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

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\textbf{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 ± 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 (Ket et al., 2014; Skoglund et al., 2014, 2012), with ancestry in Anatolia. During the Nordic Late Mesolithic period, the Ertebølle culture [EBK, c. 3500–3950 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...
The dashed line represents the approximate northern limit for TRB pottery.

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.
from c. 4000 cal BCE (Fig. S1B, see Section S1 for additional information on the archaeological background on Gotland). There are also two partially destroyed dolmens, Anzarve and Lixarve, from which only the dolmen in Anzarve has previously been excavated (Figs. S1B and S3) (Bägerfeldt, 1992; Lithberg, 1914; Martinsson-Wallin and Wallin, 2010). A minimum of 31 individuals were buried in the tomb (Wallin and Martinsson, 1986), and three mandibles have been dated to c. 3300–3000 cal BCE (Fig. S2, Table S1, and Section S1.2) (Lindqvist, 1997). Currently few TRB contexts on Gotland date after 3000 cal BCE, but the chronological time span is not fully clear (Figs. S1A and S2, Table S1). Neither is it known to which extent the culture coexisted alongside PWC, particularly since the TRB culture on the Swedish mainland survived at least up until 2800 cal BCE (Hallgren, 2008; Malmer, 2002). The different economy, cultural expressions, and possible interrelations of the two complexes on Gotland have been debated for more than a century (e.g. Andersson, 2016; Lindqvist, 1997; Lithberg, 1914; Stenberger, 1964; Stjerna, 1911; Österholm, 1989), and this debate has not yet been resolved. As the lime-stone bedrock of the island offers excellent preservation for biological remains there is great potential for archaeological genetic research. Thus, Gotland is an ideal locality to study the interactions and relationships between local farming and forager groups over time.

In this study we investigate seventeen of the individuals buried in the Anzarve dolmen and present new radiocarbon dates, isotopic analyses for diet and mobility, as well as, maternal inheritance patterns based on mitochondrial haplogroups. The genetic results are compared and discussed in light of data from nearby PWC sites on Gotland and Öland, TRB passage graves from Öland and Västergötland (Malmström et al., 2015; 2009; Skoglund et al., 2014, 2012) (Fig. 1), as well as, mitochondrial data from Neolithic sites across the European mainland (Table S4). In order to establish the Sr-baseline for the Gotland biosphere we also analyze new environmental samples from different locations on the island, together with recent Sr-isotopic data (Peschel et al., 2017).

2. Materials and methods

The human remains from the Anzarve dolmen were found com mingled and fragmented, thus we separated individuals based on previous osteological evaluation for teeth [mainly M1, loose and in situ] distinguished by position[upper, lower, and side], plus tooth wear and age of death (Wallin and Martinsson, 1986), including the three previously dated mandibles (Lindqvist, 1997) (Table S2 and Section S2). Additional bone elements were also screened for DNA preservation but were later excluded from the analyses due to low levels of endogenous DNA.

2.1. Radiocarbon dating and isotopic analyses

Sixteen samples were AMS radiocarbon dated and IRMS analyzed for Carbon and Nitrogen isotopes at Ångström Laboratorium Uppsala University, Sweden and BETA analytic Inc. (Miami, Florida) (Section S2.1-2, Table S2). The multiplot radiocarbon series were calibrated using Oxcal online software version 4.2.4 (Bronk Ramsey, 2009), based on the IntCal13 atmospheric curve (Reimer et al., 2013). A mean offset of 70 ± 40 (Eriksson, 2004), was used for the marine reservoir age correction in ans016 (Section 3.1). The M1 stable isotope results were compared to published M1 isotopic-ratios from Swedish TRB megalithic burials [Öland and Östergötland] and PWC groups [Gotland and Öland], together with local Gotlandic fauna (Eriksson, 2004; Eriksson et al., 2008; Fornander, 2011) (Section S2.2 and Table S2). Additional stable isotope results from bone of other individuals were included for marine reservoir age evaluation, and isotopic versus dating comparisons. Strontium isotope analysis [87Sr/86Sr] for eleven M1 was performed at NERC, Isotope Geosciences Laboratory (Nottingham, UK) together with sixteen additional soil and faunal tooth samples from Gotland archaeological sites (Table S2 and sections S2.3-4).

2.2. Genetic analyses; sample preparation, DNA extraction and sequencing

All samples were prepared in facilities dedicated to analyses of ancient DNA (aDNA) at Campus Gotland, and at the Evolutionary Biology Centre at Uppsala University, according to strict standards for working with degraded samples (Cooper and Poinar, 2000; Gilbert et al., 2005). DNA was extracted from bones and teeth (Yang et al., 1998) with modifications as in (Svensson et al., 2007) (Section S2.5). DNA extracts were converted into Blunt-End Illumina libraries (Meyer and Kircher, 2010) and sequenced on the Illumina HiSeq 2500 or Hi-SeqX as described in (Günther et al., 2015) (Section S2.6). Twenty-two samples were screened for human DNA (Table S2), and fourteen samples, totaling ten individuals, were used for downstream analysis.

2.3. Next generation sequence processing, alignment and authentication

Paired-end reads were merged and their adapters trimmed (Kircher, 2012) and subsequently mapped to the human reference genome using BWA (Li and Durbin, 2009) following (Lazaridis et al., 2014; Skoglund et al., 2014) (Section S2.7). PCR duplicates with identical start and end coordinates were collapsed into consensus sequences (Kircher, 2012). The data showed the characteristic deamination pattern towards the read fragment-ends (Briggs et al., 2007). Contamination was estimated based on (Green et al., 2008) (Section S2.8).

2.4. Mitochondrial haplogroup assignment, frequency histogram and PCA analyses

Mitochondrial consensus sequences were generated using ANGSD v.0.902 (Korneliussen et al., 2014), and haplogroups were assigned using HaploFind (Vianello et al., 2013) and PhyloTree mtDNA Build 17 (18 Feb 2016) (Van Oven and Kayser, 2009) (Table S3, Section S2.9). A mtDNA haplogroup frequency profile was generated based on the nine MN Ansarve individuals as described in (Brandt et al., 2013) (Table S4, for a detailed description of the ancient cultures [n = 26] see Section S2.10). The boxplots were generated with Rstudio (v0.99.903), and principal component analyses (PCA) were performed with the pcomp R function, using the ancient mtDNA haplogroup diversity profiles.

3. Results and discussion

A total of seventeen individuals of varying ages were distinguished within the archaeological material; three children [5–12 years], three juveniles [13–17 years], and eleven adults based on previous osteological evaluations (Lindqvist, 1997; Wallin and Martinsson, 1986) (Table S2, Section S1.2–3).

3.1. Radiocarbon and diet

Sixteen new radiocarbon dates were performed on teeth or bone from the human remains (Fig. 2, Table S2), which showed that the tomb was used from c. 3300–2800 cal BCE [3500 to 2630 cal BCE, 2σ], but also during the LN period; ans004 [Ua-45390, 3763 ± 30 BP, 2290–2050 cal BCE, 2σ] and ans010 [Ua-45397, 3608 ± 30 BP, 2030–1890 cal BCE, 2σ].

The stable isotope data of the Ansarve individuals show a terrestrial dietary pattern clearly distinct from the diet of PWC (Fig. 3A), although there seem to be two clusters (Fig. 3B). Some individuals show a strict terrestrial dietary pattern. The others a pattern that could be the result of mixing terrestrial protein sources with marine and/or freshwater fish similar to what has been seen in TRB on Öland (Eriksson et al., 2008) (Fig. 3A). This pattern is not as apparent when studied temporally (Fig. S5A–B). However, the majority of the individuals with a strict terrestrial diet are dated between c. 3000–2800 cal BCE indicating some level of chronological change in dietary pattern.

Three individuals [ans004, ans005 and ans016] had elevated δ15N-isotope values of 13% or more (Fig. 3B, Table S2), and one of them [ans016] also showed an elevated δ13C-value [−17.5] which indicate higher marine protein intake. The reservoir effect from marine and freshwater fish food consumption affects radiocarbon dating results, thus such results need to be corrected for carbon reservoir age before calibrated. However, due to the complex natural history of the Baltic Sea (Andrén et al., 2011) the marine reservoir effect has fluctuated over time and thus varies temporally, but also spatially due to the topography of the sea floor affecting the circulation, the saline inflow, and freshwater runoff from different river systems (Lougheed et al., 2013). Similarly, the freshwater reservoir effect in inland lakes and rivers can be problematic to evaluate as it fluctuates heavily, even within the same body of water, and time is also a factor (Philippsen, 2013).

In this study, we chose to use a mean offset of 70 ± 40 for the marine reservoir effect, which previously was suggested for the strict marine diet of MN PWC on Gotland [mean δ13C-value −15.4 ± 1.2‰] based on analyses of closed contexts in PWC burials (Eriksson, 2004). This marine reservoir offset is likely the most relevant for Gotland at this stage of the Baltic Sea. Different offsets have been suggested for other areas in the Baltic (e.g. Piličiauskas and Heron, 2015), as well as from other time periods on Gotland when the salinity was different (e.g. Boethius et al., 2017). The 70 ± 40 offset value was also applied on individuals from TRB contexts on Öland, where Eriksson et al. (2008) used an isotopic cut-off point at Carbon values higher than −18.0‰ for the marine reservoir age correction. This reservoir age correction lowers the date for ans016 [Beta-402963, 4160 ± 30 BP, reservoir 70 ± 40, 2810–2580 cal BCE, 2σ], and also extend the main period of usage of the dolmen (c. 3300–2700 cal BCE) (Fig. 2, Table 2). This new dating result is late considering the temporal range of the TRB culture in Scandinavia and could indicate secondary usage of the tomb, but also uncertain regarding the magnitude of the reservoir effect. However, the end of the TRB culture varies in different
regions, and a range between 2900 and 2700 cal BCE for the final phase of this culture complex has been suggested previously (Midgley, 2008). The other two individuals [ans004 and ans005] had lower Carbon values (−19.1 for both) (Fig. 3B), which together with elevated Nitrogen values could indicate a mixed diet including freshwater fish (Fernandes et al., 2012). Though, it has been shown that elevated nitrogen values alone cannot determine the extent of the freshwater reservoir effect (Lübke et al., 2009). Moreover, the Carbon and Nitrogen isotopic values for inland freshwater fish have not been established on Gotland, nor has the radiocarbon age offset for any inland Carbon reservoir. Thus, the radiocarbon dates from these two individuals may show dates that are too old, but they could also be correct (Lübke et al., 2009). The other fourteen individuals showed mainly a terrestrial diet and did not need reservoir age correction (Fig. 3A–B).

3.2. Mobility

Our results for the faunal and soil samples show that there are regional differences in the Sr-values from the Gotland island biosphere (Fig. S6A–C, Table S2 and Sections S2.3–S2.4). The combined Strontium isotopic values for the environmental samples range from 0.70984–0.71689. This is a much larger span than the previous suggestion for the Gotland faunal Sr-baseline of 0.7100–0.7112, 2 SD (Fig. S6C) (Preice et al., 2014; Wilhelmson and Ahlström, 2015). However, the high Häffinds soil value of 0.71689 is a bit surprising as it is quite different from the fox from the same location (0.71361), as well as a pig tooth from Hemmor in close vicinity (0.71145) (Fig. S6A–C). Soil samples can be problematic and can deviate from the local geological signals. Foxes are also quite mobile and could display a Sr-signal from another part of Gotland. More samples from Gotland need to be analyzed to confirm this result.

A recent study from the Viking Age trading port Ridanäs in Fröjel on Gotland has presented faunal Sr-values of domestic animals ranging between 0.71051 and 0.71532 (Peschel et al., 2017). The results from this single location show a large span compared to what we see for the different sites in this study (Fig. S6A and C). As Ridanäs was a trading port it is possible that some of these animals were of nonlocal origin. However, it is also possible that they came from different areas of the island, thus representing several regions on Gotland. The Ridanäs faunal values support our findings as they overlap our environmental results, with the exception of the Häffinds soil sample (Fig. S6C). The combined mean range of our study (without the Häffinds sample) and the Ridanäs faunal samples show 0.71208 ± 0.0016 (Table 1), which is somewhat lower than the mean presented for the Ridanäs samples [0.71242 ± 0.0016] (Peschel et al., 2017). This combination presents a Sr-baseline for Gotland of 0.70981–0.71534, 2 SD (n = 26). More samples from Gotland need to be analyzed to further calibrate the Gotland Sr-baseline.

3.3. mtDNA haplogroups and maternal inheritance patterns

Ten mitochondrial genomes were generated which ranged between 23 X–1593 X coverage: nine individuals from different time-periods during the MN period, and one of the LN individuals [ans010] (Table 2 and Table S2-S3).

All samples showed expected cytocine deamination patterns (Fig. S7) and a typical average read length; mtDNA contamination estimates for all samples were predicted to be low (Table 2). The results show that the haplogroups from the MN period of usage [K1a2b, T2b8, J1c5, HV0a, J1c8a, K2b1a and Hd7] resemble those of other European EN and MN individuals from a farming context (Fig. 5 and Table S4). The LN individual displayed Haplogroup U5b2a1a1.

According to the mtDNA frequency analysis the MN Ansarve individuals are most similar to the TRB group from Swedish passage graves [TRB-P], but differ from Mesolithic hunter-gatherers and PWC (Fig. 5). The Neolithic maternal affinity is also confirmed in the PCA plots where Ansarve cluster with other EN and MN groups from northcentral mainland Europe distinct from the PWC group (Fig. 6A–B).
settlement sites that show that TRB was well established on Gotland supported by TRB pottery, domestic animal remains, and the many individuals could have been local residents on the island. This is further bp = base pair, Hg = haplogroup, nd = none determined, for additional information see Tables S2–S3.

...phase displayed local Sr-signals within the 2 SD range of our Gotland 1995; Sjögren, 2003). Nine adult and juvenile individuals from the MN S1.3), which is in accordance with other MN megalithic TRB burials in (Les Noisat, 2015) although haplogroup HV0 was later condensed as haplogroup V′, which shows that these in-...
who resided on the same island as PWC for several hundred years, indicate that TRB and PWC were rather separate units and did not admit to a greater extent. This is further supported by different dietary patterns of the two cultural groups analyzed here (Fig. 3A). Though, further investigation of the extent of admixture between these groups requires analyses of genome data.

The U’ haplogroups are also lacking in the collective [TRB-C] burials in central Germany (Lee et al., 2014), contrary to the other German MN TRB groups, where Usa and Usb haplogroups have been found in contemporaneous individuals from the Ostorf flat grave burial site [TRB-F] in Mecklenburg-Vorpommern (Bramanti et al., 2009), and to some extent also in the TRB-South groups; Baalberge, Salzmünde and Bernburg in Saxony-Anhalt (Brandt et al., 2013) (Fig. 5, Table S4). The MN TRB group named FBC previously reported in Brandt et al. (2013) contained combined mtDNA haplogroup frequency data based on the Ostorf individuals (Bramanti et al., 2009), and data from the TRB passage grave burial from Gäkhem, Västergötland in southwestern Sweden (Malmström et al., 2009; Skoglund et al., 2012). However, the archaeological context of the Ostorf individuals has been described as a sub-Neolithic group, or a group of the TRB society neighboring obvious TRB farming communities, which had subsequently reverted back to a hunter-gatherer subsistence strategy (Lübke et al., 2009). This uncertainty for the Ostorf individuals suggest that they should not be considered together with the megalithic burials in Västergötland representing developed TRB farming communities (Persson and Sjögren, 2001). The higher hunter-gatherer relatedness in the Ostorf individuals is also evident in the PCA plots, where [TRB-F] fall in between PWC and the EN-MN groups from a farming context (Fig. 6A–B).

Although the sample sizes for Ansarve and some of the other MN TRB groups are limited, we note some patterns among the groups that warrant further investigation. For instance, the Ansarve group exhibits more similar variation to central European EN-MN farming groups in the PCA (Fig. 6A) (Brandt et al., 2013; Szécsényi-Nagy et al., 2015), and TRB-P (Malmström et al., 2015) cluster with the EN Gurgy group [GUR] from the Paris Basin (Rivollat et al., 2015) based on the higher frequency of haplogroup H. The southwestern affinity of the TRB-P group is further supported when adding southern European Neolithic and Chalcolithic groups (Fig. 6B and Table S4). The high frequency of haplogroup H [> 50%] is also noticed in the central European TRB collective burials [TRB-C: H, HV0 and X] (Lee et al., 2014) and the Polish Lengyel group [BKG: H, HV0, T2 and U5a] (Lorkiewicz et al., 2015), which cluster with EN Iberian populations (Chandler et al., 2005; Hervella et al., 2012). This points to interesting social relationships among and between European MN groups, but will need greater sample sizes or genome data to be explored further.

4. Conclusion

Our study investigated the relationship between two contemporaneous MN cultural complexes, TRB and PWC, on the Island of Gotland. We examined the collective burial in the Ansarve dolmen through AMS 14C dating, isotopic analyses for diet and mobility, and mitochondrial DNA. We find that the dolmen was used from c. 3300–2700 cal BCE, and also contained secondary LN burials (Fig. 2). Although few TRB locales exist after 3000 cal BCE on Gotland, the AMS results show that the tomb was used continuously during the MN phase. The stable isotope analyses show that the dietary pattern in the Ansarve group was markedly different than that of the contemporaneous PWC (Fig. 3A). Especially the individuals buried between 3000 and 2800 cal BCE showed a strict terrestrial diet (Fig. 5A–B). The other individuals showed a slightly varied terrestrial diet with some marine or freshwater fish input. One individual, ans016 from the end of the MN phase, displayed more marine protein in the diet and the dating was corrected for marine reservoir effect.

We determined the Sr-baseline for the Gotland biosphere to be 0.70981–0.71534, 2 SD (n = 26) (Table 1), and find that there are regional Sr-signals on the island (Fig. S6A–C). However, more environmental sampling is needed to fine-tune the Sr-ranges on Gotland. We find one obvious nonlocal individual from a LN secondary burial [ans010] which show that there were some mobility among individuals during the latter part of the Nordic Neolithic time period on Gotland. Two additional individuals, ans016 and the other LN individual [ans004], were just under the upper boundary of the 2 SD Sr-baseline value and could also have been of nonlocal origin. These individuals also displayed elevated marine or freshwater fish dietary signals (Fig. S5A-B) which could lower Sr-values, as well as affect radiocarbon dating results. Though, their Sr-values correspond with our result for the Västergarn soil sample located only 10 km south of Ansarve (Fig. S6C). The Sr-results for the other individuals from the MN phase, although divided into two clusters, still fall within the Sr-range we find.
for the Ansarve soil samples (Fig. S6C).

The MN Ansarve individuals show maternal continuity with central European farming populations. The mtDNA haplogroup composition closely resembles individuals buried in MN passage graves in Sweden, but differs from PWG groups on Gotland (Figs. S5 and S6A-B). Although some Ansarve individuals share the same mtDNA haplogroups, the high haplogroup variation within the group indicate that the burial site was not dominated [maternally] by one closely related group. This suggests that there were regional TRB groups present on the island which is further supported by the distinct Strontium signals in the Ansarve group (Fig. 4, A6C and Section S2.4), as well as the archaeological record (Fig. S1B and Section S1).

Even though the mtDNA haplogroup composition of the Ansarve group show close resemblance to the other Swedish megalithic burials [TRB-P] (Fig. 5) there also appears to be differences in the TRB groups that would need further investigation (Fig. 6B). The Ansarve group seems to show closer affinity to EN and MN central European groups, while TRB-P seems to have some more south western European influence. This south western influence has recently also been noticed in genomic analyses of Gok2 from the TRB passage grave in Västergötland (Cassidy et al., 2016; Martinoian et al., 2017). A similar scenario can be seen in the TRB collective burials [TRB-C] from central Europe, which cluster with EN Iberian populations based on the high frequency of haplogroup H (Figs. 6B and A8). The contemporaneous individuals at the Ostrof TRB burial site [TRB-F] cluster between PWCG and the Neolithic farmers in the PCAs (Fig. 6A-B). These individuals have also been described as a sub-Neolithic group with a hunter-gatherer-sub-

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Our results indicate that two different cultural complexes, TRB and PWG, coexisted on the island of Gotland for half a century with different cultural affiliations and subsistence strategies. Further multidisciplinary analyses of TRB megalithic burials in different geographic regions across northern mainland Europe and Scandinavia will help to clarify local and regional differences in the TRB culture.


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