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New insights on cultural dualism and population structure in the Middle Neolithic Funnel Beaker culture on the island of Gotland



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ABSTRACT

In recent years it has been shown that the Neolithization of Europe was partly driven by migration of farming groups admixing with local hunter-gatherer groups as they dispersed across the continent. However, little research has been done on the cultural duality of contemporaneous foragers and farming populations in the same region. Here we investigate the demographic history of the Funnel Beaker culture [*Trichterbecherkultur* or TRB, c. 4000–2800 cal BCE], and the sub-Neolithic Pitted Ware culture complex [PWC, c. 3300–2300 cal BCE] during the Nordic Middle Neolithic period on the island of Gotland, Sweden. We use a multidisciplinary approach to investigate individuals buried in the Ansarve dolmen, the only confirmed TRB burial on the island. We present new radiocarbon dating, isotopic analyses for diet and mobility, and mitochondrial DNA haplogroup data to infer maternal inheritance. We also present a new Sr-baseline of 0.71208 \pm 0.0016 for the local isotope variation. We compare and discuss our findings together with that of contemporaneous populations in Sweden and the North European mainland.

The radiocarbon dating and Strontium isotopic ratios show that the dolmen was used between c. 3300–2700 cal BCE by a population which displayed local Sr-signals. Mitochondrial data show that the individuals buried in the Ansarve dolmen had maternal genetic affinity to that of other Early and Middle Neolithic farming cultures in Europe, distinct from that of the contemporaneous PWC on the island. Furthermore, they exhibited a strict terrestrial and/or slightly varied diet in contrast to the strict marine diet of the PWC. The findings indicate that two different contemporary groups coexisted on the same island for several hundred years with separate cultural identity, lifestyles, as well as dietary patterns.

1. Introduction

Recent genomic analyses of humans remains from the Neolithic period from western Eurasia have revolutionized our understanding of the Neolithic transition, in that it was largely driven by migration of farmers (Gamba et al., 2014; Günther and Jakobsson, 2016; Lazaridis et al., 2014; Skoglund et al., 2014, 2012), with ancestry in Anatolia around c. 8000 years before present (Kılınç et al., 2016; Lazaridis et al., 2016; Mathieson et al., 2015; Omrak et al., 2016), that dispersed into territories previously inhabited by Mesolithic foragers (Fu et al., 2016; Posth et al., 2016; Sánchez-Quinto et al., 2012). Still, there are areas where this process is not fully understood, i.e. in Scandinavia, which

was one of the last frontiers of the Neolithic expansion on the north European mainland.

During the Nordic Late Mesolithic period, the Ertebølle culture [EBK, c. 5300–3950 cal BCE] and the central European Linear pottery culture [LBK, c. 5500–4500 cal BCE], which upheld different cultural identities and economies, coexisted in areas south of the Baltic Sea for almost a millennium (Fischer and Kristiansen, 2002; Midgley, 1992; Persson, 1999; Price, 2015). The LBK culture did not advance into Scandinavia and little is known about the cultural interactions of these different groups (e.g. Price, 2015). Instead it is the Funnel Beaker culture [TRB] that is associated to the first Neolithic phenomena in Scandinavia, with an onset from around c. 4000 cal BCE (e.g. Fischer

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Fig. 1. Map indicating distribution of TRB-North group megalithic tombs (Blomqvist, 1989; Midgley, 2008; Sjögren, 2003; Tilley, 1999) and PWC areas (Larsson, 2009) modified from (Malmström et al., 2009). Swedish megalithic TRB burial sites included in the analyses: 1. Gökhem passage grave, Falköping, Västergötland, 2. Alvastra dolmen, Östergötland, 3. Mysinge passage grave, Resmo, Öland, 4. Ansarve dolmen, Tofta, Gotland, and 5. the Ostorf TRB burial ground, Mecklenburg-Vorpommern, Germany.

and Kristiansen, 2002; Hallgren, 2008; Malmer, 2002; Midgley, 1992; Persson, 1999; Price, 2015, 2000). TRB was a large culture complex that spanned from the Netherlands to Poland and from the Czech Republic to southern Scandinavia. The culture has been divided into regional groups based on typochronology of pottery (Bakker, 1979; Müller, 2011), where present day Scandinavia and northern Germany belong to the TRB-north group (Fig. 1). The northern expansion of the TRB culture was a rapid process, beginning in northern Germany and Denmark, and continuing north into southeastern Norway and central Sweden, including the islands Gotland and Öland in the Baltic Sea, (Eriksson et al., 2008; Fischer and Kristiansen, 2002; Hallgren, 2008; Lindqvist, 1997; Papmehl-Dufay, 2012; Persson, 1999; Price, 2015). However, the mechanism for the process of dispersal of the TRB complex into Scandinavia continues to be debated (e.g. Andersson, 2016; Price, 2015).

Even though the TRB culture on the north European mainland is well studied (e.g. Bakker, 1979; Midgley, 1992; Müller, 2011), its exact origin and chronology is not known. Recent genetic studies of TRB groups in Sweden (Malmström et al., 2015, 2009; Skoglund et al., 2014, 2012) and Germany (Brandt et al., 2013; Haak et al., 2015; Lee et al., 2014) have shown that these groups have continuity with earlier Neolithic cultures on the European mainland, and differ from LM forager groups in Scandinavia and central Europe (Lazaridis et al., 2014; Skoglund et al., 2014). Other studies of mitochondrial DNA [mtDNA] and dietary isotopes have revealed the coexistence of sub-Neolithic foragers and farming populations; e.g. the TRB-North group burial ground at Ostorf in Mecklenburg-Vorpommern (Fig. 1) (Bramanti et al., 2009; Lübke et al., 2009), and the Blätterhöle cave in Hagen (Bollongino et al., 2013), in present day Germany.

Towards the end of the Nordic Early Neolithic period [EN: 4000-3300 cal BCE], a new type of burial tradition is seen in the TRB culture, largely in the form of megalithic tombs such as dolmens and passage graves. Although thousands of tombs have been located in both northern Germany and Denmark (Midgley, 2008; Müller, 2011), only c. 500-600 are known in Sweden to date. They are primarily distributed in the south and along the west coast, as well as a large group of over 250 passage graves in the Falköping area in Västergötland (Fig. 1) (Blomqvist, 1989; Sjögren, 2004, 2003; Tilley, 1999). However, only a few tombs have been located to the east, including the islands Gotland and Öland (Arne, 1923, 1909; Browall, 2016; Bägerfeldt, 1992; Janzon, 2009, 1984; Lithberg, 1914; Martinsson-Wallin and Wallin, 2010). Several of these tombs have been excavated and examined revealing that many were used for the duration of the TRB culture complex Middle Neolithic phase, also with extensions into later time periods (Eriksson et al., 2008; Fornander, 2011; Persson and Sjögren, 1995).

In the beginning of the Nordic Middle Neolithic period [MN: 3300-2400 cal BCE], cultural remains from the sub-Neolithic PWC complex appear at coastal sites in present day Sweden, northern Denmark, as well as, the islands Bornholm, Gotland, Öland, and Åland in the Baltic Sea (Fig. 1) (Larsson, 2009; Malmer, 2002; Wyszomirska, 1984). The PWC culture had distinct pottery, as well as some evidence of domesticates. Yet they were mainly hunter-gatherers with a marine economy based on sea mammals and fish (Eriksson et al., 2008, 2004; Larsson, 2009; Lindqvist and Possnert, 1997; Martinsson-Wallin, 2008). In some areas PWC sites had been established either adjacent to, or on top of, seasonal coastal sites formerly used by the TRB (Malmer, 2002). Hybridization of pottery have also been discovered at some of these locations, and it has been suggested that TRB groups in these areas abandoned farming in favor to a marine hunter-gatherer lifestyle (Larsson, 2009; Malmer, 2002). While in eastern Denmark there is evidence of cultural hybridization between local TRB and PWC groups (Iversen, 2016). The PWC culture performed inhumation burials in large grave fields, often located in older PWC cultural layers, and although many sites exist on the Swedish mainland, few have well preserved human remains (Wyszomirska, 1984). On Gotland, however, there are several PWC sites and burial grounds totaling over 200 burials (Fig. S1B). Which through more than 130 years of investigation has generated much information on the PWC (e.g. Bartholin and Burenhult, 1997; Brandt and Burenhult, 2002; Eriksson, 2004; Hansson, 1897; Hildebrand, 1887; Janzon, 1974; Lithberg, 1914; Martinsson-Wallin, 2008; Molnar, 2008; Nihlén, 1927; Norderäng, 2008; Wallin, 2016; Wallin and Martinsson-Wallin, 2016; Wallin and von Hackwitz, 2015; Österholm, 2008, 1989).

Malmström et al. (2015, 2010, 2009) and Skoglund et al. (2014, 2012) presented the first direct insights into the genetic makeup of these two contemporary cultures in Sweden. Analyses of mtDNA from TRB passage grave burials from Västergötland and Öland (Fig. 1), as well as PWC contexts on Öland and Gotland revealed some overlap in haplogroup distribution [K, T and H] between the two groups (Malmström et al., 2015). However, haplogroups unique to both cultures such as: J1 and J2 in TRB, plus U4 and U5 exclusively in PWC were also observed. Further genomic analyses of the TRB passage grave burial in Gökhem, Västergötland and PWC groups on Gotland demonstrated that the two groups had different demographic origins (Skoglund et al., 2012). Skoglund et al. (2014) also revealed evidence of admixing from foragers into the Gökhem TRB group.

TRB on Gotland represents the northeastern most extension of this culture complex, and several sites with TRB pottery have been located

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