

Mesolithic domestic pigs at Rosenhof – or wild boar? A critical re-appraisal of
ancient DNA and geometric morphometrics

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Abstract

We challenge the claim by Krause-Kyora et al. (2013) that there were domestic pigs at Mesolithic sites in northern Germany. A small number of animals from Rosenhof and Poel have Ancient DNA and Geometric Morphometric signatures elsewhere associated with domestic animals. At this time Neolithic farming settlements were present 150 km to the south, but the Mesolithic specimens are however metrically wild boar, much larger than domestic pigs, and cannot be domestic individuals acquired from the farmers. A more likely explanation for these ‘domestic’ traits is that animals that escaped from farmers’ pig herds interbred with local wild boar. Their descendants were morphologically and behaviourally wild, and were shot by Mesolithic foragers in the course of normal hunts. Their presence at Mesolithic sites is not a precursor to agriculture.

Key words

wild boar, domestic pig, Mesolithic, ancient DNA, Geometric Morphometrics, Rosenhof

Introduction

In a paper entitled ‘Use of domesticated pigs by Mesolithic hunter-gatherers in northwestern Europe’, the authors state that ‘our results reveal that the northern European Mesolithic Ertebølle hunter-gatherers did not only possess domestic pigs like those of their agricultural neighbours, but that these animals were present in the region ~500 years earlier than has previously been demonstrated’ (Krause-Kyora et al. 2013, 2). If this claim were substantiated, it would be of massive importance for our understanding of the spread of farming, and also for the ways we study domestication.

The recognition of domestic animals is not always straightforward. The authors briefly allude to potential complications such as feral animals, and do not explicitly claim that Ertebølle people actively *managed* or *domesticated* these animals, and they acknowledge that the Ertebølle continued to concentrate on hunting and gathering for many hundreds of years. But they strongly imply that these animals had a relationship with Ertebølle foragers distinct from that of hunted wild boar when they say that the Ertebølle ‘*possessed* domestic pigs also kept by their agricultural ... neighbours’ (Krause-Kyora 2013: 5, emphasis added). The whole thrust of the paper is that Mesolithic people had domestic pigs. This is reiterated many times, and the concluding sentence states that ‘these domestic pigs do, however, represent not only the first domestic animals identified from Mesolithic sites in continental northern Europe, but also the earliest domesticates from the region’ (Krause-Kyora et al. 2013, 5).

This paper was rapidly picked up by the scientific media around the world, which have universally understood it to claim that Mesolithic people had domestic pigs. *Science* reported the conclusions under the heading ‘European hunter-gatherers dined on domestic pigs’ (Balter 2013, 950). The NERC website reported it under the heading ‘European hunter-gatherers owned pigs as early as 4600 BC’ (NERC 2013). The claim was widely hyped in the world’s media and received considerable attention.

The claim is based on three lines of evidence:

- Mitochondrial DNA (mtDNA) of the Near Eastern Y1 haplotype, showing descent through the female line from introduced domestic pigs.
- Nuclear DNA (nDNA) homozygous for the *MC1R* E^P allele 501, indicating a spotted coat of the kind found in domestic pigs.
- Geometric morphometrics (GMM) revealed molars of domestic shape.

Using these criteria, the authors identify four specimens from Ertebølle sites as domestic pigs. Mandible E24 from Rosenhof, directly dated to the Mesolithic, has the Y1 haplotype, the spotted coat, and a domestic GMM shape. The authors conclude that the genetic and GMM data together ‘strongly indicate that E24 represents the remains of a domestic animal’ (Krause-Kyora et al. 2013, 3). Two additional specimens from Ertebølle sites, Rosenhof E44 and Poel E69, are identified as domestic just on the basis of their having the Near Eastern Y1 haplotype. A final Ertebølle specimen, Rosenhof E151, has the European haplotype, but is nevertheless identified as domestic on the basis of nDNA evidence that it carried the *MC1R* mutation associated with spotted coat coloration.

Here we critically re-assess this claim for Mesolithic domestic pigs. We conclude that the animals were most probably wild boar with some domestic ancestry, but not domestic pigs. Metrical evidence points clearly in this direction, and more plausible explanations are advanced to account for the DNA and GMM data.

Rosenhof – the background

The current claim for Mesolithic domestic animals at Rosenhof is just the latest of several going back nearly 40 years. Rosenhof belongs to the Ertebølle hunter-fisher-gatherer culture, well known for its shell middens in Denmark, dating to 5300-3900 cal BC. Contemporary foragers of the Swifterbant culture occupied the Low Countries. The Neolithic LBK and Rössen cultures were present to the south at this time, and there was a long static boundary between foragers and farmers (fig. 1). Forager-farmer interactions have long been discussed. Numerous stone axes were traded from farmers to foragers (Klassen 2002; Verhart 2012).

In the 1950s the Danish palynologist Jørgen Troels-Smith argued that domestic animals had also spread to the Ertebølle (Troels-Smith 1953). Radiocarbon dating and other evidence have subsequently shown that this is incorrect (see Rowley-Conwy 1999), but during the 1950s this argument was quite influential. Working in northern Germany, Hermann Schwabedissen suggested that the later Ertebølle should be termed the *Altneolithikum*, ‘oldest Neolithic’. He expected that a few domestic animals might be found (Schwabedissen 1958).

Schwabedissen excavated Rosenhof in 1969/70 (Schwabedissen 1972). A few of the *Bos* bones were indeed identified as domestic cattle (Nobis 1975). Renewed excavations in 2001/02 apparently produced a few more (Hartz 2005) but no details are available. Recent aDNA and isotopic work has however shown that these cattle were wild, not domestic (Noe-Nygaard et al. 2005; Scheu et al. 2008). A few other domestic cattle have been claimed, from Dąbki in Poland to Schokland P14 in the Netherlands (fig. 1). These are all problematic. The Dąbki claim is no longer accepted (Kabacinski et al. 2009), and the Schokland P14 claim is not based on metrical evidence (Rowley-Conwy 2013, 300-301). Domestic cattle bones occasionally turn up in Mesolithic sites, recent examples including Smakkerup Huse and Åkonger (fig. 1); but when directly dated these specimens are shown to be intrusions from the Neolithic (Price and Gebauer 2005; Heinemeier and Rud 1999). Some authorities appear to assume that a few domestic cattle could be traded north as easily as if they were stone axes (e.g. Zvelebil 2006, 185), but this is unlikely: hunter-gatherers would find it very difficult to integrate a couple of domestic cattle into their nomadic foraging lifestyle (Rowley-Conwy 2013, 301). Domestic pigs and caprines have also been claimed. From Rosenhof, a small pig scapula was claimed to come from a domestic animal (Nobis 1975), but the scapula grows substantially *after* it fuses and appears adult. This individual might thus be a juvenile wild boar (Rowley-Conwy 2013). Caprines are claimed at Hardinxveld-Giessendam de Bruin in the Netherlands (Oversteegen et al. 2001). These are more convincing because sheep and goat are not native to Northwest Europe – but they have yet to be directly dated by radiocarbon. In view of this long debate and the continuing uncertainties, the latest claim for domestic animals at Rosenhof must be evaluated carefully.

Rosenhof mandible E24

Zooarchaeology has long used biometry to distinguish wild from domestic. Ludwig Rüttimeyer established that wild boar M3s measured 40mm or more in length, domestic pigs 39mm or less, as long ago as 1862 (Rüttimeyer 1862). Subsequent work has shown that things are somewhat more complex: wild boar size varies from region to region (e.g. Groves 1981; Albarella et al. 2009), so that 39mm is not universally appropriate, and there is a modest metrical overlap between wild and domestic; but in

northern Europe Rüttimeyer's threshold holds reasonably true (Rowley-Conwy et al. 2012).

The Rosenhof E24 mandible is from an adult male. It is broken and lacks M3, but does have an M2. Metric data are not reported by Krause-Kyora et al (2013), but we have been sent E24's M2 measurements by Allowen Evin, taken from her photographs used for the GMM study reported in that paper, and also by Ulrich Schmölcke, the zooarchaeologist responsible for the Rosenhof assemblage. Schmölcke's measurements were taken directly on the specimen using callipers; each was taken five times and then averaged to produce the results given below. There is damage to the posterior end of the tooth, so the original length may have been slightly greater than listed here (Schmölcke, *pers. comm.* to PR-C, 19 December 2013). Evin cautions that measurements from a photograph may be quite different from those taken with callipers (Evin, *pers. comm.* to PR-C, 24 October 2013). Their measurements are as follows, with the true measurement using callipers universally larger than those taken from photographs:

	Evin	Schmölcke
length (L)	23.9	24.5
anterior width (WA)	15.5	15.7
posterior width (WP)	16.4	17.6

These measurements are plotted in fig. 2, compared to assemblages of domestic pigs from Troldebjerg (Early Neolithic Denmark) and Durrington Walls (Late Neolithic England), and three assemblages of wild boar from Late Mesolithic Denmark (see fig. 1 for locations). Schmölcke's measurements, taken by an experienced zooarchaeologist and using the same method as for the other assemblages, are directly comparable to the other assemblages plotted.

In Fig. 2, the wild and domestic distributions are largely separate. This is the common pattern for wild and domestic pig measurements in northern and central Europe (e.g. Payne and Bull 1988; Rowley-Conwy et al. 2013). There is a small overlap between some of the smaller animals from Mesolithic Sludegaard and the largest specimens

from the Neolithic sites, but the zone of uncertainty is small. Neolithic farmers may also have hunted some wild boar, but no clear instances can be seen in Fig. 2. Two anomalously small teeth from Mesolithic Bloksbjerg stand out clearly. As has proven the case with other proposed domesticates in Mesolithic sites (see above for examples involving cattle), it is possible that these specimens are intrusive domestic animals from a later period, a possibility that should be checked by accelerator dating.

Rosenhof E24 falls in the wild scatter, most clearly so when using Schmölcke's calliper measurements. E24 is metrically a wild boar. If Mesolithic people from Rosenhof had acquired a domestic pig from the farmers to the south, it could never have been so large an animal: the farmers simply did not have any domestic animals that big. This is a major problem for the claim that E24 was domestic.

Krause-Kyora et al. (2013, 3) acknowledge the large size of E24, but downplay the value of biometrics. They cite mandible L320 from Zauschwitz, a Neolithic site deep in farming territory (see fig. 1). This animal is also of wild boar size – but like Rosenhof E24, it is identified as domestic because it carries the Near Eastern Y1 mitochondrial haplotype, and GMM indicates a domestic molar shape (but note this determination is not reported in Krause-Kyora et al. 2013, table 3), thus 'further underscoring the unreliability of molar size as a definitive marker for domestic or wild status' (Krause-Kyora et al. 2013, 3). Genetics and molar shape do not always trump size in the authors' designation of specimens as wild or domestic however. Specimen L308 from the farming site of Brodau is of domestic size, but possesses a European mitochondrial haplotype and a wild molar shape. It is nevertheless identified as a domestic animal. The authors do not say whether this is based on the specimen's small size, or its context in a Neolithic farming site, underscoring a problematic lack of consistency (and clarity) on the criteria used here to make these wild/domestic determinations.

In support of their dismissal of traditional biometric techniques for distinguishing wild from domestic pigs Krause-Kyora et al. (2013) cite a paper by a partly overlapping group of authors, Evin et al. (2013). Evin et al. (2013) examined samples of modern wild boar and domestic pigs. They conclude that GMM discriminates more accurately between wild and domestic animals than established biometry. They

buttress their dismissal of established biometrical techniques, citing several published papers in support of their position:

‘...the ranges of molar length measurements show significant overlap between the two groups (Albarella and Payne, 2005; Albarella et al., 2006; Mayer et al., 1998; Payne and Bull, 1988). Despite decades of research, size variation between wild and domestic pigs remains inadequately studied, raising doubts about the accuracy of size measurements to discriminate wild and domestic forms (Mayer et al. 1998)’ (Evin et al. 2013, 736).

These earlier studies are, however, inaccurately characterised here. Albarella and Payne (2005) considered the domestic pigs from Durrington Walls; their molars do not approach the mean size of wild boar from Turkey to which they were compared (Albarella and Payne 2005, fig. 2), and overlaps with wild boar are not discussed. Albarella et al. (2006) plot only one minor wild/domestic overlap – from Portugal, where the wild boar are relatively small (Albarella et al. 2006, fig. 15.1); metrical overlaps are otherwise not discussed. Payne and Bull (1988), moreover, showed that wild and domestic pigs overlapped (not surprisingly) at the early agricultural site of Jarmo in Iraq, while in Europe there was little overlap between them (Payne and Bull 1988, figs. 7, 8 and 9). Mayer et al. (1998), cited twice, conclude from their study of modern animals that using 95% confidence limits ‘the present study confirms the value of second and third molar size as a basis for differentiating wild boar from early domestic swine’ (Mayer et al. 1998, 46), and that they have ‘generally validated the use of molar size criteria to distinguish Eurasian wild boars from smaller primitive domestics’ (Mayer et al. 1998, 51). None of these papers thus supports Evin et al.’s (2013) statement.

On the basis of their own measurements of modern animals Evin et al. (2013) claim that only 77.9-87.5% can be correctly identified using measures of size. However, in this study they combine wild boar from a variety of populations from Russia to Morocco (Evin et al. 2013, supplementary table 1), despite there being widely recognized regional variation in dental biometrics (Groves 1981; Albarella et al. 2009). So it is not surprising that the picture is unclear. In individual regions, established zooarchaeology can identify much higher proportions. When one

compares specimens from a more geographically restricted area, as is the case in Fig. 2, most animals can be classified as wild or domestic fairly easily.

Most recently, some of the same authors (Evin et al. 2014) present a new statistical method based on biometrical data extracted from their 2013 GMM study, now with a claimed success rate mostly above 90%. They identify a cut-off separating wild and domestic, but specimens nearer the cut-off are at greater risk of mis-diagnosis – exactly the situation in established biometrics. Their cut-off for M3 length is 37.9 mm. If GMM measurements taken from photographs used to calculate those lengths are consistently smaller than calliper measurements (see table above), the calliper cut-off would be closer to 39 mm. This is precisely where Rüttimeyer placed it in 1862 (see above), so the statement that this new method provides ‘a more robust and rigorous statistical tool for use in identifying the domestic or wild status of *Sus scrofa* remains from archaeological sites’ (Evin et al. 2014, 10) seems somewhat overstated. It is also interesting to note that by the standards established in Evin et al. 2014 Rosenhof E24 would be classified as wild based on both the M2 GMM and calliper length and width measurements.

Paradoxically, having claimed improved metrical accuracy, Evin et al. (2014, 11) go on to argue that there were nevertheless ‘large but clearly domestic pigs’ at both Mesolithic and Neolithic sites, ‘contradicting the traditionally accepted view that domestic pigs are small, and wild boar are large’ (Evin et al. 2014, 12). In support of this they cite Krause-Kyora et al. (2013), so these ‘large domestic pigs’ are evidently Rosenhof E24 and Zauschwitz L320. We have no measurements for L320. For E24, however, we have demonstrated that established biometrical methods are robust, despite the attempts to downplay them: E24 is clearly a wild boar.

Wild boar with ‘domestic’ aDNA and GMM signatures

If Rosenhof E24 can be reasonably argued to be a wild boar, despite its genetic signatures and molar shape, then this raises questions about the status of the other Ertebølle specimens identified here as domestic pigs. There is, in fact, a quite straightforward explanation for this mix of ‘wild’ and ‘domestic’ characteristics

observed in these specimens, if we bear in mind the archaeological context of a static boundary between foragers and farmers lasting more than a millennium (fig. 1).

Domestic pigs must intermittently have escaped from their owners throughout the LBK and Rössen periods, and run wild in the forests. Some, particularly females, would encounter wild boar and be incorporated into the wild population. Given (a) the long period of co-existence between foragers and farmers, (b) the likelihood that the LBK domestic pigs were managed in a loose pannage system (Albarella et al. 2006), and (c) the documented extent to which wild and domestic pigs freely interbreed (Albarella, Tagliacozzo et al. 2006; Albarella et al. 2007; Dwyer 1996), it is not surprising that genetic signatures of these introduced LBK domestic animals crop up among indigenous wild boar solely through introgression between escapes and native animals. Thus metrically and behaviourally wild boar would sometimes have the spotted coat inherited from a domestic ancestor – we see no reason why this trait should always be eliminated in the wild (contra Krause-Kyora et al 2013, 2). In fact, the domestic form of the *MC1R* allele identified in Rosenhof E24 is used today as an indicator of just such hybridization, present in 5% of free-ranging wild boar in Greece (Koutsogiannouli et al. 2010). Humans hunting wild boar would thus encounter a behaviourally wild population of large size, containing some genes and tooth shapes that derived from (possibly quite distant) domestic ancestors. This would apply both to the farmers who shot Zauschwitz L320 and to the foragers who shot Rosenhof E24.

Krause-Kyora et al. (2013) however argue that such introgression is unlikely, stating that ‘Near Eastern mtDNA haplotypes have so far not been observed in ancient or modern European wild boar, suggesting that even if this did occur, the wild–domestic crosses have not left a significant mtDNA footprint in ancient or extant indigenous European wild boar populations’ (Krause-Kyora et al. 2013, 5). The absence of the Near Eastern mtDNA haplotype among modern European boar is not surprising; these haplotypes are also no longer evident among modern domestic pigs (Larson et al., 2005, 2007). As to the ancient populations, we argue that Krause-Kyora et al.’s (2013) study provides precisely such evidence of the presence of domestic genetic signatures among a population of wild boar. The variable mix of both ‘domestic’ and ‘wild’ genetic and morphological signatures in these animals is what one might

expect from hybrid offspring of European wild boar and introduced Near Eastern domestic pigs.

Defining Domestication in the Ertebølle context

The demonstration that some Ertebølle pigs have domestic ancestry is not the same as a demonstration that these animals were either behaviorally domestic or, importantly, were treated by the Ertebølle people that consumed them as domestic animals. There is more to domestication than genetics or the phenotypic expression of genetic traits. A core, defining characteristic of a domesticate is that it be engaged in a mutualistic relationship with humans in which humans provide some level of control over breeding, nutrition, and protection in return for a sustainable off-take of resources from a managed herd (Zeder 2012). There is no evidence that the Ertebølle people managed these animals in a way consistent with keeping domesticates (Zeder 2006). Aside from asserting that pigs with spotted coats must have seemed ‘strange and exotic’ to Ertebølle hunters (Krause-Kyora et al. 2013, 5), the authors provide no evidence that animals with some domestic ancestry, even the spotted ones, were treated any differently from hunted boar of more pure European ancestry.

They go on to assert that possession of these domestic pigs ‘...ultimately open[ed] a gateway to lifeways centred on the continuous use of livestock as a dietary staple’ (Krause-Kyora et al. 2013, 5), concluding that ‘the acquisition of domestic pigs by these last hunter-gatherers was one (perhaps critical) component of a broader socioeconomic process by which the Ertebølle acquired and assimilated agricultural elements, eventually leading to the emergence of the Trichterbecher culture’ (Krause-Kyora et al. 2013, 5). By failing to make the important distinction between (a) the genetic heritage of an animal, and (b) its cultural and economic context, they go far beyond the supportable conclusion that these animals possessed some domestic ancestry, to the unsupportable conclusion that there was something special in the relationship between Ertebølle people and these animals, something that contributed to the radical restructuring of Ertebølle society nearly 1000 years after the earliest of these animals turn up in an Ertebølle assemblage.

Conclusion

We have argued that Krause-Kyora et al. (2013) are almost certainly mistaken in their claim that Rosenhof E24 was a domestic pig, raising questions about the domestic status of the other pigs from Ertebølle assemblages that possess some genetic and morphometric characteristics found in domestic pigs. The claims of domestic status for these animals is based on a too narrow reliance on the results of two new techniques, and a too narrow appreciation of both the general archaeological and the zooarchaeological contexts and background. Future studies need to take these aspects more into account if they are to avoid similar errors.

Rather than providing the ‘earliest evidence of the first domesticated pigs introduced the region’ (Krause-Kyora et al. 2013, 3), what this interesting study instead provides is evidence that pigs with some domestic ancestry were hunted by Mesolithic people. This is interesting and important, and an impressive demonstration of the utility of mixing both morphological and genetic approaches to document the complex processes of domestication and dispersal. But it is not an indication that Mesolithic people ‘possessed’ domestic pigs, or that possessing these animals somehow paved the way for the eventual adoption of an agricultural way of life.

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Figure Captions

Figure 1. Map showing locations of sites and archaeological cultures mentioned. Culture distributions combined from Müller 2011, figs. 2 and 4.

Figure 2. Scatter plot of pig lower M2 measurements. Durrington Walls from Albarella and Payne (2005); Troldebjerg measured by Rowley-Conwy (unpublished); Sludegaard, Bloksbjerg and Nivaa measured by Keith Dobney and Peter Rowley-Conwy as part of the Durham Pig Project.



