



ELSEVIER

Journal of Archaeological Science xx (2007) 1–8

 Journal of  
**Archaeological  
 SCIENCE**
<http://www.elsevier.com/locate/jas>

## Ancient DNA provides no evidence for independent domestication of cattle in Mesolithic Rosenhof, Northern Germany

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Received 22 May 2007; received in revised form 7 August 2007; accepted 24 August 2007

### Abstract

Recent studies of modern and ancient mtDNA in domesticated and wild cattle has indicated that members of the extinct Near Eastern aurochs population (*Bos primigenius primigenius*) were the wild progenitors of European domesticated cattle (*Bos taurus*) (Bollongino, R., Edwards, C.J., Burger, J., Alt, K.W., Bradley, D.G., 2006. Early history of European domestic cattle as revealed by ancient DNA. *Biol. Lett.* 2, 155–159; Edwards, C.J., Bollongino, R., Scheu, A., Chamberlain, A., Tresset, A., Vigne, J.-D., Baird, J.F., Larson, G., Ho, S.Y.W., Heupink, T.H., Shapiro, B., Freeman, A.R., Thomas, M.G., Arbogast, R.-M., Arndt, B., Bartosiewicz, L., Benecke, N., Budja, M., Chaix, L., Choyke, A.M., Coqueugniot, E., Döhle, H.-J., Göldner, H., Hartz, S., Helmer, D., Herzig, B., Hongo, H., Mashkour, M., Özdogan, M., Pucher, E., Roth, G., Schade-Lindig, S., Schmölcke, U., Schulting, R.J., Stephan, E., Uerpmann, H.-P., Vörös, I., Voytek, B., Bradley, D.G., Burger, J., 2007. Mitochondrial DNA analysis shows a Near Eastern origin for domestic cattle and no indication of comestication of European aurochs. *Proc. Biol. Sci.* 274, 1377–1385; Troy, C.S., MacHugh, D.E., Bailey, J.F., Magee, D.A., Lotfus, R.T., Cunningham, P., Chamberlain, A.T., Sykes, B.C., Bradley, D.G., 2001. Genetic evidence for near-Eastern origins of European cattle. *Nature* 410, 1088–1091). This observation is generally consistent with the observation of archaeo-zoologists, but there are exceptions. As cattle domestication is associated with size reduction, wild and domesticated individuals have usually been differentiated by measuring the size of the bones. But this criteria is complicated by a pronounced sexual dimorphism that makes it difficult to discriminate between male domestic cattle and female aurochs. In particular, several bone samples from the mainly terminal Mesolithic site Rosenhof LA 58 in northernmost Germany have provoked intense discussion because they are smaller than the minimum known size of Scandinavian female aurochs. Therefore, some scholars have argued that they represent the first and possibly locally domesticated bovines of the northern European Mesolithic.

To clarify the status of the Rosenhof “cattle”, we determined the mtDNA-haplotype and sex of four of these presumed Mesolithic domesticates. We also analysed one early Neolithic sample and four Mesolithic robust and therefore morphologically definite wild aurochs from Rosenhof. For the purposes of comparison, we also determined the mtDNA haplotypes of seven samples from the adjacent Neolithic site of Wangels.

The Neolithic samples from Wangels and Rosenhof revealed lineages that are typical of imported taurine cattle. In contrast, the four wild aurochs and the four presumed Mesolithic domesticates from Rosenhof yielded mtDNA sequences that are characteristic for European aurochs. Furthermore, all the proposed domestics from Rosenhof were female individuals while three out of four remains from Rosenhof's confirmed aurochs were males.

As the four bones in question are too large to belong to female domesticates it is highly likely that they stem from wild female aurochs that were smaller than previously thought. Our data thus indicate that the beginning of cattle husbandry in Northern Germany did not predate, but is rather linked to the Neolithic transition. The single Neolithic Rosenhof domestic revealed an early radiocarbon date of 4000 ± 50 cal BC and marks the onset of the Neolithic in Northern Europe.

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**Keywords:** Ancient DNA; Mitochondrial DNA; *Bos primigenius primigenius*; *Bos taurus*; Domestication; Ertebølle culture; Neolithisation; Cattle

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## 1. Introduction

### 1.1. Archaeological background

According to recent  $^{14}\text{C}$  dates, the transition from the Mesolithic Ertebølle/Ellerbek culture to the Neolithic Funnel Beaker Culture in northern Germany dates back to approx. 4100 cal BC (Hartz and Lübke, 2005) and therefore predates only marginally the Neolithic transition in the earliest layers at the Danish Åmose (Zealand) and along the shore of northeast Jutland (approx. 3950 cal BC; Andersen, 1993; Fischer, 2002). However, because the Ertebølle culture in northernmost Germany coexisted for several hundred years with adjacent Neolithic cultures south and east of the river Elbe, acculturation processes led to the adoption of Neolithic elements by the Mesolithic population. Recovered artefacts like shaft hole axes (T-axes), imported perforated Danubian solid rock axes and axes made from non-native rocks or copper are evidence of regular contact with farming cultures. Additionally, palynological analyses show that agriculture might even have been practiced on a small scale (Hartz et al., 2002; Kalis and Meurers-Balke, 1998). In particular, the Rosenhof LA 58 site has played a key role in the discussion about the neolithisation of northern Germany. It is the oldest excavated settlement in East Holstein and was occupied from approx. 4900/4800 cal BC until the middle Neolithic (approx. 3000 cal BC; Hartz, 2005; Hartz et al., 2002). The settlement, believed to be several thousand square meters in size, was built at the edge of a moraine knoll called *Jarbock* on the Wagrien Peninsula and benefited from an adjacent backwater that now forms the dry lowland of Grube-Wessek (Fig. 1).

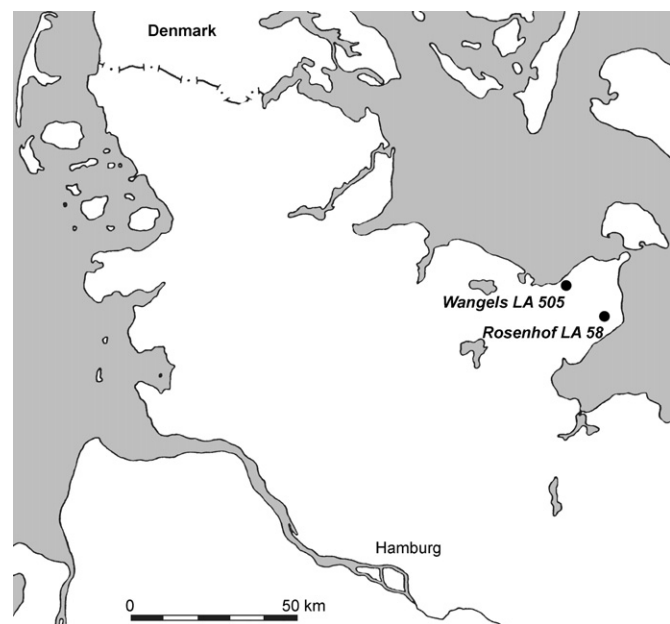


Fig. 1. Location of the coastal sites Wangels LA 505 (Neolithic) and Rosenhof LA 58 (terminal Mesolithic/early Neolithic) in northern Germany.

### 1.2. Archaeo-zoological background

Observations have established that a drastic reduction in size occurs in bovines after only a few generations of domestication. However, even if domesticated cattle are normally significantly smaller and more gracile than their wild ancestors (Fig. 2), the morphological distinction between the two groups is often ambiguous. Some bones and teeth are of intermediate size and could therefore be either small aurochs or large cattle. Some scholars have pointed out that individuals within an overlapping size range may represent the initial state of domestication of the indigenous aurochs (e.g. Bökönyi, 1974; Döhle, 1997; Herre, 1949; Müller, 1964; Nobis, 1975). Therefore they have been called the “wild-domestic-transitional-field” (Nobis, 1975; Bökönyi, 1962). In contrast, Degerbøl (1970) deduced on the basis of measurements on Danish aurochs remains that the overlapping size range is a result of broad sexual dimorphism within the wild type. Degerbøl and others concluded that European domesticated cattle were not local domesticates but imported cattle from the domestication centre in the Near East (Bogucki, 1989; Benecke, 1994; Rowley-Conwy, 1985,1995,2003).

At the Rosenhof site, the aggregate of faunal and archaeological remains indicates a permanent base-camp of hunter-gatherers (Hartz, 2005), but earlier and recent publications (e.g. Nobis, 1975; Hartz et al., 2002; Hartz, 2005; Schmölcke, 2005a) postulate that several bones from terminal Mesolithic layers represent domesticated cattle. In contrast to the bones

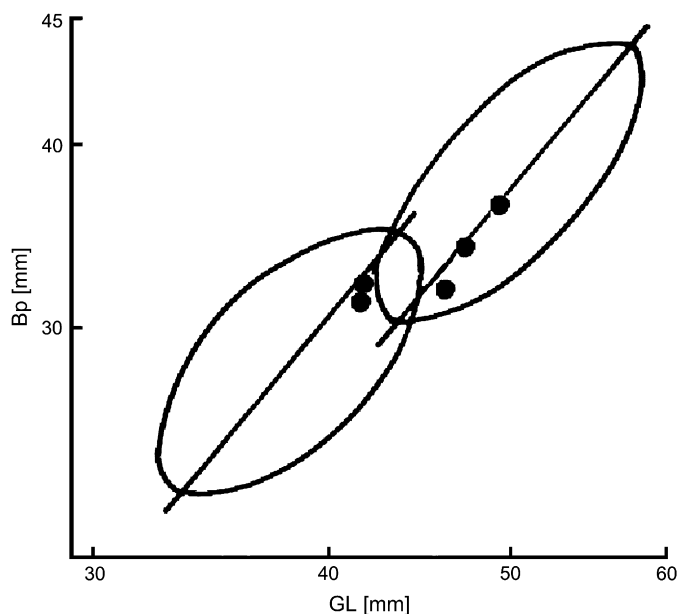


Fig. 2. Allometric relationship between the greatest length (GL) and the greatest proximal breadth (Bp) of the 2nd phalanx. Left ellipse: domesticated Neolithic cattle ( $n = 15$ ;  $r = 0.66$ ); right ellipse: aurochs ( $n = 81$ ,  $r = 0.75$ ). The ellipse contains 95% of the individual data. Measurements as defined by Driesch von den (1976). The data originate from Danish and northern German individuals (Degerbøl, 1970; Hübner et al., 1988). Five 2nd phalanges from Rosenhof were added as black dots. Two of them fall in the left ellipse and therefore in the size range of domesticated Neolithic cattle. For further details about these bone samples see SI 2.



in southern Italy. They concluded that the P-carrying aurochs of the British Isles could not longer be regarded as typical representatives of the European aurochs population and that consequently the mitochondrial DNA of bovines is no suitable genetic marker of domestication. But the authors base their reasoning upon the lacking significance of six British aurochs with P-haplotypes described by Bailey et al. (1996) and Troy et al. (2001). The subsequent study of Edwards et al. (2007) revealed further 49 P-carrying aurochs from many places across Europe. The T-carrying aurochs population in Italy seems to be exceptional and their post-glacial expansion restricted by the Alps like it has been already discussed by Edwards et al. (2007). Due to this geographic isolation we state that the findings of Beja-Pereira et al. (2006) have no impact on studies on the northern German aurochs population.

On the basis of those previous results, the aim of our current study was to examine whether the mtDNA haplotypes of the proposed domesticates from Rosenhof are of the P-haplotype or the T-haplotype. If domesticated individuals were imported from or came with Neolithic settlers, one would expect to see T-haplotypes. If there was cross-breeding of indigenous aurochs and imported domesticates, both haplotypes (T and P) might be seen, depending on female and male introgression patterns. If we were dealing with independent domestication one would expect *primigenius*-like haplotypes (P) similar to those of the wild European aurochs. Finally, if the presumed domesticated cattle are in fact small wild females, P-haplotypes would be expected. To figure out whether the small size of the bones could be due to pronounced sexual dimorphism, we also established the sex of all nine Rosenhof samples by analyzing parts of homologous zinc finger genes on the X and Y chromosomes.

## 2. Materials and methods

### 2.1. Samples

The archaeological bone material was collected from two adjacent coastal sites in northern Germany (Fig. 1). Seven samples from the Wangels LA 505 site and one sample from the Rosenhof LA 58 site are from early Neolithic layers (Lab code: Wan1, Wan2, Wan4, Wan5, Wan7, Wan9, Wan10, Ros9). Ros9 had formerly been considered a Mesolithic domesticated individual, but recent radiocarbon dating showed it to be of early Neolithic age of  $4000 \pm 50$  BC (KIA 28210). Five samples of four individuals from the Rosenhof site are terminal Mesolithic and had been morphologically established as aurochs (Lab codes: Ros2A, Ros2B, Ros3, Ros5, Ros7; the samples Ros2A and Ros2B belong to the same individual Ros2). Four additional Rosenhof samples that are likely to be of Mesolithic origin are of special interest because they are small-sized and therefore presumed domesticated individuals (Lab codes: Ros1, Ros10, Ros11, Ros12). This made a total of 16 individuals under consideration. Measurements of the bones, the dating and further details are given in Table 1 and in the electronic supplementary information (SI 1).

### 2.2. Extraction and PCR amplification

The samples were analyzed in the laboratories of the Institute of Anthropology in Mainz. To avoid contamination, the pre-PCR procedures were conducted in a clean-room-laboratory which is free from molecular work. Amplification of 361 bp (np 15903–16312) of the mtDNA control region was performed using three primer pairs as previously described by Bollongino et al. (2006). The nuclear primers amplify 27 bp of the X and Y

Table 1  
Summary of results and additional information on all archaeological *Bos* samples

Lab code	Morphological phenotype	mtDNA-haplotype	Sex (zf gene)	Dating	Skeletal element	Archaeological code
Ros2	A <i>B.p.</i> B <i>B.p.</i>	P	Female	Late Mesolithic	<i>Tibia</i>	S 95,5–96 O 113,5–114 T.: –4,21
Ros3	<i>B.p.</i>	P	Male	Late Mesolithic	<i>Calcaneus</i>	S 112,68 O 168,21 T.: –4,25
Ros5	<i>B.p.</i>	P	Male	Late Mesolithic	<i>Metatarsus</i>	test pit 2001 S 8–18, O 108–110 T.: –3,50–4,50
Ros7	<i>B.p.</i>	P	Male	Late Mesolithic	<i>3rd phalanx</i>	test pit 2001 S 8–18, O 108–110 T.: –3,50–4,50
<b>Ros1</b>	<b><i>B.t./B.p?</i></b>	<b>P</b>	<b>Female</b>	<b>4840 ± 80 cal BC (OxA 3327)</b> <b>4740 ± 60 cal BC (AAR 5000)</b>	<b><i>Metatarsus</i></b>	<b>Ros74 VI □ 148 i</b>
Ros9	<i>B.t./B.p?</i>	T3	Female	4000 ± 50 cal BC (KIA 28210)	<i>Scapula</i>	Ros 80 XIX □ 337 h
<b>Ros10</b>	<b><i>B.t./B.p?</i></b>	<b>P</b>	<b>Female</b>	<b>4770 ± 40 cal BC (KIA 31641)</b>	<b><i>Metacarpus</i></b>	<b>Ros 73 Ia □ 44 h</b>
<b>Ros11</b>	<b><i>B.t./B.p?</i></b>	<b>P</b>	<b>Female</b>	<b>Late Mesolithic/early Neolithic</b>	<b><i>Praemaxille</i></b>	<b>Ros 75 VIII □ 191 g</b>
<b>Ros12</b>	<b><i>B.t./B.p?</i></b>	<b>P</b>	<b>Female</b>	<b>Late Mesolithic/early Neolithic</b>	<b><i>3rd phalanx</i></b>	<b>Ros 80 XIX □ 350 I</b>
Wan1	<i>B.t.</i>	T3	–	3946 ± 79 cal BC (AAR 4998)	<i>Metatarsus</i>	Wa 505 – 98/518
Wan2	<i>B.t.</i>	T3	–	Early Neolithic	<i>1st phalanx</i>	Wa 505 – 97/15
Wan4	<i>B.t.</i>	T3	–	Early Neolithic	<i>Metatarsus</i>	Wa 505 – 97/48
Wan5	<i>B.t.</i>	T3	–	Early Neolithic	<i>Metatarsus</i>	Wa 505 – 98/390
Wan7	<i>B.t.</i>	T3	–	Early Neolithic	<i>2nd phalanx</i>	Wa 505 – 97/105
Wan9	<i>B.t.</i>	T3	–	Early Neolithic	<i>2nd phalanx</i>	Wa 505 – 97/262
Wan10	<i>B.t.</i>	T3	Female	Early Neolithic	<i>Talus</i>	Wa 505 – 97/182

The individual Ros2 is represented by two bones, A and B. The presumed Mesolithic domesticated individuals from Rosenhof are in bold. *B.p.* = *Bos primigenius*, *B.t.* = *Bos taurus*.

linked zinc finger gene homologues that carry chromosome-specific differences. Primer sequences and positions and further methodological details on the ancient DNA work, including DNA extraction, PCR and sequencing, are given in the electronic supplementary information (SI 4).

### 2.3. Phylogenetic analysis

Both control region and zinc finger genes sequences were aligned using the program MegAlign™ from the DNA Star Software package (version 7.0.0). Reduced median networks of T3 and P sequences (Fig. 3) were constructed with the Network 4.2.0.0 programme (Fluxus Technology Ltd. Clare, Suffolk, UK; <http://www.fluxus-technology.com>). Default weights were used.

### 3. Results

The amplification of the 361 bp control region product was successful for all seventeen bone samples. The sequences were compared to the corresponding 361 bp of the control region from 24 Neolithic and 7 Bronze Age European *B. taurus* samples and 15 European *B. primigenius* samples as previously published (Bollongino et al., 2006; Edwards et al., 2007) (GenBank accession numbers of the aurochs sequences: DQ915519, DQ915521, DQ915522, DQ915523, DQ915540–44, DQ915552, DQ915554–57, DQ915560, DQ915571, DQ915573).

All eight Neolithic samples from Wangels and Rosenhof revealed T3 haplotypes similar or identical to those present in modern and ancient taurine samples from Europe (Bollongino et al., 2006; Troy et al., 2001). Wan1, Wan5, Wan9, Wan10 exhibited haplotypes that match the reviewed Anderson Sequence (GenBank accession number V00654; Anderson et al., 1982) while Wan2, Wan4 and Ros9 are one, and Wan7 is two mutational steps away. By contrast, all four terminal Mesolithic robust aurochs samples from Rosenhof belong to haplogroup P that has been shown to be predominant among European aurochs (Edwards et al., 2007). Three of them belong to the central node of the P haplogroup that is twelve mutational steps away from the central node of the T3 haplogroup.

All four presumed terminal Mesolithic domesticated individuals from Rosenhof (Ros1, Ros10, Ros11, Ros12) possess P haplotypes, with two of them (Ros10, Ros11) being identical. Fig. 3 shows the mtDNA haplotype diversity within the sixteen individuals of the current study in the median reduced networks of the Neolithic and Bronze Age specimen. A compilation of all polymorphic positions among the 16 individuals is given in the supplementary information (SI 5).

Amplification of 27 bp sex-linked zinc finger gene products was attempted for the nine Rosenhof individuals the study was focussed on and one additional Wangels specimen for comparison. The molecular sexing was successful in each case. The early Neolithic sample from Wangels (Wan10), one of the late Mesolithic confirmed aurochs from Rosenhof (Ros2) and the five presumed domesticated individuals from Rosenhof (Ros1, Ros9, Ros10, Ros11, Ros12) revealed exclusively X chromosomal sequences. False identification favouring females could occur if the Y chromosome had not been amplified due to DNA degradation in ancient samples. The samples of our current study show an overall excellent preservation state. Since we independently replicated the zinc finger gene sequences from two different DNA extracts and 4 PCRs with an amplification success of 100%, this phenomenon is very unlikely. By contrast, the three remaining confirmed terminal Mesolithic aurochs samples from Rosenhof (Ros3, Ros5, Ros7) yielded both X chromosomal and Y chromosomal sequences (Fig. 4). Therefore, the presumed domesticated individuals from Rosenhof, one Neolithic bovine from Wangels and one terminal Mesolithic wild aurochs from Rosenhof are all female, while three of the terminal Mesolithic wild aurochs from Rosenhof are male. An overview of all results is given in Table 1. The mitochondrial sequences of the eight Rosenhof individuals with P haplotypes have been deposited in the GenBank database (accession numbers DQ915561–69).

### 4. Discussion

On the basis of the archaeological record, the site of Rosenhof LA 58 in northern Germany is considered a permanent

450		460		470		480																								
G	T	G	T	C	T	G	A	C	A	T	T	G	G	A	C	A	C	G	T	T	G	T	T	C	A	T	G	ZFX NM_177490		
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-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Ros3 X	
-	-	-	-	-	-	-	-	-	-	T	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	Ros3 Y
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-	-	-	-	-	-	-	-	-	-	T	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	Ros5 Y
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Ros7 X	
-	-	-	-	-	-	-	-	-	-	T	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	Ros7 Y
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Ros1 X	
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Ros9 X	
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Ros10 X	
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Ros11 X	
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Ros12 X	

Fig. 4. Alignment of the 27 bp product of sex-linked zinc finger genes of the nine Rosenhof individuals. Only sites that differ from the X chromosomal reference sequence with the GenBank accession number NM\_177490 are shown. The Y chromosomal sequence with the GenBank accession number NM\_177491 is also shown. Numbering is according to the reference sequence. Identical positions are denoted with periods. The letter after the sequence name shows whether it is an X or Y chromosomal sequence.

base-camp of a Mesolithic hunter-gatherer population. Interestingly, there is some evidence for direct contact and exchange with neighbouring Neolithic settlers. However, the archaeozoological evidence for pre-Neolithic cattle husbandry is disputed, since some *Bos* bones seem to be too small to stem from wild indigenous aurochs according to the present morphological criteria. By applying stringent ancient DNA methods to mitochondrial and nuclear DNA, we can show that: (1) all Neolithic samples from the Wangels and Rosenhof sites carry the imported taurine haplogroup T3; (2) all samples from the Rosenhof site that could be of Mesolithic origin belong to the European aurochs lineage P; (3) all Rosenhof presumed domesticates are female individuals; and (4) three out of four remains from Rosenhof's robust late Mesolithic aurochs stem from males. These data allow us to re-evaluate various hypotheses concerning Rosenhof during the terminal Mesolithic era.

#### 4.1. Import of domesticated individuals?

As in previous ancient DNA studies on *Bos* specimens from central and northern Europe, the Neolithic *Bos* bones from northern Germany, without exception, carry imported T3 haplotypes, while morphologically confirmed terminal Mesolithic Rosenhof aurochs carry P-lineages. The proposed terminal Mesolithic Rosenhof domesticates also show P haplotypes. This means the scenario of imported domesticated cattle from adjacent Neolithic settlers can no longer be supported, since we would then expect T haplotypes among these morphologically gracile individuals. The single T3 haplotype individual in Rosenhof (Ros9) provides the earliest direct evidence for domesticated bovines in northern Germany and southern Scandinavia. The dating of  $4000 \pm 50$  cal BC is in agreement with the first evidence of domesticated sheep or goat in Rosenhof that dates back to about 4100 cal BC (AAR 1459, KIA 7127, KIA 7129; Hartz et al., 2002).

Rowley-Conwy (1985, 1995) argued resolutely against the presence of domesticated bovines in terminal Mesolithic Rosenhof layers and none of Nobis' (1975) presumed domesticates or transitional individuals passed his critical review. For example, according to Nobis (1975), the specimen Ros10 represents a Neolithic domesticated animal because its measurements are smaller than the smallest known Scandinavian aurochs. Rowley-Conwy, however, argues that it is located at the edge of the domesticated bull/female aurochs overlap region and should therefore be regarded as a female aurochs. Molecular sexing was of vital importance for further clarification. It showed that we are indeed dealing with a female individual. All the small Rosenhof samples (including Ros10) turned out to be female, but they are too large to stem from fully domesticated cows. Therefore, our data strongly support Rowley-Conwy's hypothesis of small female aurochs.

#### 4.2. Hybridisation of indigenous aurochs and imported cattle?

Using mitochondrial DNA sequences, hybridisation of wild aurochs and Neolithic cattle would only be observable in the

case of female introgression. Since mitochondrial DNA is strictly maternally inherited, female introgression of T3 haplotypes in a herd of P haplotypes and female introgression of P haplotypes in a herd of T haplotypes could be detected. On the other hand, due to the lack of suitable Y chromosomal markers, there is so far no way to demonstrate male introgression. Nevertheless, one of the strongest arguments against common hybridisation events in Europe is the absence of the P-haplogroup among modern and ancient central European domesticated cattle (Bollongino et al., 2006; Troy et al., 2001). Additionally, Edwards et al. (2007) convincingly showed that the impact of P haplotype-carrying females on the modern mitochondrial gene pool of European domesticated cattle was negligible. At a minimum, that means there is no evidence of female cattle introgression among the Rosenhof samples. Introgression of a domestic male into the Mesolithic aurochs population seems to be very unlikely, especially considering the fact that we found no male individuals in Rosenhof carrying T3.

#### 4.3. Independent domestication of local aurochs?

The idea of independent domestication of indigenous aurochs was primarily postulated by Nobis (1975). He proposes three separate stocks in Rosenhof: imported domesticated cattle, individuals of the "wild-domestic-transitional-field" including locally domesticated animals, and wild aurochs. This supports Schwabedissen's view (Schwabedissen, 1994) that the Neolithic transition in northern Germany occurred as early as ca. 4400 cal BC. This idea was supported by ceramics from the Rosenhof site differing from the typical wide-mouthed terminal Mesolithic Ertebølle vessels with a pointed base. Instead, they showed affinities to the Central European Neolithic Michelsberg culture (Schwabedissen, 1979). However, due to unclear stratigraphic classification and the results of recent palynological dating the current consensus in the archaeological community is that these Neolithic artefacts are import articles that may be even younger (Hartz et al., 2002; Hartz, 2005; Kalis and Meurers-Balke, 1998; Rowley-Conwy, 1985). Since the Rosenhof settlers are presently believed to be mainly Mesolithic hunter-gathers, the occurrence of cattle husbandry would be extraordinary and its detection unique. Rowley-Conwy (1995) emphasizes that local domestication of indigenous aurochs in particular would have been unnecessarily troublesome for the Mesolithic settlers, compared to importing and further breeding of Neolithic cattle — a possibility that we have qualified above. However, our genetic analysis of the presumed Mesolithic domesticates ultimately revealed that we are dealing with four females that carry three different P haplotypes (Ros1, Ros10, Ros11, Ros12; see Fig. 3b). If there were independent domestication of local aurochs by the Mesolithic settlers, it is likely that we would see a lower degree of variability. Unfortunately our sample size is too small to draw final conclusions on this. However, a strong argument against local domestication is the lack of male individuals among the assumed domesticates whose size is clearly greater than that of domesticated cows.

#### 4.4. Unusual small aurochs cows?

The Rosenhof bones of presumed domestics show no signs of pathology. Nor does current knowledge of contemporary ecological conditions provide an explanation for their small size. Therefore, the only remaining explanation for the small size of the Rosenhof bovines is that the maximum size of wild female aurochs has been underestimated. Degerbøl (1970) had already concluded from his study of Stone Age Danish bovines that the transitional individuals represent female aurochs. We propose reconsidering the actual size variation of female aurochs. The Danish aurochs collection that was used for comparison clearly contains more aurochs bulls than cows. The numbers of the reference individuals per skeletal element that are relevant for the present study are as follows: Metatarsus: ♂24/♀17; scapula: ♂22/♀12; metacarpus: ♂27/♀20; praemaxille: none; 3rd phalanx: ♂3/♀2 (Degerbøl, 1970). Accordingly, only about 40% of the bone material stem from female individuals. The small number of female aurochs reference samples has probably hindered a representative assessment of their size variation.

A further methodological problem is estimating individual age. For instance, since 3rd phalanges do not have distinct ossification centres, it is always difficult to know if growth is complete. It is possible that the individual Ros12, represented by a 3rd phalanx, is small not because it had been domesticated but because it was a subadult animal. Further, there is evidence from dietary isotopes that the Rosenhof metatarsal of Ros1 stems from an aurochs and not from a domesticated animal (Noe-Nygaard et al., 2005).

## 5. Conclusions

Our joint analysis of morphological and genetic data revealed that four presumed domesticated individuals from terminal Mesolithic layers in Rosenhof are female aurochs. The fact that all samples that are possibly of terminal Mesolithic origin carry P haplotypes, as well as the sex molecular identifications, confirms that there were unusually small females among the northern German aurochs population, and there is no evidence of local domestication or hybridisation. Thus, even if the southwestern Baltic region functioned as a bridge between Neolithic settlers to the south and east of the Elbe River and the Mesolithic hunter-gatherers of Scandinavia, the exchange was restricted to smaller objects like stone tools and ceramics, but did not include livestock husbandry, one of the core aspects of the Neolithic life style. The beginning of livestock husbandry began with the transition to the Neolithic Funnel Beaker Culture and is evidenced by the earliest direct proof of an imported Neolithic bovine with T3 haplotype in Rosenhof at  $4000 \pm 50$  cal BC.

## Acknowledgement

We thank Julia Elsner and Dirk Heinrich for collaboration, and Mark G. Thomas, Wolfgang Haak, Helmut Hemmer, Christine Weber, and Frank Zachos for helpful discussion.

The project was financially supported by the Bundesministerium für Bildung und Forschung.

## Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jas.2007.08.012.

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