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The long and winding road: identifying pig domestication through molar size and shape

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The ability to document the effects of domestication from archaeological remains of animals and plants is essential for reconstructing the history of one of the most important transitions in human prehistory – the shift from hunting and gathering to farming. In mammals, teeth are well preserved in archaeological remains and are known to be taxonomically informative. In this study, we compare three sets of dental morphometric descriptors in wild and domestic pigs (*Sus scrofa*) – maximum length, size and shape variables from 2D geometric morphometrics – in order to assess which of the three provides the best ability to correctly distinguish current wild and domestic West Palaearctic pigs. For this purpose, we used predictive linear discriminant analysis with cross-validation taking into account potential bias due to heterogeneous sample sizes and important number of predictors. Classification accuracy of wild and domestic status ranged between 77.3 and 93% depending of the tooth and the descriptor analyzed. However, individual posterior probabilities of correct classification were appreciably smaller when using tooth length and centroid size compared to shape variables. Size appeared to be a poor indicator of wild and domestic status, contrary to shape which in addition provides a high degree of confidence in the wild versus domestic predictions. Our results indicate that geometric morphometrics offers an extremely powerful alternative to more traditional biometric approaches of length and width measurements to capture the elusive morphological changes induced by the domestication process in archaeological remains.

1. Introduction

Over the past 10,000 years human subsistence has been transformed by the domestication of plants and animals. Though the differences between 'wild' and 'domestic' animals is generally understood, fundamental questions regarding this basic dichotomy, along with the processes involved with the biological and cultural transformations leading to domestication, remain largely unanswered (Dobney and Larson, 2006; Vigne et al., 2005). The bones and teeth of animals recovered from archaeological sites can provide direct evidence of this important transition in human history, as they exhibit phenotypic and genotypic changes associated with natural and artificial selection. Wild and domestic forms of the same species are often morphologically, behaviourally and/or ecologically distinct (Price, 2002). In mammals, the most significant physical changes to occur with domestication involve a decrease in brain and body size, changes in body proportions, and a modification of external morphological characters such as emergence of piebald coat colour, wavy or curly hair, rolled and shortened tails, or floppy ears (e.g. Dobney and Larson, 2006; O'Regan and Kitchener, 2005). Notably, a decrease in body size during domestication has

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been demonstrated in many mammals including dogs, cattle, goats, sheep and pigs (e.g. Albarella et al., 2005; Davis, 1981; Hongo et al., 2009; Peters et al., 1999; Zeder et al., 2006).

Identifying domestic forms of *Sus scrofa* is particularly challenging for zooarchaeologists as wild boar are distributed throughout Eurasia (Albarella et al., 2006; Rowley-Conwy et al., 2012). Traditional size measurements (linear distances) of teeth and bones have commonly been used to infer the wild or domestic status of archaeological remains (Vigne et al., 2005). Thus, a reduction in size is generally recognized as one of the primary indicators of the transition from wild to domestic in the archaeological record (e.g. Boessneck and von den Driesch, 1978; Bökönyi, 1974; Meadow, 1989). As a consequence, small individuals are commonly classified as 'domestic' and large ones as 'wild' (see reviews in Albarella et al., 2006; Rowley-Conwy et al., 2012). Although the maximum length of the lower third molar (most frequently used for wild/domestic determinations in zooarchaeological analyses) is generally considered longer in wild pigs (e.g. Rütimeyer, 1862; Boessneck et al., 1963; Flannery, 1982; Rowley-Conwy et al., 2012; Ervynck et al., 2001), 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). More accurate morphometric methods are, therefore, required to first describe specific morphometric differences between wild and domestic dentitions, and second to determine the best morphometric descriptors to classify specimens more accurately.

Although traditional morphometrics provide important reference data on quantitative variation in morphology, they have inherent limitations such as the difficulty in separating size from shape information, the lack of an effective visualization of analytical results (generally interpreted using summary statistics and coefficients tables) and, more importantly, their inability to accurately preserve the relative positions of the anatomical landmarks between which distances are measured (Adams et al., 2004; Rohlf and Marcus, 1993). To overcome these limitations, developments in morphometric methods during the 1980s and '90s, provided new ways of separating size from shape, to accurately capture the geometric relationships amongst the parts being measured and to visualize analytical results using intuitive shape diagrams (Adams et al., 2004; Rohlf and Marcus, 1993; Bookstein, 1996). This approach known as geometric morphometrics (GMM) has become the mainstream set of techniques used in biological and palaeontological studies and are now increasingly being employed in zooarchaeology to tackle taxonomic issues at the specific and sub-specific level in groups with a complex taxonomy, such as murids (Cucchi et al., 2011a; Valenzuela-Lamas et al., 2011; Cucchi, 2008), equids (Bignon et al., 2005) or cave bear (Seetah et al., 2012). In pigs GMM have already been employed to clarify taxonomy and dispersal in Island South-East Asia (Cucchi et al., 2009; Larson et al., 2007) and the beginnings of its domestication in China (Cucchi et al., 2011b). However, these studies have not dealt specifically with estimating the accuracy of assigning archaeological remains to either wild or domestic forms.

Previous molecular analysis has revealed the likely existence of multiple centres of pig domestication in Eurasia (Larson et al., 2005). In order to exclude phenotypic differences potentially due to independent domestication events this study focuses on modern wild and domestic *S. scrofa* from the West Palaearctic. Analyses were undertaken using lower second (Cucchi et al., 2011b) and lower third (Larson et al., 2007; Cucchi et al., 2009) as well as upper second and third molars.

Classification in morphometrics is commonly achieved using a well established parametric method called linear discriminant function analysis (LDA). LDA looks for linear combinations of variables that maximize differences between predefined groups relative to within group variation. Thus, discriminant functions can be derived using measurements on modern domestic and wild pigs that aid with the classification of archaeological material. LDA is sensitive to assumptions that are easily violated by real data; it is affected by sampling error (small sample size as well as unbalanced designs) and the number of variables used as group predictors; also, LDA tends to over fit the data (i.e., its results are often 'over-optimistic' – Kovarovic et al., 2011). This is why classifications from LDA must be cross-validated and the robustness of their results assessed. This is particularly important in archaeology, where sample sizes are often unbalanced. Furthermore, when using GMM approaches, shape analysis tends to generate numerous variables, whose number may be reduced using ordination techniques such as principal component analysis (PCA) (i.e. Sheets et al., 2006; Baylac and Friess, 2005).

This study aims to: (1) describe the variability of modern wild and domestic West Palaearctic *S. scrofa* using a commonly used traditional measurement (maximum molar length) as well as size and shape variables from geometric morphometrics on lower and upper second and third molars; (2) assess the classification accuracy of the different morphometric descriptors – taking into account how the number of predictors and unequal sample size might affect results; (3) estimate the confidence in the classification accuracy when using the different morphometric descriptors.

This study is the first of a series of analyses designed at developing more definitive standards that could be used to improve the identification of wild and domestic forms in the zooarchaeological record. Accuracy of classification and detailed quantitative descriptions of morphometric differences are fundamental for a better understanding of animal domestication history and the often subtle patterns of variation and covariation produced by human-induced selection over millennia.

2. Material

A total of 972 teeth were analyzed, including 327 upper M2, 163 upper M3, 311 lower M2 and 171 lower M3 (Table 1). The geographic range of wild boar specimens in our samples covers the entire West Palaeartic (i.e. North Africa, Western and Eastern Europe, Russia and Near East, see more details in Supplementary Table 1), whilst domestic pigs represent eleven different modern European breeds (Supplementary Table 1). Due to a complex history of pig domestication, including local domestications and population replacements (Larson et al., 2005, 2007), we focused only on the overall signature of domestication (i.e. differences between wild and domestic pigs). Teeth were measured unilaterally, preferentially from the right side. Third molars erupt later than the second molars (Bull and Payne, 1982), which explains the smaller number of M3 in our dataset. Our samples include adults only (older than 12–14 months), both males and females. Since the sex of archaeological *S. scrofa* specimens is often difficult to

Table 1
Sample sizes for wild and domestic pigs per tooth with the ratio between the numbers of wild boars and domestic pigs.

	UpperM2	UpperM3	LowerM2	LowerM3
Wild	268	123	258	129
Domestic	59	40	53	42
Total	327	163	311	171
Domestic/wild	0.18	0.25	0.17	0.25