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The zooarchaeological application of quantifying cranial shape differences in wild boar and domestic pigs (*Sus scrofa*) using 3D geometric morphometrics



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ABSTRACT

The process of domestication increases the variety of phenotypes expressed in animals. Zooarchaeologists have attempted to study these changes osteologically in their search for the geographic and temporal origins of initial animal domestication during the late Pleistocene and early Holocene. Traditional biometric approaches have explored broad changes in body size over time, but this approach provides poor resolution. Here we investigate whether geometric morphometric (GMM) analyses of cranial shape can be used to provide better resolution between wild and domestic pigs (*Sus scrofa*), since shape is less affected by environmental factors than size. GMM combined with traditional multivariate statistics were applied to the crania of 42 modern domestic pigs (representing 6 breeds), 10 wild × domestic first generation hybrid pigs and 55 adult wild boar. Further analyses were carried out on morphologically discrete portions of the crania to simulate the fragmented nature of archaeological mammal remains. We found highly significant discrimination between wild and domestic pigs, both on the whole crania, and subsets including the parietal, the basicranium, the angle of the nasal and the zygomatic. We also demonstrate that it is possible to discriminate different domestic breeds on the basis of cranial morphology, and that 1st generation hybrid wild × domestic pig morphology more closely resembles wild pigs than domestic, suggesting that a wild phenotype (here represented by morphology) is dominant over a recessive domestic one. Our data demonstrate that GMM techniques can provide a quantifiable, clear classification between wild and domestic *Sus* (even using partial cranial remains) which has significant implications for zooarchaeological research.

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1. Introduction

A key part in the transition of human subsistence strategies from hunting and foraging to farming was the domestication of plants and animals during the early Neolithic. Studies of this transition includes locating and analysing the origins of animal domestication (Rowley-Conwy et al., 2012), which requires the ability to reliably

identify between the wild and domestic remains of the same species. The morphological determination of wild vs. domestic relies upon the presence of derived or altered characters in the domestic forms relative to their wild ancestors. The traditional methodology of wild-domestic assignment in the archaeozoological record is largely based on size reduction of either dental or skeletal elements in early domesticated animals (e.g. Albarella, 2002; Eryvnck et al., 2001; Mayer et al., 1998; Payne and Bull, 1988; von den Driesch, 1976). Yet, there is a major issue with this assumption in that size is affected by both genetic and epigenetic factors such as temperature, climate, diet, sexual dimorphism and individual variation (Vigne et al., 2005). Climatic and environmental conditions

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(especially precipitation) have a significant impact on body size, as moisture is linked to primary productivity and food availability (Cardini and Elton, 2009; Meiri and Dayan, 2003). Thus comparative morphology can only be informative of the wild or domestic status of animals in the past if the issues associated with size are controlled. For example, the effects of climatic variation can be overcome by comparing samples from similar habitats and with adequate temporal sequences (to eliminate the effect of climate change over time). Such corrections are subject to the availability of well-dated, large zooarchaeological datasets and relevant climatic data, the dearth of which often precludes inter-regional comparisons (Rowley-Conwy et al., 2012). Alternatively, methodologies that study shape instead of size – e.g. Geometric Morphometrics (GMM) – can provide an approach that is less affected by such biases (Vigne et al., 2005; Evin et al., in press). Shape is determined more by genetically inherited traits and less by environment or diet, and is thus more informative than size if studied in a multivariate statistical environment (Zelditch et al., 2004).

The morphological changes caused by domestication have been well documented (e.g. Clutton-Brock, 1988). Darwin, in his two part volume dedicated to the evolution of domestic species (and the differences between them and their wild progenitors) was the first to note that virtually all domesticated animals had undergone similar phenotypic and physiological changes (Darwin, 1868). These include the appearance of dwarf or giant varieties, piebald colouring, curly hair, shortened or rolled tails, floppy ears and changes in the reproductive cycle of most domesticated species (Trut, 1999). Changes also include proposed 'paedomorphic' characters of the crania, expressed as snout shortening and increased concavity of the face, braincase reduction, tooth crowding and tooth length reduction, which can be linked to overall size reduction in many species, including pigs and dogs (Clutton-Brock, 1988; Coppinger et al., 1987; Moray, 1992, 1994; Zeder, 2012).

The causal mechanisms of morphological change brought about by domestication are poorly understood. Some of the modifications may result from hormonal changes due to environmental conditions and the stress of captivity, i.e. without human intent (Arbuckle, 2005; Künzl et al., 2003). Others may stem from epigenetic/developmental changes, or as expressions of genetic mutations directly selected for by humans (Price, 1984, 1999; Vigne, 2011). Experimental data suggest that morphological changes may be triggered by selection along developmental pathways that control the physiological systems responsible for reduced aggressiveness (Arbuckle, 2005; Trut, 1999; Zeder, 2012). This has been demonstrated in a breeding experiment of silver foxes (*Vulpes vulpes*) (Belyaev, 1969, 1979), where selection was solely based on reduced aggression towards their human handlers (Trut, 1999). The experiment produced a suite of phenotypic changes commonly found in domestic animals within 8–10 generations (Trut, 1999). Rapid development of the domestic phenotype has been explained by the process of heterochrony – alterations in the rate of development (Gould, 1977; Hare et al., 2012), and suggestions that domestication may have accelerated the attainment of sexual maturity (Price, 1999). However, the traditional methodology used to test for heterochrony has recently been challenged (Mitteroecker et al., 2005) and the theory that dogs (*Canis lupus*) are paedomorphic wolves rejected (Drake, 2011). Despite the uncertainty about the root causes of morphological change in domestic animals, the point stands that wild and domestic animals can be distinguished by their morphology.

The changes seen in domestic animals resulted in a diversification of morphologies far beyond that which exists in the wild (Drake and Klingenberg, 2010), with many of these morphologies (recognised today as domestic breeds) created through intense

artificial selection. Selective breeding to 'improve' domestic stock and promote desired traits has a long history, that most certainly goes back well before the agricultural revolution of the 18th century (Davis et al., 2012), a time traditionally associated with the appearance of most modern improved livestock breeds. However, the origin of other (more traditional) or so-called 'rare breeds' remain unknown. Although early evidence for deliberate (human-induced) stock improvement has relied upon changes in the size of their excavated skeletal remains (Davis, 2008), this approach suffers from the same problems as using simple changes in the size of teeth and bones to determine the wild-domestic status of zooarchaeological remains.

To quantify the differences between wild and domestic cranial morphologies, and further explore the effect of hybridisation and breed variation, we applied a three dimensional landmark based Geometric Morphometric approach to pig crania. Pigs were chosen for this study as they have been an important resource throughout human history, and remain a major global food source and of central importance to the development of human societies across the world. They were one of the earliest livestock species to be domesticated, and unlike some other major domesticates (e.g. cattle) their wild progenitor still exists in abundance in the wild (Vigne, 2011). The evolution of pig morphology and behaviour in response to domestication, and the co-adaptation of pigs and humans, has also been intensively studied (Clutton-Brock, 1988; Price, 1984; Rosenberg and Redding, 1998; Scandura et al., 2011; Vigne, 2011; Zeder, 2006, 2012; Zeuner, 1963). We focused specifically on crania, since they have a noted response to domestication (Darwin, 1868) and have been used as a proxy for reconstructing body size in studies of other mammals (Cardini et al., 2007).

This principal aims of this study were to (1) determine whether, and how accurately, cranial morphology can be used to distinguish between wild and domestic pigs; (2) analyse specific regions of the skull, and quantify differences in morphology between wild and domestic pigs, in order to replicate the effects of taphonomic processes bones are subjected to in the archaeological record (e.g. breaking or abrasion (Lyman, 1994)); (3) investigate whether hybrid wild × domestic (Tamworth) pigs are morphologically distinct from wild or domestic pigs – the presence of hybrids often proves confounding to the determination of wild/domestic status in the archaeological record when analysed using size alone (Rowley-Conwy et al., 2012) so we assessed whether a shape-based approach could provide better discrimination; (4) determine whether it is possible to distinguish different domestic pig breeds on the basis of cranial morphology.

2. Materials

Our dataset consisted of 52 recent domestic and 58 wild adult (>18 months) *Sus scrofa* crania. The domestic pigs were recorded in the "Julius Kühn" Museum für Haustierkunde in Halle, East Germany where they were born, bred and slaughtered. The wild boar crania are located in the Natural History Museum in Berlin and derive from *S. scrofa* populations inhabiting the Białowiecki national park in East Poland, or the vicinity of Nysa, South-West Poland. We chose wild specimens from a limited region to reduce the confounding effects of geographic and climatic induced morphological variation that is known to exist in *Sus* (Albarella et al., 2009; Groves, 1981). The domestic *S. scrofa* specimen breeds were Berkshire (5), Cornwall (8), Tamworth (5), Veredeltes Landschwein (13), Hannover–Braunschweig Landschwein (3) and Deutsches Edelschwein (8), as well as a small sample (10) of first generation Tamworth × Wild pig hybrids (domestic sows bred with wild boars).

2.1. Issues with modern proxies

Using modern pigs as proxies for past pig populations could introduce additional sources of error, which must be accounted for if the results are to be applicable to the archaeological record. In this context the possible recent introgression of Asian pig breeds into European pig breeds must be considered. To minimise this effect, we used older established breeds that are thought to have been subject to less improvement (intensive breeding) (Porter, 1993). Theoretically error could be introduced through interbreeding between wild and domestic animals, contaminating the modern wild sample. However, recent DNA studies have suggested that the amount of Asian DNA from improved modern domesticates is negligible in European wild boar (Scandura et al., 2011).

2.2. Methods

Forty-four unilateral three-dimensional landmark coordinates (Fig. 1 and Supplementary Table S1) were digitised from the right side of the cranium, using a Microscribe® GLS (Microscribe Inc), by the first author, and analysed using Geometric Morphometric methods (Bookstein, 1991; O'Higgins, 2000; Mitteroecker and Gunz, 2009). Specimens were standardised (scaled, transposed and rotated) using a Generalised Procrustes Analysis (GPA) superimposition (Rohlf, 2003; Zelditch et al., 2004). A separate GPA was conducted for each separate dataset (e.g. Wild vs. Domestic and domestic breed datasets). Although GPA standardises size, size can be reintroduced into the analysis as Centroid Size (CS), where CS is a geometric scale defined as the square root of the sum of squared distances between all landmarks and the configurations centroid (Zelditch et al., 2004). Differences in CS between sample groups were assessed using one-way ANOVA in Morphoj (Klingenberg, 2011). GPA does not completely remove the effect of size, as allometry, the relationship between size and shape,

remains. To test for the presence of allometries, a multivariate regression of cranial shape against log centroid size on pooled within-group variation was conducted on the wild and domestic samples using Morphoj, both for the complete sample and for the main individual principle components (those comprising more than 1% of the total variation of the sample). Allometry free shape was investigated by conducting a Principal Components Analysis (PCA) on the regression residuals of a multivariate regression of cranial shape against log centroid size on pooled within group variation, also conducted using the Morphoj software. GPA was conducted in either the Morphoj software (Klingenberg, 2011) or R (version 2.15.2 R Development Core Team) for each analysis as noted below.

PCA was used for initial data exploration of morphological relationships between individuals and their respective groups (in Morphoj). The morphological differences between group means in the initial PCA were visualised using a 3D surface scan morphed to different landmark configurations using the (EVAN Toolbox, 2010). The surface scan was taken from a wild adult male *S. scrofa* specimen held in the Durham University collections, using a non-contact Konica Minolta Digitiser (v-910).

Significance of differences in shape between groups – including wild vs. domestic and between domestic breeds – was assessed using a procrustes Analysis of Variance (ANOVA) in Morphoj (analogous to a MANOVA) and Canonical Variates Analysis (CVA) with 10,000 permutations, following a separate GPA fit for each analysis (Klingenberg, 2011). Discriminant functions (DF) with leave-one-out cross-validation were applied to the principal component scores to assess the discriminatory power of shape and size differences between groups. Differences between the extreme ends of the discriminant function were visualised using wireframes, and the distribution of the discriminant functions shown with histograms (using R).

To avoid the dangers of over-fitting data (Kovarovic et al., 2011) – caused by small sample size and a high number of variables – a dimensionality reduction method was used for analysis following the methodology set out in Evin et al. (2013) (see also Baylac and Friess, 2005) in R. This reduces the number of predictors by replacing the original shape variables with PC scores. By using only a limited sub-set of PCs, the number of predictors can be reduced to below that of the number of individuals within the dataset. We chose the number of PCs by iteratively selecting a number of PCs and exploring whether adding or removing variables affect classification scores, attempting to attain the minimum number of PCs with at least 95% of the total variance within the dataset. We settled on 30 PCs as the most parsimonious number. Additionally, all DF and CVA were accompanied by leave-one-out-cross-validation and permutation tests respectively. Despite this caution, it should be noted that the number of variables is still larger than the sample size of the smallest group – a trait regarded as desirable for robust results (Kovarovic et al., 2011). As such, the data presented here should be regarded with caution and as preliminary until a larger dataset can be obtained and analysed.

The dataset was further broken down into smaller subsets of landmarks (Fig. 1 and Supplementary Table S2), chosen to represent specific regions of the skull in order to determine areas of maximum discrimination that could then be applied to fragmentary archaeological material. These were 1. the parietal; 2. the zygomatic; 3. the angle of the nasal; 4. the orbit; 5. the tooth row and 6. the basicranium (numbers refer to those in Fig. 1). The skull regions were chosen on their likely ability to distinguish between wild and domestic *Sus* and their frequent preservation in the archaeological record. Sub-sets of landmarks were analysed following the same steps as for the whole crania, with separate GPA fits for each individual analysis.

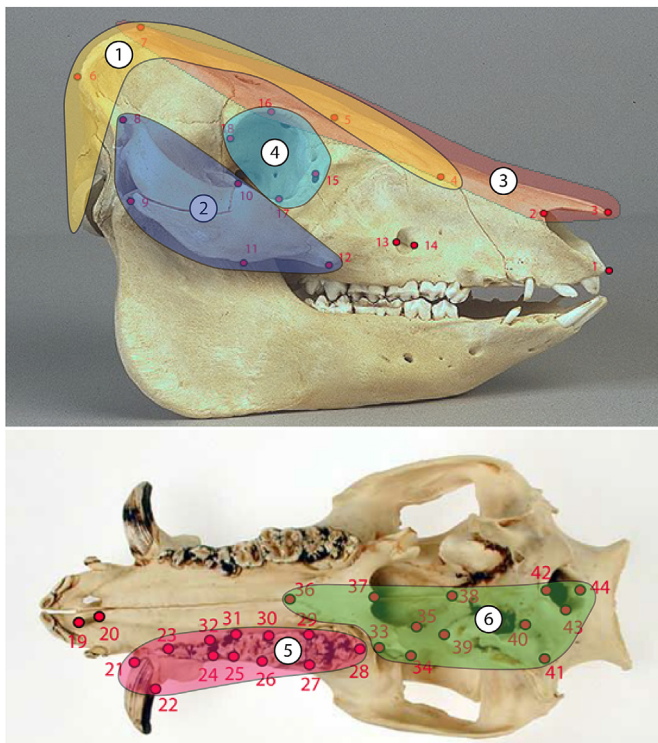


Fig. 1. Illustration showing the position of landmarks and the sub-set regions of the crania.

2.3. Measurement error and sexual dimorphism

Possible effects of inter-observer error were tested with repeated digitisation following the methodology of O'Higgins and Jones (1998) and found to be insignificant.

The dataset was tested for the effect of sexual dimorphism, both in the wild and domestic pig samples, and in the pooled sample containing both wild and domestic pigs. Sexual dimorphism was found to be not significant in wild boar, both for centroid size ($p = 0.71$, $df = 1$, $F = 0.14$), or shape ($p = 0.27$, $df = 125$, $F = 1.07$), but was significant in domestic pigs (size $p = 0.004$, $df = 1$, $F = 9.11$, shape $p \leq 0.001$, $df = 125$, $F = 2.5$). For the pooled sample of wild and domestic pigs, there was no sexual dimorphism in size ($p = 0.37$, $df = 1$, $F = 0.83$), but there was in shape ($p \leq 0.001$, $df = 125$, $F = 5.07$). Due to the small sample sizes available, we conflated males and females into a single sample – being aware that sexual dimorphism in the domestic sample could potentially be a source of bias. However, mixing the male and female groups replicates conditions found when analysing archaeological material, as it is difficult to assess the sex of pigs, especially in the absence of canines (von den Driesch, 1976; Payne and Bull, 1988; Mayer and Brisbin, 1988).

3. Results

3.1. Size differences between wild vs. domestic *S. scrofa*

There are small, but statistically significant cranial size differences between the wild and domestic samples (ANOVA $p = 0.035$, $df = 1$, $F = 4.49$). Size differences can be seen in Fig. 2, which shows that wild pigs are often larger than domestic pigs, but also that the size ranges of the wild and domestic samples overlap and the median centroid size of the wild sample is similar to the domestic sample. The Tamworth \times Wild cross-breed is similar in size to the

mean of the Wild, Tamworth and Hannover–Braunschweig Land-schwein specimens. Multivariate regression of complete cranial shape against log CS revealed only a weak relationship (7.7% of total shape variation explained, $p \leq 0.01$).

Discrimination between wild and domestic pigs on the basis of size, using discriminant functions with leave-one-out cross validations, returned low cross-validation scores (Table 1). When compared with partial skull analyses, the whole crania and basi-cranium had the highest proportion of correctly assigned individuals at 72.2%, followed by the zygomatic (62.9%), and the remaining cranial sub-sets returning scores around the random mark of 50%.

3.2. Shape differences between wild vs. domestic *S. scrofa*

Principal components analysis of the complete skull (Fig. 3) shows a clear structuring of individual variation, with no overlap between wild and domestic *Sus* on PC1 (68.6% of total variance). Wild boar scored positively on PC1, while domestic pigs scored negatively. The sample of Tamworth \times Wild crosses overlap with the wild boar group on all PCs, although they score slightly more negatively on PC1 than the majority of the wild boar.

The morphological changes explained by PC1, and subsequently those that separate domestic from wild boar include a relative straightening of the snout, an elongation of the parietal and a more slender zygomatic in wild boar. Increasing scores on PC2 (7.1% of variance) show a shortening of the palate, an increase in the overall size of the orbit and a slight increase in the angle of the slope of the parietal. A Procrustes ANOVA on shape differences between wild and domestic individuals confirm that there are significant differences between them ($p \leq 0.0001$, $df = 125$, $F = 144.0$). Discriminant functions with leave-one-out cross-validations, correctly classified 100% of domestic and wild specimens (Table 1).

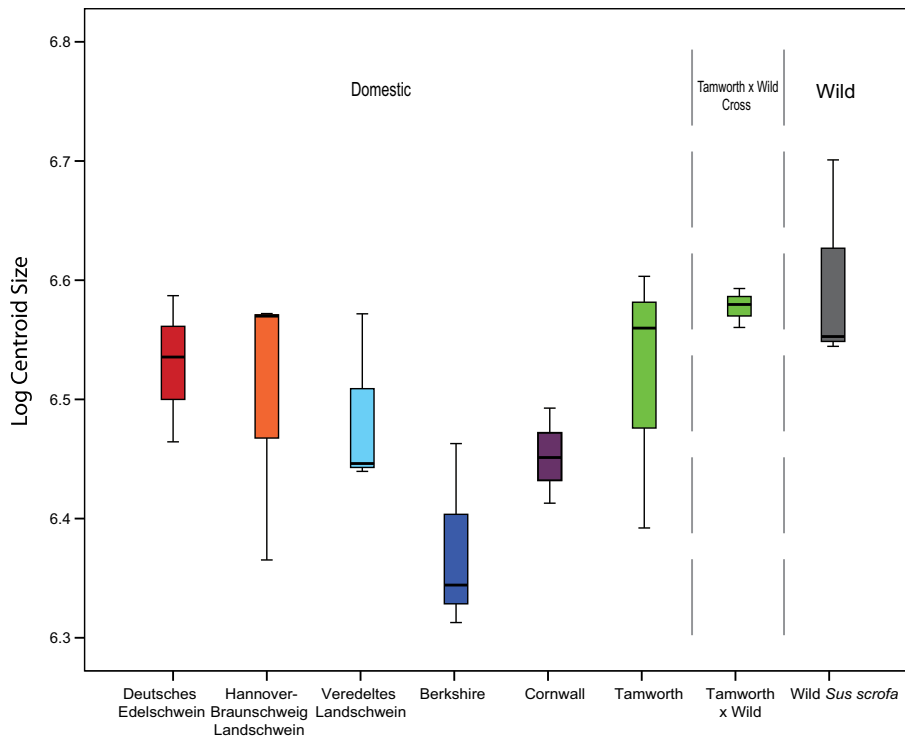


Fig. 2. Box plot showing centroid sizes of domestic breeds, wild-domestic cross breeds and wild pigs. Boxes show the median and 50% of the population, with the tails and whiskers showing the upper and lower 25%. The colours refer to breed, or wild/domestic status, and are the same as in Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Cross validation percentages of discriminant functions between wild and domestic pigs. Showing results for the whole and partial crania, and for both shape and size. Rows show the region of the crania investigated. Columns detail number of landmarks associated with each region, the total correctly assigned cross validation percentages (CVP) based on shape, and number of principal components used in the discriminate function (nComp); followed by the correctly assigned percentages of domestic (DP) and wild (WB) pigs. The results for discriminant functions based on size follow the same layout.

| Region of crania | Number of landmarks | nComp | Shape | | | Size (centroid size) | | |
|------------------|---------------------|-------|---------|-------------------------|-------------------------|----------------------|-------------------------|-------------------------|
| | | | CVP (%) | % Correctly assigned DP | % Correctly assigned WB | CVP (%) | % Correctly assigned DP | % Correctly assigned WB |
| Whole cranium | 44 | 20 | 100 | 100 | 100 | 72.2 | 66.7 | 76.4 |
| Parietal | 5 | 5 | 97.94 | 95.2 | 100 | 43.3 | 0 | 100 |
| Nasal | 6 | 6 | 97.94 | 95.2 | 100 | 50.5 | 14.3 | 78.2 |
| Orbit | 4 | 4 | 88.66 | 78.6 | 100 | 52.6 | 31 | 69.1 |
| Zygomatic | 5 | 4 | 97.94 | 95.2 | 100 | 62.9 | 47.6 | 74.6 |
| Tooth Row | 12 | 17 | 87.63 | 85.7 | 89 | 48.5 | 2.38 | 83.6 |
| Basicranium | 9 | 12 | 100 | 100 | 100 | 72.2 | 66.7 | 76.4 |

The cranial sub-sets also demonstrate significant differences between wild and domestic *Sus* morphology. Table 1 shows the results of discriminant functions, with leave-one-out cross validation. The parietal (98% correct classification), nasal (98% correct), zygomatic (98% correct) and basicranium (100% correct) all returned excellent discriminant scores. The orbit (89%) and tooth row (88%) returned lower scores. Closer examination of the results revealed that wild boar was more likely to be correctly assigned than domestic pigs. The results of the discriminant functions are shown in the histograms of Fig. 4 and the associated shape changes shown by the wireframes. In wild pigs the parietal is swept backwards at an acute angle, whereas in domestics the angle is wider. The nasal region is deeply concave in domestic pigs and flat in the wild boar, whilst the zygomatic is considerably wider and more robust in domestics. On the basicranium, the positions of notable protuberances (i.e. the pterygoid bone and the tympanic bulla) are more crowded together in domestic pigs than in wild boar.

The results in Table 1 and Fig. 4 demonstrate that both whole and partial crania can be used to discriminate between wild and domestic pig morphologies. The strength of discrimination varies slightly, with the basicranium, parietal, zygomatic and angle of the nasal bone

giving best results. The orbit and tooth row, whilst correctly assigning most of the wild individuals, misclassify many domestic individuals and are less reliable indicators of domestic status.

3.3. Allometry

Multivariate regressions of log CS against the first seven PC's (see Supplementary Table S3) – from the PCA of the complete skull (those explaining more than 1% of total variance) – shows that PC1 has no significant relationship between size and shape (1.1% of total shape variation explained, $p = 0.28$), that PC2 has highly significant allometry (74% of total shape variation explained, $p \leq 0.001$), PC3 (9.2% of total shape variation explained, $p = 0.001$) and that subsequent PCs have insignificant proportions of variation explained by allometry.

Examination of non-allometric shape space through PCA (Supplementary Fig. 1) shows that there is little difference between it and allometric shape space. There is a clear separation of wild and domestic pigs on PC1 (72.4% total variance), with wild pigs scoring more positively and the domestic pigs more negatively. The Tamworth \times Wild specimens overlap with the wild pigs on all PCs. When these results are combined with the investigation of log CS on

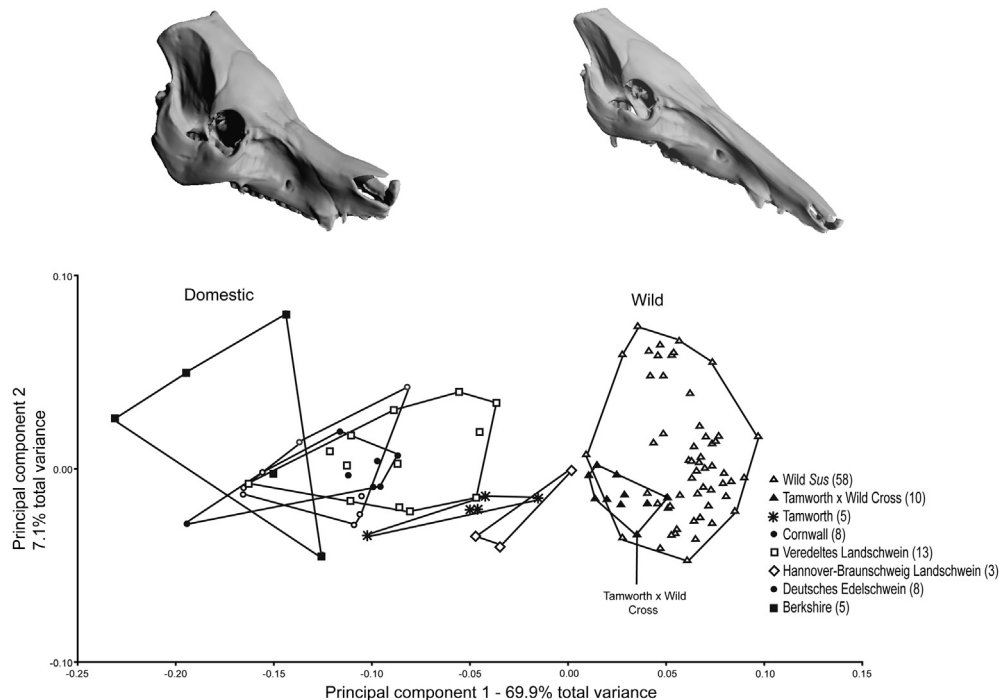


Fig. 3. PCA of full crania: PC1 (69.9% of total variance) vs. PC2 (7.1% of total variance). Visualisations show a surface scan warped to the mean shape configuration of domestic and wild *Sus*.

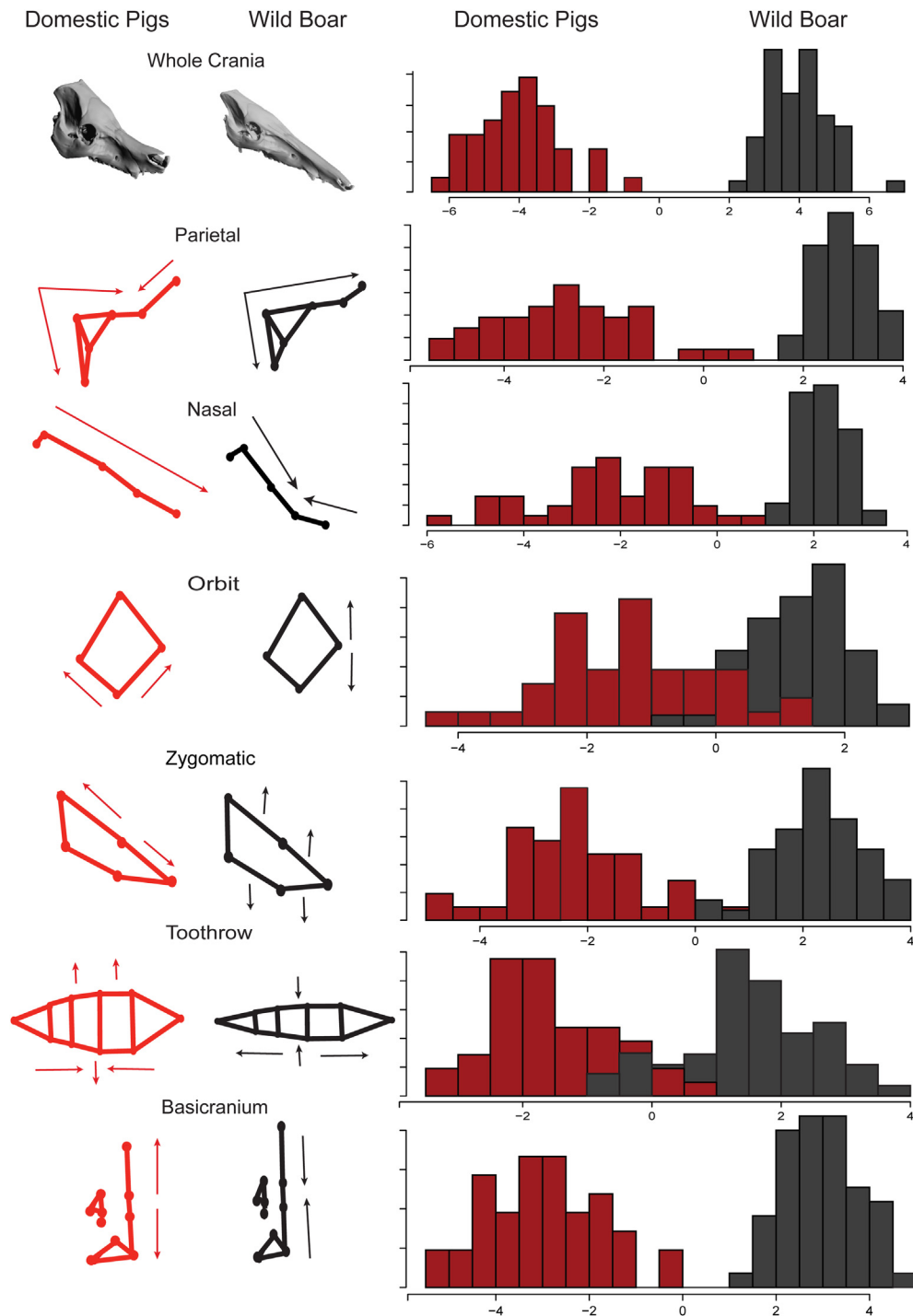


Fig. 4. Histograms of the linear discriminant analysis values computed between wild (grey) and domestic (red) pigs, for both the complete crania and the partial cranial subsets. The y-axis shows the frequency and the x-axis the discriminant function score. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

individual PCs, they show that there are significant allometries within the dataset (e.g. PC2). However, these allometries are not driving the morphological differences between wild and domestic pigs, which is described by PC1 in both allometric and non-allometric shape space.

3.4. Shape and size differences between domestic *S. scrofa* breeds

There are significant differences between domestic breeds in both shape (procrustes ANOVA $df = 750$, $F = 10.32$, $p \leq 0.0001$) and

size (ANOVA $df = 6$, $F = 6.53$, $p \leq 0.0001$). In a discriminant function analysis – with leave-one-out cross validation – the majority of pigs were correctly assigned to breed (Table 2). CVA on only the domestic breeds (after a separate GPA) shows that there are significant differences between the breeds (Supplementary Fig. S2, and Supplementary Tables 4–7) with the exception of Hannover–Braunschweig Landschwein and Tamworth pigs, a result that must be treated with caution because of the very small number of Hannover–Braunschweig Landschwein specimens (3).

Table 2

Cross validation percentage scores from discriminant functions with leave-one-out cross validation between domestic breeds and wild pigs. Bold values show the percentage correctly assigned to each group. The table should be read from left to right for correct interpretation. Note that the Hannover–Braunschweig sample was omitted from this analysis due to small sample size.

| | Berkshire | Cornwall | Edelschwein | Tamworth–Cross | Tamworth | Veredeltes | Wild |
|------------------------|-----------|-------------|-------------|----------------|-----------|-------------|-----------|
| Berkshire | 80 | 20 | – | – | – | – | – |
| Cornwall | – | 87.5 | – | – | – | 12.5 | – |
| Edelschwein | – | 12.5 | 75 | – | – | 12.5 | – |
| Tamworth–Cross | – | – | – | 90 | – | – | 10 |
| Tamworth | – | – | – | – | 80 | – | 20 |
| Veredeltes Landschwein | – | 7.7 | 7.7 | – | – | 84.6 | – |
| Wild | – | – | – | 3 | 1 | – | 96 |

These results suggest that, although the cranial morphologies of domesticated pig breeds may appear similar, they are specific enough to allow statistical discrimination between them. However, due to the small number of individuals within the domestic pig groups, these results should be treated as preliminary until further analyses can be conducted with a larger sample size.

3.5. Hybrid wild-Tamworth *S. scrofa*

The majority (9) of the wild domestic hybrids were correctly re-assigned to group (Table 2), with the single misclassified individual assigned to wild boar, suggesting that the hybrid morphology is distinct from both wild and domestic forms. However, with the misclassified individual assigned to the wild group, and the position of the hybrid group in the PCA of Fig. 3 lying close to the wild population, it can be posited that this population of first generation wild Tamworth pigs has a cranial morphology that is dominated by the ancestral wild parentage and not the domestic one.

4. Discussion

Wild and domestic pig crania have distinct, quantifiable morphologies. Wild pig crania are more slender, with straighter snouts, whilst domestic pigs have deeply concave snouts and are relatively more robust. Our results show that these morphological differences have very good discrimination power, demonstrating that wild and domestic pigs can be identified with a considerable degree of confidence on the basis of cranial morphology. These results both contrast with and supplement the more traditional biometric techniques and approaches used in zooarchaeology. Application of GMM provides much greater resolution than traditional biometry, with well-supported and statistically quantifiable results. In addition we have shown that GMM can be used to differentiate between some modern pig breeds, which could have significant impact in the study of the origins of domestic animal breeds, and the development of breed improvement in the past.

4.1. Partial crania

Few complete crania are recovered from archaeological sites, especially in taxa bred or hunted for human consumption. Dividing the crania into separate components allows us to simulate (to some degree at least) the effects of ante-, peri- and post-mortem taphonomic processes. Our study shows the parietal, nasal, zygomatic and basicranium provide particularly good discrimination between wild and domestic *Sus*. That these areas of the skull exhibit a strong domestic signal compared to other regions (e.g. the orbit, tooth row), suggests that physical stresses focused upon specific areas of the crania are important in forming specific domestic morphotypes. These results also suggest that discriminating between wild

and domestic morphologies can be achieved in fragmented archaeological assemblages.

4.2. Explaining changes seen in the domestic morphology

Artificial selection, through intensification in breeding and direct selection for specific characters, has produced a far wider variety of morphotypes in domestic animals than exists in their wild progenitor. For example variation in the cranial shape of dogs is comparable to, or exceeds that of the entire order Carnivora (Drake and Klingenberg, 2010). Domestication has also resulted in unintentional changes to both phenotype and behaviour, through modified natural selection in the captive environment and relaxation of selective pressures essential to survival in the wild, which in turn may be linked to possible changes in the rate and/or pattern of growth during ontogeny (Price, 1999).

It is possible that some changes in cranial morphology between wild and domestic *Sus* may be caused by biomechanical stress. Increased muscle activity results in increased robusticity in areas of attachment. Following Wolff's Law, bone will remodel in response to stress loads placed upon it (Dinu, 2009; Wolff, 1986; O'Regan and Kitchener, 2005). Changes in diet affect the muscles associated with mastication, including the masseter, the temporalis and the pterygoid, in turn affecting the morphology of the parietal fossa, nuchal crest and zygomatic, which we have shown to be more robust in domestic pigs than wild boar. Thus if domestic pigs have a different diet to wild boar, one that requires more physical processing, it perhaps explains the morphological changes we have identified.

Changes in behaviour, specifically increases in rooting behaviour, would also affect cranial morphology. Pigs root for buried food such as roots, tubers and truffles (Sack, 1982). They have a highly developed sense of smell, and a hyper-mobile nasal plate and rostrum with robust muscles (the levator nasolabialis, levator labii superioris, and depressor labii superioris) for manipulating the rostrum (Groves, 1981; Sack, 1982; Sisson and Grossman, 1910). Increased rooting would likely develop the muscles in the nasal and the neck (trapezius) regions, exerting greater stress on these points of attachment and modifying their morphology in ways which could also explain the changes observed in the angles of the parietal and nasal. Biomechanical effects on cranial shape do not preclude genetic or other reasons (e.g. stress response, heterochrony) for morphological change, but are additional factors that need to be considered when explaining changing morphology during domestication.

4.3. Cross-bred wild-domestic *S. scrofa*

One aspect of this study that requires further discussion is the inclusion of first generation wild (male) × domestic (female) cross breeds. These specimens derive from the early stages of the Halle museum breeding experiments (early 20th century) and not all the

details of their provenance are known, only that they are wild boar crossed with domestic (Tamworth) pigs that were bred at Halle. The cross-breeds morphological similarity to their wild form parentage implies that inherited characteristics from the wild males are dominant over recessive domestic inherited characteristics from the females. That this occurred while the hybrids were raised in the same conditions as their domestic mothers suggest that the domestic morphotype is more dependent on genotype than environment. Whether this would be the case if the parentage were reversed is not known.

Rapid reversal of domestic morphotypes has been identified in the genetically inherited coat colour gene, MC1R (Fang et al., 2009), where coat colour is the product of strong positive selection in captivity that quickly reverts to the original wild colour once this selective pressure is removed. Conversely, studies of feral animals have suggested that domestic morphologies (such as brain size reduction and coat colouration) remain even once the selective pressures of domestication are removed (Kruska and Röhrs, 1974; Rowley-Conwy and Dobney, 2007; O'Regan and Kitchener, 2005; Zeder, 2012). Thus it is inconclusive whether the causal factor in the retention of a domestic phenotype is environmental pressure or the continuation of inherited traits, but studies of feral, and hybrid wild and domestic animals could prove to be productive avenues of future study.

5. Conclusion

Four conclusions can be drawn from our results: (1) cranial morphology can be used to discriminate between wild and domestic *S. scrofa*, which is true for both whole and (2) partial crania, as the parietal, zygomatic, angle of the nasal and the basicranium returned excellent discriminant values. (3) Hybrid offspring of wild and domestic pigs can be identified through their morphology and (4) that some domestic pig breeds have distinct cranial morphologies. Prudence should be exercised with these results due to the small sample sizes involved. Although this is a problem not unique to GMM studies, it does present an additional challenge because of the high dimensionality of the data involved. However, with adequate precautions GMM studies can at least partially negate these problems and deliver robust results.

This proof of concept study, showing that GMM can be used to discriminate between wild, domestic and hybrid *Sus* crania has significant implications for the field of zooarchaeological research in further exploring the domestication process and refining our ability to establish the proportion of wild and domestic animals from archaeological sites. Additionally, the non-destructive nature of GMM data gathering is attractive where rare specimens are involved, or where ancient biomolecules do not survive. There have been a number of recent successful applications of GMM to archaeological and fossil animals remains, (Cucchi et al., 2011; Dobney et al., 2008; Evin et al., 2013; Bignon et al., 2005; Curran, 2012) where the resolution it affords is providing new ways resolving old questions and exploring new ones.

Based on our preliminary results, GMM can also be used to distinguish between domestic varieties/breeds which has important consequences for the study of livestock improvement and intentional selection, where past breed improvement, for e.g. traction or increased meat yield, will be better reflected in morphology than simply in size. Targeted application of GMM to the archaeological record could potentially trace breed evolution and development back to its origins.

Geometric morphometrics is a rapidly evolving and important tool in the study of human origins (Harvati et al., 2004; O'Higgins, 2000) and variation (Viðarsdóttir et al., 2002), and in the study of evolution and development (Lawing and Polly, 2010). Archaeology

has been slow in the uptake and application of this important tool, but as has been shown with recent work (Cucchi et al., 2009; Dobney et al., 2008; Evin et al., 2013; Larson et al., 2007), GMM can provide complex insights into the processes, evolution and history of animal domestication and improvement.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jas.2013.12.010>.

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