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Neolithic dairy farming at the extreme of agriculture in northern Europe

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The conventional 'Neolithic package' comprised animals and plants originally domesticated in the Near East. As farming spread on a generally northwest trajectory across Europe, early pastoralists would have been faced with the challenge of making farming viable in regions in which the organisms were poorly adapted to providing optimal yields or even surviving. Hence, it has long been debated whether Neolithic economies were ever established at the modern limits of agriculture. Here, we examine food residues in pottery, testing a hypothesis that Neolithic farming was practiced beyond the 60th parallel north. Our findings, based on diagnostic biomarker lipids and δ^{13} C values of preserved fatty acids, reveal a transition at *ca* 2500 BC from the exploitation of aquatic organisms to processing of ruminant products, specifically milk, confirming farming was practiced at high latitudes. Combining this with genetic, environmental and archaeological information, we demonstrate the origins of dairying probably accompanied an incoming, genetically distinct, population successfully establishing this new subsistence 'package'.

1. Introduction

Since the end of the last Ice Age, some 12 000 years ago, the high northern latitudes of the globe became permanently settled by humans of Late Palaeolithic and/or Mesolithic cultures. Their sole subsistence mode for millennia, and for most of them to the present day, was hunting, fishing and gathering, thereby making use of the plentiful wild resources. While there is no evidence for farming on the North American Continent and in Siberia above the 60th parallel north prior to the European colonization, earlier examples of agro-pastoral farming appear in Iceland in the ninth century AD Viking Age, and an episode (10-15th century AD) in southwest Greenland [1]. In order to make farming viable, these inhabitants of the high northern latitudes had to overcome extreme climatic and environmental conditions. The forced abandonment of the south Greenland settlements at the onset of the Little Ice Age [2] demonstrates the vulnerability of any productive subsistence economy to climate change at these high latitudes. Hence, it has long been doubted whether more ancient prehistoric subsistence economies based on agriculture would have been viable, especially given the limited adaptations in stock animals and domesticated plants, most of which originated in the warm and semi-arid climes of the 'Fertile Crescent' of the Levant approximately 11000 years ago [3]. However, at least in northwestern Europe, thanks to the warming effects of the Gulf

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Figure 1. Integrated maps of: (*a*) the northern hemisphere relative to the North Pole. Highlighted are the modern borders of Finland (in red) and the 60th parallel north (in light blue), (*b*) the location of all Finnish prehistoric sites from which sherds were sampled (numbers correspond to table 1), and (*c*) the distribution of the Corded Ware culture within Finland. Mapped (black dots) are finds of typical stone battle axes, used as a proxy (data from [8]). The red isolines indicate average permanent snow cover period from 1981 to 2010 (data from [9]). A recent study estimates the snow cover period *ca* 4500 years ago would have been 40-50 days less than today [10]. Overlying coloration refers to the lactose persistance (LP) allele gradient in modern northeastern Europe (see the electronic supplementary material, appendix B: Material and methods and table 1, for details); lozenge dots specify the dataset mean points for the triangulation.

Stream, Early Neolithic fourth millennium settlers were reaching as far north as to between the 55th and 58.5th parallel, and probably intermittently beyond, establishing the sustainable farming economies in all of Britain, southern Norway and even east-central Sweden [4–7].

Here, we explore the possibility for prehistoric farming in Finland at sites located beyond the 60th parallel north. These sites were located at the same high latitude as southern Greenland, Canada's Northwestern Territories, Anchorage in Alaska, Kamchatka Peninsula and near Yakutsk in Siberia, and lying further to the east, were thus exposed to a harsher continental climate. Farming in Finland would have been extremely challenging on account of the low average temperatures and several months of snow cover (figure 1 [8–10]) limiting vegetation periods [11]. The year was often interrupted by cold spells with snow and ice even in summertime, such that cereal agriculture is nowadays only just possible, and stock require considerable periods of shelter and

foddering during the long winters. The date of the earliest practices of domestication at this latitude in Europe has been questionable owing to the paucity of surviving cultural and biological evidence from the prehistoric period. There is, at present, neither evidence to suggest that animal domestication was established during the climatic and demographic optimum of the first half of the fourth millennium BC [12], nor even that it was associated with the subsequent appearance of people using pottery belonging to the Pan-European Corded Ware phenomenon in the third millennium BC. Indeed, it appears to have a much later date [13], despite the people associated with the latter culture being strongly associated with pastoral farming economies elsewhere in Europe [14], and who were thought to have carried with them the ability to digest milk into adulthood (lactase persistence, LP) into southern Finland in the third millennium BC [15]. Nowadays, both the prevalence of LP and consumption of dairy products in this part of northern Europe are among the highest in the world [16,17].

The exceptionally poor survival of archaeological remains in the acidic soils of southern Finland normally only leave small pieces of burnt (cremated) animal bones for further analysis [18], and with macrofossil plant remains never systematically investigated, it has thus far been impossible to reconstruct whether these pioneer Corded Ware 'pastoral farmers' were ever able to establish farming above the 60th parallel north or whether there was a return to the plentiful wild resources, driven by the harsh climatic conditions [19,20]. To date, the earliest domesticate bone recovered from southern Finland is a sheep/goat dated to the Final 'Neolithic' Kiukainen culture, ca 2200-1950 BC [18], with the earliest cattle and horse not dated earlier than the Bronze Age [18]. Infrequently recovered domesticate bones from potential Corded Ware contexts have recently been directly dated to the historic or modern period [18].

Fortunately, the acidic soils that preclude survival of bones have the advantage of offering favourable conditions for the survival of certain classes of ancient biomolecules, such as lipids in the walls of ancient ceramic cooking vessels, represented by sherds recovered in considerable numbers. The carbon isotopic compositions of such biomolecules can be used to assign organic residues to their origins, in particular, to distinguish aquatic fats from those of terrestrial species, and dairy fats from carcass fats [21,22]. Additionally, specific diagnostic biomarkers that survive include isoprenoid fatty acids originating from marine organisms and long-chain ω-(o-alkylphenyl)alkanoic acids (APAAs) and vicinal diols (DHYAs) that arise from heating or oxidation of the highly reactive mono- and polyunsaturated fatty acids, characteristically found in abundance in aquatic fats [23-25]. Based on the above biomarkers and carbon isotope proxies, we now have tools to allow us to robustly investigate the economy and pottery function of prehistoric hunter-fisher-foragers (people using so-called Comb Ware) and the potentially earliest farmers (so-called Corded Ware, Final 'Neolithic' Kiukainen Ware and Early Metal Age prehistoric pottery people) and explore their inter-relationship with the environment.

Settlement sites from which we obtained pottery sherds for biomarker lipids and isotopes analyses are located in southern and southwestern Finland, all being north of the 60th parallel (see the electronic supplementary material, appendix A, for details and figure 1b for their exact geographical location). We have chosen these sites owing to their importance in Finnish prehistoric research, their excavated archaeological features, relative abundance and good preservation of pottery remains, and chronological range spanning from the fourth to the first millennium BC. These are the Typical/Late Comb Ware (fourth millennium BC) site of Vantaa Stenkulla/Maarinkunnas; the Corded Ware (third millennium BC) sites of Tengå Nyåker, Koivistosveden and Backisåker 1 (Kvarnåker), all near the southern Finnish town of Kirkkonummi; the Kiukainen Ware (around 2000 BC) site of Nakkila Uotinmäki, near the town of Pori in southwest Finland; the Late Bronze Age (around 1000 BC) sites of Raasepori Kroggård Hagnäs llb and Kaarina Toivola Hulkkio in southwestern Finland; and the Morby Ware (first millennium BC) site of Espoo Bolarskog I. As is typical for this region, few if any, identifiable fragments of animal bone were reported (electronic supplementary material, appendix A).

2. Results

Seventy prehistoric sherds were investigated according to well-established analytical procedures described in the Material and methods. Well-preserved lipids were recovered from 19 sherds. These include Comb Ware sherds deriving from the multiphase site of Vantaa Stenkulla/Maarinkunnas (table 1), dating to ca 3900-3300 cal. BC, at which time the settlement was located at a narrow Litorina Sea bay opening to a second outer bay. Subsistence was probably based upon a hunting-fishing-foraging subsistence economy, with the recovered faunal remains and fishing equipment suggesting a significant role of marine resources. The lipid residues from the Comb Ware pointed- and round-base pots all originate from a predominantly or exclusively marine origin, displaying high concentrations of palmitic acid (figure 2 [26-29]), enriched carbon isotope signatures, long-chain APAAs and DHYAs and isoprenoid acids. The lipid residues thus suggest highly specialized subsistence strategies and/or specialized or selective vessel use for processing marine commodities, possibly for storage or exchange [30]. Although it has been debated whether Typical Comb Ware pottery would have been able to withstand cooking, the formation of APAAs requires temperatures of approximately 270°C [21,23,25] and therefore processing of marine products using heat seems highly likely. Comb Ware settlements, faunal assemblages and the size and fragility of Comb Ware vessels suggest that these populations were probably sedentary. A specialized economy based upon coastal resources in close proximity would have permitted such reduced mobility, while the use of pots would have facilitated heat-processing and storage from episodes of over-killing. It is therefore likely that there was a very close inter-reliance between subsistence patterns, frequent pottery use and sedentism.

Three sites of the Corded Ware culture yielded preserved organic residues. No faunal remains were reported from any of these sites, with the exception of a single fragment of burnt wild mammal bone from *Tengå Nyåker* [27]. However, in contrast with the Comb Ware sherds, the organic residues preserved in diagnostic Corded Ware sherds from sites at Kirkkonummi (*Tengå Nyåker* and *Backisåker*), dated to *ca* 2500 cal. BC, display stable carbon isotope signatures typical of the fats of terrestrial ruminants, despite their locations being less than 2 km from the contemporary coastline [31]. While theoretically, the stable carbon isotope values could



Figure 2. Lipid compositions, aquatic biomarker distributions and stable isotope values of extracts from prehistoric sherds. Typical partial gas chromatograms of lipid extracts from (*a*) Comb Ware and (*b*) Corded Ware; CX:Y FA denotes fatty acid with carbon chain length X and degree of unsaturation Y, *denotes phthalate. Panels (*c*) and (*d*) are mass chromatograms from Comb and Corded Ware lipid extracts, respectively, analysed by GC/MS-SIM, showing the distribution of C₁₈ (inverted triangle) and C₂₀ (black circle) APAAs present only in (*c*). Panel (*e*) shows $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values from Typical/Late Comb Ware (orange), Corded Ware (pink), Kiukainen Ware (green) and Metal Age (grey) residues; when shown as stars, this indicates aquatic biomarkers were also observed in the residue. Numbers refer to the KM-number, as assigned in table 1. Shaded reference ellipses derive from modern reference fats [21,22]. The timeline shows the archaeological cultures discussed here alongside actual sherds sampled and typical vessel forms (after [26–28]) (latter not shown to scale). Distribution maps show the geographical range of (*f*) Typical Comb Ware, (*q*) Corded Ware, (*h*) Kiukainen Ware and (*i*) Bronze Age cultures in the region (after [10,20,29]).

originate from domesticated (e.g. cattle) or wild (e.g. elk, forest reindeer) ruminants, half of these residues are milk fats, which must have originated from domesticated stock (figure 2). Intriguingly, the three dairy fat residues were all associated with beaker-type 'drinking' vessels, often occurring in grave deposits, and not with the amphorae and S-shaped pots more typical of settlements.

Only one residue from a Corded Ware vessel, deriving from a third site at Kirkkonummi (*Koivistosveden*), contained fatty acids exhibiting enriched stable carbon isotope values and long-chain DHYAs, indicating a marine origin. Although lying less than 2 km from the aforementioned Corded Ware sites, *Koivistosveden* would have had the closest proximity to the contemporary coastline and demonstrates that pottery vessels were not used exclusively for terrestrial resources by Corded Ware users.

The Final 'Neolithic' Kiukainen culture, whose ceramic inventory shows similarities with Late Corded Ware and local hunter-fisher-forager ware (Pyheensilta Late Comb Ware), is believed to be a cultural amalgamation emerging locally during a period of climatic deterioration [20,32]. While the low number of residues recovered makes interpretation preliminary, this intriguingly appears mirrored in the pottery residues, because the fatty acid stable carbon isotope values fall along a mixing line between ruminant and nonruminant/marine products. Although the isotope signatures reflect at least some contribution of terrestrial fat, both residues contain biomarkers for aquatic fats, including longchain APAAs and isoprenoid fatty acids. As neither the Comb Ware, nor the Corded Ware pottery residues exhibited evidence for mixing of terrestrial and aquatic products, these findings indicate either that this culture practiced a

Typical/Late Comb Ware Comb Ware 1 Vanida Maanihkunas 209 bowl -20.4 -19.5 0.9 FFAs (G ₁₄ - 2 Vanida Maanihkunas -19.4 -11.1 -11.7 FFAs (G ₁₄ - 2 Vanida Stenkulia -19.4 -21.1 -11.7 FFAs (G ₁₄ - 29954 : 2128 -29954 : 2137 -21.1 -11.7 FFAs (G ₁₄ - 29954 : 2135 60 H.E.S bowl -23.2 -23.1 0.1 FFAs (G ₁₄ - 29954 : 2135 60 H.E.S bowl -23.2 -23.1 0.1 FFAs (G ₁₄ - 29954 : 3105 53 151 -23.2 -23.1 0.1 FFAs (G ₁₄ - 29954 : 3105 53 -23.8 -24.4 0.4 FFAs (G ₁₄ - 29954 : 3105 273 H.E.S bowl -25.8 -24.4 0.4 FFAs (G ₁₄ - 29954 : 4932 KM-30 10.6 FFAs (G ₁₄ - 20954 10.0 7.4 29954 : 4732 KM-40 146 H.E.S bowl	(C ₁₄ -C ₂₀); C ₁₈ -C ₂₂ APAAs; C ₁₈ -C ₂₂ DHYAs (C ₁₄ -C ₂₀); C ₁₈ -C ₂₂ APAAs; TMTD, Phy; C ₁₈ -C ₂₀ DHYAs (C ₁₄ -C ₂₀); C ₁₈ -C ₂₀ APAAs; TMTD, Phy; C ₁₈ -C ₂₀ DHYAs (C ₁₂ -C ₂₀); C ₁₈ -C ₂₀ APAAs; TMTD, Pris, Phy; C ₁₈ -C ₂₀ HYAs (C ₁₂ -C ₂₀); C ₁₈ -C ₂₂ APAAs; TMTD, Pris, Phy; C ₁₈ -C ₂₀	marine fat marine fat marine fat marine fat
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KM-36 151 H.E.S bowl -23.2 -23.1 0.1 FFAs (G ₁₄ - 29954 : 2357 29954 : 2357 60 H.E.S bowl -24.8 -24.4 0.4 FFAs (G ₁₂ - 29954 : 3105 29954 : 3105 0.4 FFAs (G ₁₂ - 0HYAs 29954 : 3105 273 H.E.S bowl -24.8 -24.8 0.4 FFAs (G ₁₂ - 29954 : 4932 105 1.0 FFAs (G ₁₂ - 0HYAs 29954 : 4932 146 H.E.S bowl -25.8 -24.8 1.0 FFAs (G ₁₂ - 29954 : 4932 20954 : 7738 0.2 FFAs (G ₁₂ - 0HYAs 29954 : 7738 K.M-41 204 H.E.S bowl -23.2 -22.7 0.5 FFAs (G ₁₄ -	(C ₁₄ -C ₂₀); C ₁₈ -C ₂₀ APAAS; Phy; C ₁₈ -C ₂₀ DHYAs (C ₁₂ -C ₂₀); C ₁₈ -C ₂₀ APAAS; TMTD, Pris, Phy; C ₁₈ -C ₂₀ HYAs (C ₁₂ -C ₂₀); C ₁₈ -C ₂₂ APAAS; TMTD, Pris, Phy; C ₁₈ -C ₂₀	marine fat marine fat marine fat
29954 : 2357 29954 : 2357 KM-38 60 H.E.S bowl -24.8 -24.4 0.4 FFAs (f ₁₂ - 29954 : 3105 29954 : 3105 DHYAs DHYAs 29954 : 4932 1.0 FES bowl -25.8 -24.8 1.0 FFAs (f ₁₂ - 29954 : 4932 146 H.E.S bowl -25.8 -24.8 1.0 FFAs (f ₁₂ - 29954 : 4932 146 H.E.S bowl -19.1 -19.0 0.2 FFAs (f ₁₄ - 29954 : 7738 XM-40 126 H.E.S bowl -13.1 -19.0 0.2 FFAs (f ₁₄ - 29954 : 7738 XM-41 204 H.E.S bowl -23.2 -22.7 0.5 FFAs (f ₁₄ -	(C ₁₂ -C ₂₀); C ₁₈ -C ₂₀ APAAs; TMTD, Pris, Phy; C ₁₈ -C ₂₀ HYAs (C ₁₂ -C ₂₀); C ₁₈ -C ₂₂ APAAs; TMTD, Pris, Phy; C ₁₈ -C ₂₀	marine fat marine fat marine fat
KM-38 60 H.E.S bowl -24.8 -24.4 0.4 FFAs (f ₁₂ - 29954 : 3105 29954 : 3105 0.4 FFAs (f ₁₂ - 0HYAs 29954 : 4932 273 H.E.S bowl -25.8 -24.8 1.0 FFAs (f ₁₂ - 29954 : 4932 146 H.E.S bowl -19.1 -19.0 0.2 FFAs (f ₁₂ - 29954 : 7738 29954 : 7738 M.41 204 H.E.S bowl -23.2 -22.7 0.5 FFAs (f ₁₄ -	(C ₁₂ -C ₂₀); C ₁₈ -C ₂₀ APAAs; TMTD, Pris, Phy; C ₁₈ -C ₂₀ HYAs (C ₁₂ -C ₂₀); C ₁₈ -C ₂₂ APAAs; TMTD, Pris, Phy; C ₁₈ -C ₂₀	marine fat marine fat marine fat
2954:3105 DHYAs 2954:3105 273 H.E.S bowl -25.8 -24.8 1.0 FFAs (f ₁₂ - 2954:4932 146 H.E.S bowl -25.8 -24.8 1.0 FFAs (f ₁₂ - 2954:4932 146 H.E.S bowl -19.1 -19.0 0.2 FFAs (f ₁₄ - 2954:7738 2054:7738 H.E.S bowl -23.2 -22.7 0.5 FFAs (f ₄ -	HYAs (C ₁₂ —C ₂₀); C ₁₈ —C ₂₂ APAAs; TMTD, Pris, Phy; C ₁₈ —C ₂₀	marine fat marine fat
KM-39 Z73 H.E.S bowl -25.8 -24.8 1.0 FFAs (r ₁₂ - DHYAs 29954 : 4932 DHYAs DHYAs DHYAs DHYAs 29954 : 7738 146 H.E.S bowl -19.1 -19.0 0.2 FFAs (r ₄ - 23954 : 7738 29954 : 7738 KM-41 204 H.E.S bowl -23.2 -22.7 0.5 FFAs (r ₄ - 24.4	(C ₁₂ -C ₂₀); C ₁₈ -C ₂₂ APAAs; TMTD, Pris, Phy; C ₁₈ -C ₂₀	marine fat marine fat
29954 : 4932 DHYAs KM-40 146 H.E.S bowl -19.1 -19.0 0.2 FFAs (C ₁₄ - 29954 : 7738 2054 H.E.S bowl -23.2 -22.7 0.5 FFAs (C ₁₄ -		marine fat
KM-40 146 H.E.S bowl — 19.1 — 19.0 0.2 FFAs (C ₁₄ – 29954 : 7738 KM-41 204 H.E.S bowl — 233.2 — 23.7 0.5 FFAs (C ₁₄ –	HYAS	marine fat
29954:7738 KM-41 204 H.E.S bowl -23.2 -22.7 0.5 FFAs (C. ₄ -	$(C_{14} - C_{20})$; $C_{18} - C_{20}$ APAAs; TMTD, Phy; $C_{18} - C_{20}$ DHYAs	
KM-41 204 H.E.S bowl -23.2 -22.7 0.5 FFAs (C ₄₄ -		
	$(C_{14} - C_{20})$; $C_{18} - C_{20}$ APAAs; TMTD, Pris, Phy; $C_{18} - C_{20}$	marine fat
29954 : 9074	HYAs	
KM-42 66 H.E.S bowl -20.2 -19.6 0.5 FFAs (C ₁₄ -	$(C_{14}-C_{20})$; $C_{18}-C_{20}$ APAAs; TMTD, ?Pris, Phy	marine fat
29954 : 1840		
rded Ware		
Kirkkonummi Tengå Nyåker		
KM-1 2398 beaker – 28.6 – 34.3 – 5.8 FFAs (C ₁₄ –	$(C_{14} - C_{24})$	dairy fat
8709:52		
KM-31 342 'S-shaped' amphora -27.1 -29.8 -2.7 FFAs (C ₁₂ -	(C ₁₂ -C ₂₀); TMTD, ?Phy	ruminant carcass fat
8709:35		
KM-47 105 large beaker, impressed – 27.7 – 30.0 – 2.3 FFAs (C ₁₄ –	$(C_{14} - C_{18})$	ruminant carcass fat
8709 : 17 decoration		

Table 1. Description of sherds containing significant concentrations of preserved lipids. (Site descriptions are given in the electronic supplementary material, appendix A. H.E.S. bowl, half egg-shaped bowl; FFAs, free fatty acids; APAAs,

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	lipid			, , ,	. 12		
ຮ	onc (µg g ^{_1})	form	$\delta^3 c_{16:0}$	$\delta^3 c_{16:0}$	לני∆	lipid composition	classification
50	32	large beaker	— 25.8	—31.4	5.5	FFAs (C ₁₂ -C ₂₂); C ₁₈ DHYAs	dairy fat
oivistosveder	1						
1	305	beaker	-24.2	- 23.8	0.4	FFAs (C ₁₄ – C ₂₀); C ₁₈ – C ₂₀ DHYAs	?marine fat
ackisåker l	(Kvarnåker)						
5	57	large 'S-shaped'	- 26.5	— 29.8	-3.3	FFAs (C ₁₄ -C ₂₂); C ₁₈ DHYAs	ruminant carcass fat
		amphora					
46	1826	decorated beaker	-27.7		-4.1	FFAs (C ₁₂ -C ₂₄), ?Phy	dairy fat
inen) Uotir	ımäki						
	484	large funnel-type	- 25.4	- 25.6	-0.1	FFAs (C ₁₄ -C ₁₈); C ₁₈ -C ₂₀ APAAs; TMTD, ?Pris, Phy; C ₁₈ -C ₂₀	marine and
						DHYAs	ruminant fat
	323	unknown	— 26.9	— 29.7	- 2.8	FFAs (C ₁₂ -C ₂₀); C ₁₈ -?C ₂₀ APAAs;?TMTD, Phy; ?C ₁₈ DHYAs	ruminant fat,
							?marine fat
iaa) Krogg	ård Hagnäs Ilb						
	5851	amphora-type, flat	-27.2	-33.2	-6.0	FFAs $(C_{14} - C_{24})$	dairy fat
		bottom					
1 Hulkkio							
	233	bowl with flat bottom	-27.3	-33.6	—6.3	FFAs (C ₁₂ -C ₂₀)	dairy fat
/Early Iror	ı Age)						
g I							
	1372	small roundish pot	- 26.5	-33.1	-6.6	FFAs (C ₁₄ -C ₂₄)	dairy fat
		with flat bottom					

Table 1. (Continued.)

б

7

less-specialized economy, perhaps re-introducing aquatic resources as a buffer against deteriorating or fluctuating climatic conditions, or that use of vessels for varied purposes was now practiced.

Finally, residues from Early Metal Age pottery (*ca* 1200–500 BC) all derived from dairy fats. Increasing population size despite the continuing climatic deterioration of the Late Holocene is believed to have arisen from the intensification of agriculture by the later Metal Ages [33] which overcame environmental constraints upon population size. Certainly, such a scenario of established stock-rearing would be supported by the prevalence of dairy fats in the pots.

3. Discussion

It has been observed that the global prevalence of the LP phenotype is associated with cultures with a history of milk exploitation, with patchy distributions of LP in Africa and the Middle East associated with nomadic pastoralists, in contrast to their non-pastoralist neighbours [34]. These findings presented here demonstrate the antiquity of dairy product processing in southern and southwestern Finland, a tradition reflected by both the high frequency [35] and distribution of the LP allele in present-day Finland. The SW-NE gradient in the frequency of the LP allele in Finland (figure 1) is the product of recurrent, substantial immigrations from the west and east over the past 6000 years [15,36] and its highest frequency exhibits close correlation with the distribution of Corded Ware settlements in southern and southwestern Finland. Genetic evidence suggests that low frequencies of LP in some parts of the eastern Baltic may reflect long-lasting 'genetic refugia' for hunter-fisher-forager populations [37]. However, the age estimate for the only LP haplotype in Finland, H98 containing the T-13910 allele shows divergence ca 5000 years ago [38]. This is consistent with a correlation between immigrating Corded Ware people, their milk use in the far north and the probable first appearance of the LP, still reflected in the LP gradient of modern-day Finland more than 4500 years later.

Our investigations into organic residues preserved in hunter-fisher-forager and 'early farmer' pottery vessels from Finland provide, to our knowledge, the first direct evidence that animal domestication, specifically including dairy production, was practiced by early prehistoric farmers beyond the 60th parallel north. With the earliest directly dated domesticate bone currently dating to the Kiukainen culture, at least 500 years later [18], the identification of dairy fats associated with Corded Ware pottery now pushes the date for domestication back to ca 2500 BC and for the first time, directly associates the appearance of a new cultural horizon with the arrival of animal domestication. The strong contrast between the marine products processed in hunterfisher-forager Comb Wares and terrestrial and domesticated secondary products processed in Corded Wares supports the hypothesis that Corded Ware pottery represents the successful introduction of novel subsistence practices into Finland and, moreover, places the prehistoric origins of farming and milk consumption, at the most northerly latitudes so far, some 4500 years ago. However, the biomarker and stable isotope compositions of residues from the Final 'Neolithic' Kiukainen period tentatively indicate reversion to aquatic foods probably associated with episodic climate deterioration [10,39] showing vividly the vulnerability of any early farming system.

When viewed alongside evidence for dairying from other parts of northern and northwestern Europe [5,7,22,40], the importance of milk, cattle and stock-keeping, alongside cereal agriculture, in the demic farming colonization of Europe's northern latitudes [41] is unequivocally established. But whereas in northern Britain, a terrestrial subsistence economy remains the sole food source for more than 1500 years after the initial colonization [5], southern Scandinavia shows the continuation of the exploitation of aquatic resources as an additional food resource alongside agricultural products [7,40]. A third more opportunistic way may have been chosen by the Late Corded Ware inhabitants of Finland, and their Kiukainen successors, by adopting again hunting–fishing– gathering practices after some generations as the later third millennium BC annual temperatures continued to fall [42].

This rather episodic character of prehistoric farming is probably symptomatic of cultivation in marginal landscapes above the 60th parallel north also evident later in Bronze and Iron Age records [13,33,43] and in historical times [44]. Even today, Finland is one of the most northerly agricultural zones of Europe and the inhabitants of northerly latitudes have to overcome unfavourable extreme climatic conditions to make 'conventional' farming viable [11]. Although predicted global warming raises the possibility of modern-day populations extending agriculture to higher latitudes in the future on a global scale, our results show how climatic instabilities at such frontier zones will make continuous farming extremely challenging [45,46].

4. Material and methods

The protocol briefly comprised cleaning of a small portion of the external surfaces of the potsherd using a modelling drill and the removal of this cleaned piece using a chisel. Cleaned sherd fragments were crushed in a solvent-washed mortar and pestle and an internal standard added ($20 \ \mu g \ n$ -tetratriacontane) prior to solvent-extraction using $2 \times 10 \ ml \ CHCl_3/MeOH \ 2:1 \ v/v$ via sonication ($20 \ min$). After centrifugation, the solvent was decanted and blown down to dryness under a gentle stream of N₂. Aliquots of the total lipid extract were filtered through a silica column and treated with $40 \ \mu l \ N$, *O-bis*(trimethylsilyl)trifluoroacetamide (BSTFA, 70° , 1 h) prior to screening using high-temperature gas chromatography (GC).

Aliquots from selected sherds were then hydrolysed (0.5 M NaOH/MeOH; 70°, 1 h) and methylated (100 µl BF₃/MeOH; 75°, 1 h) for the structural identification of components using GC/mass spectrometry (GC/MS) and highly sensitive detection of specific biomarkers using selected ion monitoring (GC/MS-SIM; scanning for ions m/z 105, 262, 290, 318 and 346). The isotopic composition of individual fatty acids was determined using GC-combustion-isotope ratio MS (GC/C/IRMS). The δ^{13} C values were derived according to the following expression and are relative to the international standard vPDB: δ^{13} C ‰ = ((*R* sample – *R* standard)/*R* standard) × 1000, where $R = {}^{13}$ C/ 12 C. The δ^{13} C values were corrected for the carbon atoms added during methylation using a mass balance equation [47].

The 'bound' fraction from selected sherds was released through the alkaline extraction of solvent-extracted pottery, using 5 ml 0.5 M NaOH/MeOH in DCM-extracted doubledistilled water (9:1 v/v; 70°, 1 h). After acidification to pH3, these 'bound' lipids were extracted using 3×3 ml DCM. The bound fraction was treated with 40 µl BSTFA (70°, 1 h) prior to analysis using a GC/MS fitted with a non-polar column, operated in full scan and SIM mode (*m*/*z* 215, 317, 517, 345, 545, 243 and 573). Acknowledgements. We are grateful to Alison Kuhl and James Williams from the NERC Life Sciences Mass Spectrometry Facility and Helen Whelton from the University of Bristol for technical assistance. We thank Helen Grant of the NERC Life Sciences Mass Spectrometry Facility (Lancaster node) for stable isotopic characterization of reference standards and derivatizing agents. Wesa Perttola, University of Helsinki, and Dr Martin Furholt, University of Kiel/Germany, are also thanked for graphical assistance.

Data accessibility. Archaeological GC and GC/MS data: Bristol University Research Data Repository (doi:10.5523/bris.13kidnrls4jnl1m806eyf

References

- Arneborg J, Lynnerup N, Heinemeier J, Møhl NR, Sveinbjörnsdóttir ÁE. 2011–2012 Norse Greenland dietary economy ca. AD 980–ca. AD 1450: introduction. J. North Atlantic 3, 1–39. (doi:10. 3721/037.004.s303)
- Dugmore AJ, McGovern TH, Vésteinsson O, Arneborg J, Streeter R, Keller C. 2012 Cultural adaptation, compounding vulnerabilities and conjunctures in Norse Greenland. *Proc. Natl Acad. Sci. USA* 109, 3658–3663. (doi:10.1073/pnas.1115292109)
- Price TD, Bar-Yosef O. 2011 The origins of agriculture: new data, new ideas. *Curr. Anthropol.* 52, 163–174. (doi:10.1086/659964)
- Sheridan SA. 2010 The Neolithisation of Britain and Ireland: the big picture. In *Landscapes in transition* (eds B Finlayson, G Warren), pp. 89–105. Oxford, UK: Oxbow Books.
- Cramp LJE, Jones J, Sheridan A, Smyth J, Whelton H, Mulville J, Sharples N, Evershed RP. 2014 Immediate replacement of fishing with dairying by the earliest farmers of the northeast Atlantic archipelagos. *Proc. R. Soc. B* 281, 20132372. (doi:10.1098/rspb.2013.2372)
- Østmo E. 2007 The northern periphery of the TRB: graves and ritual deposits in Norway. *Acta Archaeol.* 78, 111–142. (doi:10.1111/j.1600-0390.2007. 00102.x)
- Isaksson S, Hallgren F. 2012 Lipid residue analyses of Early Neolithic funnel-beaker pottery from Skogsmossen, eastern Central Sweden, and the earliest evidence of dairying in Sweden. *J. Archaeol. Sci.* 39, 3600–3609. (doi:10.1016/j.jas.2012.06.018)
- Huurre M. 1995 9000 vuotta Suomen esihistoriaa. Helsinki, Finland: Otava, Helsinki.
- 9. Finnish Meteorological Institute. See http://en. ilmatieteenlaitos.fi/home.
- Solantie R. 2005 Aspects of some prehistoric cultures in relation to climate in southwestern Finland. *Fennoscandia Archaeol.* 22, 28–42.
- 11. Finnish Ministry of Agriculture and Forestry. See http://www.mmm.fi.
- Tallavaara M, Seppä H. 2012 Did the mid-Holocene environmental changes cause the boom and bust of hunter-gatherer population size in eastern Fennoscandia? *Holocene* 22, 215–225. (doi:10. 1177/0959683611414937)
- Lahtinen M, Rowley-Conwy P. 2013 Early farming in Finland: was there cultivation before the Iron Age (500 BC)? *Eur. J. Archaeol.* 16, 660–684. (doi:10. 1179/1461957113Y.000000000040)

- Kriiska A. 2009 The beginning of farming in the eastern Baltic Area. In *The east European plain on the eve of agriculture* (eds PM Dolukhanov *et al.*), pp. 159–179. British Archaeological Reports, S1964. Oxford, UK: Archaeopress.
- Vuorisalo T, Arjamaa O, Vasemägi A, Taavitsainen J-P, Tourunen A, Saloniemi I. 2012 High lactose tolerance in North Europeans a result of migration, not *in situ* milk consumption. *Perspect. Biol. Med.* 55, 163 – 174. (doi:10.1353/pbm.2012.0016)
- Itan Y, Jones BL, Ingram CJE, Swallow DM, Thomas M. 2010 A worldwide correlation of lactase persistence phenotype and genotypes. *BMC Evol. Biol.* **10**, 36. (doi:10.1186/1471-2148-10-36)
- Food and Agriculture Organisation of the United Nations Statistics Division. *FAOStat*. See http://www. faostat.fao.org/.
- Bläuer A, Kantanen J. 2013 Transition from hunting to animal husbandry in Southern, Western and Eastern Finland: new dated osteological evidence. *J. Archaeol. Sci.* 40, 1646–1666. (doi:10.1016/j.jas. 2012.10.033)
- Halinen P, Heyd V, Lavento M, Mannermaa K. In press. When south meets north: Corded Ware in Finland. In *A Corded world* (ed. P Włodarczak). Kraków, Poland: Instytut Archeologii i Etnologii Pan.
- Lavento M. 2012 Cultural reproduction from Late Stone Age to Early Metal Age: a short discussion of the cultures in Finland, the northern part of Fennoscandia and Karelia, 3200 cal. BC to 1500 cal. BC. In *Becoming European. The transformation of third millennium Northern and Western Europe* (eds C Prescott, H Glorstad), pp. 144–155. Oxford, UK: Oxbow Books.
- Cramp LJE, Evershed RP. In press. Reconstructing aquatic resource exploitation in human prehistory using lipid biomarkers and stable isotopes. In *Treatise on geochemistry*, 2nd edn, vol. 12 (ed. T Cerling). Oxford, UK: Elsevier.
- Copley MS, Berstan R, Dudd SN, Docherty G, Mukherjee AJ, Straker V, Payne S, Evershed RP. 2003 Direct chemical evidence for widespread dairying in prehistoric Britain. *Proc. Natl Acad. Sci. USA* **100**, 1524–1529. (doi:10.1073/pnas.0335955100)
- Hansel FA, Copley MS, Madureira LAS, Evershed RP. 2004 Thermally produced ω-(*o*-alkylphenyl)alkanoic acids provide evidence for the processing of marine products in archaeological pottery vessels. *Tetrahedron Lett.* **45**, 2999–3002. (doi:10.1016/j. tetlet.2004.01.111)

d8h6z). Archaeological single compound stable isotope data: Bristol University Research Data Repository (doi:10.5523/bris.upjtf9os1dzr 154phmgvrupib).

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- Hansel FA, Bull ID, Evershed RP. 2011 Gas chromatographic mass spectrometric detection of dihydroxy fatty acids preserved in the 'bound' phase of organic residues of archaeological pottery vessels. *Rapid Commun. Mass Spectrom.* 25, 1893–1898. (doi:10.1002/rcm.5038)
- Evershed RP, Copley MS, Dickson L, Hansel FA. 2008 Experimental evidence for the processing of marine animal products and other commodities containing polyunsaturated fatty acids in pottery vessels. *Archaeometry* 50, 101–113. (doi:10.1111/j.1475-4754.2007.00368.x)
- 26. Finnish National Board of Antiquities. See http:// www.karttaikkuna.fi/susa/4.pdf.
- Edgren T. 1970 Studier över den snörkeramiska kulturens keramik i Finland. *Finska Fornminnesföreningens Tidskrift 72*. Helsinki, Finland: The Finnish Antiquarian Society.
- Meinander CF. 1954 Die *Kiukaiskultur*. Suomen Muinaismuistoyhdistyksen Aikakauskirja 53. Helsinki, Finland: The Finnish Antiquarian Society.
- Nordqvist K, Herva V-P, Ikäheimo J, Lahelma A.
 2012 Early copper use in Neolithic north-eastern Europe: an overview. *Estonian J. Archaeol.* 16, 1–22. (doi:10.3176/arch.2012.1.01)
- Pesonen P, Leskinen S. 2010 Hunter-gatherer ceramics in Stone Age Finland. In *Ceramics before farming* (eds P Jordan, M Zvelebil), pp. 299–318. Chicago, IL: Left Coast Press.
- Kylli J. 2001 Asutussysteemi ja toimeentulo muinaisessa Espoossa ja lähiympäristössä. *Muinaistutkija* 2001, 2–13.
- Sundell T, Heger M, Kammonen J, Onkamo P. 2010 Modelling a Neolithic population bottleneck in Finland: a genetic simulation. *Fennoscandia Archaeol.* 27, 3–19.
- Taavitsainen J-P, Simola H, Grönlund E. 1998 Cultivation history beyond the periphery: early agriculture in the North European boreal forest. *J. World Prehistory* 12, 199–253. (doi:10.1023/ A:1022398001684)
- Ingram CJE, Liebert A, Swallow DM. 2012 Population genetics of lactase persistence and lactose intolerance. *eLS*. (doi;10.1002/97804700 15902.a0020855.pub2)
- Leonardi M, Gerbault P, Thomas MG, Burger J. 2012 The evolution of lactase persistence in Europe. A synthesis of archaeological and genetic evidence.

Int. Dairy J. **22**, 88–97. (doi:10.1016/j.idairyj.2011. 10.010)

- Lappalainen T, Laitinen V, Salmela E, Andersen P, Huoponen K, Savontaus M-L, Lahermo P. 2008 Migration waves to the Baltic Sea region. *Ann. Hum. Genet.* 72, 337–348. (doi:10.1111/j.1469-1809.2007.00429.x)
- Malmström H *et al.* 2009 Ancient DNA reveals lack of continuity between Neolithic hunter–gatherers and contemporary Scandinavians. *Curr. Biol.* 19, 1758–1762. (doi:10.1016/j.cub.2009.09.017)
- Enattah NS *et al.* 2007 Evidence of still-ongoing convergence evolution of the lactase persistence T₋₁₃₉₁₀ alleles in humans. *Am. J. Hum. Genet.* 81, 615–625. (doi:10.1086/520705)
- Sundell T, Kammonen J, Halinen P, Pesonen P, Onkamo P. In press. Can archaeology and genetics together identify prehistoric population bottlenecks? *Antiquity* 88.

- Craig OE *et al.* 2011 Ancient lipids reveal continuity in culinary practices across the transition to agriculture in Northern Europe. *Proc. Natl Acad. Sci. USA* **108**, 17 910–17 915. (doi:10.1073/pnas. 1107202108)
- Rowley-Conwy P. 2011 Westward Ho: the spread of agriculturalism from Central Europe to the Atlantic. *Curr. Anthropol.* 52, 431–451. (doi:10.1086/658368)
- Seppä H, Bjune AE, Telford RJ, Birks HJB, Veski S. 2009 Last nine-thousand years of temperature variability in Northern Europe. *Clim. Past* 5, 523–535. (doi:10.5194/cp-5-523-2009)
- Viklund K. 2011 Early farming at Umea in Västerbotten. Charred cereal grains dated to the Bronze Age. *Fornvännen* **106**, 238–242.
- Gissel S, Jutikkala E, Österberg E, Sandnes J, Teitsson B. 1981 Desertion and land colonization in the Nordic Countries c.1200–1600. Comparative

report from the Scandinavian research project on deserted farms and villages. Stockholm, Sweden: Almqvist and Wiksell.

- Olesen JE, Trnka M, Kersebaum KC, Skjelvåg AO, Seguin B, Peltonen-Sainio P, Rossi F, Kozyra J, Micale F. 2011 Impacts and adaptation of European crop production systems to climate change. *Eur. J. Agronomy* **34**, 96–112. (doi:10.1016/j.eja. 2010.11.003)
- Juday GP et al. 2005 Forests, land management, agriculture. In Arctic climate impact assessment: scientific report (ed. 'Arctic Council'), pp. 781–862. Cambridge, UK: Cambridge University Press.
- Rieley G. 1994 Derivatization of organic-compounds prior to gas-chromatographic combustion-isotope ratio mass-spectrometric analysis: identification of isotope fractionation processes. *Analyst* **119**, 915–919. (doi:10.1039/an9941900915)