and Table S9). Filled circles represent samples containing the APAA C_{20} biomarker; open circles - no aquatic biomarker. $\delta^{13}C_{16:0}$ values against the $\Delta^{13}C$ values for (C) the Middle and Upper Don basin pottery and (D) the Middle Volga basin pottery. %SRR against the $\Delta^{13}C$ values for (E) the Middle/Upper Don pottery and (F) the Middle Volga pottery. %SRR range for aquatic and ruminant resources are based on reported values in (Lucquin et al., 2016a).

5.2. Does environmental context influence the resources available and, therefore, the foods processed in pottery?

All sites investigated here are located in a single zone of the Köppen-Geiger classification indicating warm summer continental climates (Dfb) with the exception of the Cherkasskaya sites (hot summer continental climate; Dfa; (Willmes et al., 2014; Willmes et al., 2017). Even though microregional paleoenvironmental reconstructions are lacking nowadays to evaluate local variability, this suggests relatively analogous environmental conditions and therefore no clear difference would be expected in the faunal or floral resources available. Given the similar environmental conditions, it is reasonable to assume that wild animal populations were evenly distributed across the whole ancient steppe and forest-steppe (Dataset 1) including amongst others elk, wild boar (only identified in the Middle Don area), tur, wild horse, saiga, deer, beaver, marten, otter and hare (Andreev and Vybornov, 2017; Vybornov, 2011). In the Middle Don area, wild mammals (e.g. wild boar, deer) do not seem to have been processed in pottery vessels despite being hunted (Skorobogatov et al., 2018; Yanish et al., 2019). This indicates a preference for processing mammal carcasses differently (e.g. spit roasting) in the Don. Mammals are the main residue-type processed in pots in the Volga basin. The aquatic resources documented in the Don river basin (Skorobogatov et al., 2018; Yanish et al., 2019) are also common in the Volga river (Górski, 2010). Fish bones have seldom been recorded at Middle Volga sites, but this can be explained by poor preservation and/or recovery bias. Overall, there is no evidence for differences in resource availability between sites in the Middle Don and Middle Volga, hence this does not adequately explain the observed differences in pottery use.

5.3. Does the type of site influence pottery use?

The nature of the sites, whether more permanent settlements or seasonal camps, may have had an impact on the way that pottery was used. However, such attributions are difficult to establish from the available archaeological evidence. Perhaps the best evidence comes from Cherkasskaya 3 and 5, located on a lakeshore in the Middle Don. At Cherkasskaya 5, aquatic bird bones, dominated by mallard, represent more than half of the osteological remains and a further c. 10 % are fish, notably pike, catfish and carp. Both sites are interpreted as seasonal, short-term camps intensively used for net-fishing, hunting waterfowl and turtle and collecting molluscs (Skorobogatov et al., 2018). It seems that pottery was also largely used for this purpose, with aquatic biomarkers identified in the majority of vessels from these sites, mirroring a specialist function observed elsewhere (Bondetti et al., 2021a). In the Middle Volga, some sites with dwellings hint at a longer occupation but there is no consistent difference in $\Delta^{13}C$ values between sites with and without structures in our sample. Indeed, a greater proportion of samples from sites without structures contain ruminant fats (i.e. $\Delta^{13}C < -1$; 29/44) than those with (4/11), perhaps indicating use as hunting camps. However, overall, there is no evidence that the site type or length of occupation had an effect on pottery use.

5.4. Does chronology have an effect?

Despite a change in pottery style, there is no obvious shift in ingredients over a time span of ca. 1500 years in Middle Volga basin pottery. For example, nearly identical distributions of the molecular proxies (SRR%) and isotopic values ($\delta^{13}C_{16:0}$ and $\Delta^{13}C$) are found when comparing Elshanskaya pottery and the later Middle Volga pottery. As for the early pottery in the Middle and Upper Don basin, it remains difficult to study the impact of time because the early phase is solely represented by the pottery found at the fishing camps of Cherkasskaya 3 and 5. Nevertheless, it seems that the focus on aquatic resources in the Don basin includes many sites over a significant area, encompassing different pottery types and over a considerable timespan, at least 1500 years.

6. Conclusions

Microscopic, molecular and isotopic analysis of ceramic vessels provides new insights into the preparation and consumption of food in the Eastern European forest-steppe during the Early Neolithic. The observed differences in pottery function between the Don and Volga basins are seemingly unrelated to local environmental conditions, the availability of resources or the length of site occupation. An alternative explanation is that pottery use was under strong cultural control, recognisable as separate sub-regional culinary traditions. If so, the origins of these different culinary practices may have evolved separately among aceramic hunter-gatherers of each sub-region, perhaps by replacing pre-existing technologies such as perishable containers or other food preparation regimes, including spit roasting and pit cooking. In some cases, pottery vessels did not entirely replace alternative container technologies or non-vessel food preparation regimes but functioned alongside extant culinary practices for a considerable period. A similar explanation has been suggested to explain differences in early pottery use by other Northern European hunter-gatherers (Courel et al., 2020). This would imply a 'soft transition' to pottery with a gradual evolution in container technology with no specific functional constraints relating to use.

The almost complete absence of 'soft' containers and other predecessors of pottery in hunter-gatherer wetland sites conducive to organic preservation (i.e., Zamostje 2 and Veretje sites (Lozovski et al., 2014; Oshibkina, 1997); does not support this hypothesis. Nevertheless, in the forest-steppe region, it is difficult to meaningfully assess cultural continuity between 'Mesolithic' aceramic and 'Neolithic' ceramic hunter-gatherers due to the small number of Late Mesolithic 'aceramic' sites (Fedyunin, 2018). From the little evidence available from the Middle Volga basin, Vasiliev and Vybornov have highlighted differences in flint technology between Mesolithic and Elshanskaya groups, which they attribute to the non-local nature of the latter (Vasiliev and Vybornov, 1998). Likewise, Fedyunin has suggested an abrupt change in cultural traditions (Fedyunin, 2007), despite the fact that both aceramic and pottery-producing groups used similar landscape settings. From these, albeit limited, lines of evidence it can be argued that the introduction of pottery had a more profound impact, associated with pioneering populations, new food traditions and new settlements located at highly productive aquatic ecotones. If so the differences in pottery use observed might be related to dispersal dynamics (i.e., route and timing), including a demographic component, both of which remain to be determined. Large open steppe zones reached as far north as the Upper Don region in the early Atlantic period, potentially facilitating extremely rapid dispersals.

The prevalence of aquatic resources in hunter-gatherer-fisher pottery in the Middle and Upper Don supports the wider notion that for many Holocene hunter-gatherers, pottery was indeed a major asset for processing and cooking aquatic resources, as shown for hunter-gatherers of the Eastern Baltic (Courel et al., 2020), East Asia (Craig et al., 2013; Lucquin et al., 2016b; Shoda et al., 2017), North America (Taché and Craig, 2015) and the Russian Far East (Gibbs et al., 2017). Here, it seems pottery is well suited for managing surpluses created by intensive fishing perhaps during periods of seasonal abundance. However, the 'aquatic Neolithic' hypothesis for the uptake of pottery is not supported in other regions and sub-regions; organic residue analyses of hunter-gatherer pottery from the Middle Volga (this study) and Upper Volga (Bondetti et al., 2019), southeastern Baltic, Western Baltic (Courel et al., 2020), cis-Baikal (Bondetti et al., 2020) and the middle Amur (Shoda et al., 2020) show much greater diversity in use. Interestingly, such patterns are maintained over extensive geographical areas and through multiple phases of occupation. They also show little correspondence with their respective paleoenvironmental settings. Together this implies that pottery function was under strong cultural control governed principally by culinary choices. Whether distinct culinary practices can be tracked through space and time perhaps with other pottery attributes, such as manufacturing techniques and decoration, remains to be seen.

Credit author statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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