Morphological Variation in Wild and Domestic Suids

JOSEPH THOMAS DAVID OWEN

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Joseph Thomas David Owen

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Department of Anthropology
Department of Archaeology
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Table of Contents

List of Figures

List of Tables

Declaration

All work submitted within this thesis was conducted and written by the author, with the following exceptions. The analysis of the mode of evolution in manuscript 2, which was jointly conducted by the author and Prof. P.David Polly (University of Illinois), and the computation of angles between regression trajectories in manuscript 4, which was collaborative work between the author and Prof. Kieran McNulty (University of Minnesota).

Statement of Copyright

Acknowledgements

'The time has come,' the Walrus said,
'To talk of many things:
Of shoes - and ships - and sealing wax -
Of cabbages - and kings -
And why the sea is boiling hot -
And whether pigs have wings.'

(Lewis Carroll – 1871)

It is a pleasure to thank the many, many people who made this thesis possible.

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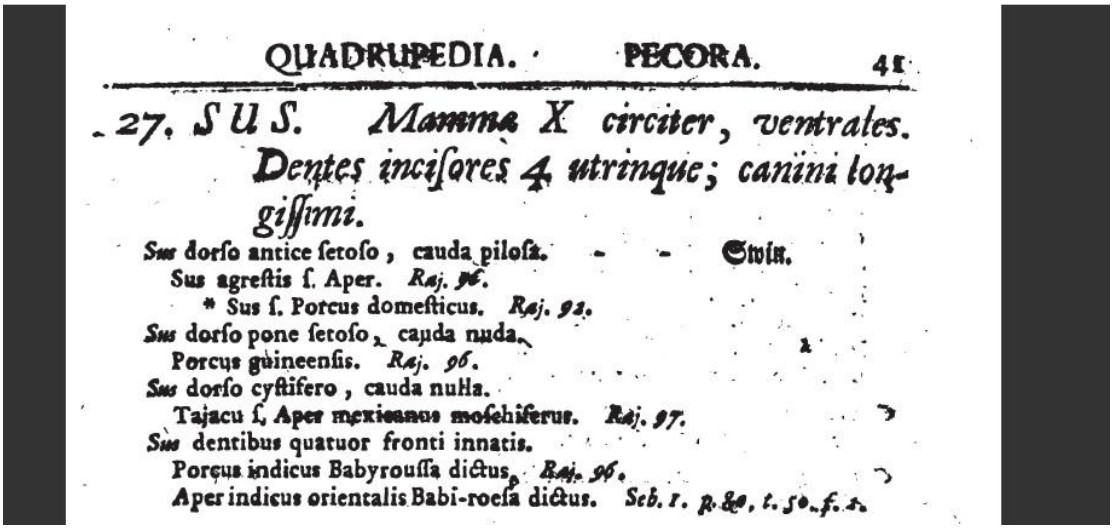
Morphological Variation in Wild and Domestic Suids

1.1 Introduction

Pigs occupy a special place in the human psyche. They are kept both as stock domesticates, like cattle and sheep, and they are treated as companions and aids, like cats and dogs. There are currently nearly two billion (c.1,984,607,000) domesticated pigs in the world kept as stock animals bred for slaughter (Foreign Agricultural Service (FAS), 2012). Keeping pigs as pets has become increasingly popular in western society in recent years and commensalism with pigs is a long-held tradition in Island South East Asia (McDonald-Brown, 2009). Pigs are a key economic resource; however, they are also an animal that inspires strong emotions of attachment or revulsion; seen as loyal, intelligent, courageous and resourceful or unclean, licentious, gluttonous and ignorant (Albarella et al., 2007, Phillips, 2007). As such pigs and pig products are extensively referenced in classical literature and modern pop culture; examples include George Orwell's *Animal Farm*, Circe, a minor Greek goddess who transforms Odysseus' men into pigs when they feast at her table in Homer's *Odyssey*; the warthog Pumba from the movie The Lion King, Miss Piggy from The Muppets and Spiderpig in the Simpsons; pigs continued popularity is a testament to their enduring importance.

As a result of this unique dual positions of pet and produce, pigs have been intensively studied both as domestic and wild animals. The earliest studies of domestic pigs, their form and origins, come from Charles Darwin (1868) and Ludwig Rutimeyer (1860, 1864), whilst the first scientific description of wild *Sus* was by Karl Linnaeus (1740, 1758) (see figure 1).



QUADRUPEDIA. PECORA. 41

27. SUS. Mamma X circiter, ventrales. Dentes inciſores 4 utrinque; canini longiſſimi.

Sus dorſo antice ſetoſo, cauda piloſa. - - Stwin.
Sus agreſtis ſ. Aper. Raj. 96.
* Sus ſ. Porcus domeſticus. Raj. 92.
Sus dorſo pone ſetoſo, cauda nuda.
Porcus guineenſis. Raj. 96.
Sus dorſo cyſtifero, cauda nulla.
Tajacu ſ. Aper mexicanus moſchiferus. Raj. 97.
Sus dentibus quatuor fronti innatis.
Porcus indicus Babyrouſſa dictus. Raj. 96.
Aper indicus orientalis Babi-roeſa dictus. Seb. 1. p. 80, t. 50. f. 2.

Figure 1: Excerpt from Linnaeus Systema Naturae (1740: second edition)

Here I continue the investigation of the pig, particularly the evolution of wild and domestic pigs, through a geometric morphometric analysis of cranial form. Whist the original concept of this study was derived from a grant concerned with the spread of domestic pigs across Europe at the beginning of the Neolithic, this thesis encompasses wider studies. By applying geometric morphometrics to questions of suid evolution and variability and domestication, we can effect a deeper understanding of how pigs colonised Africa, how suid morphology is affected by climate and geography, that wild and domestic pig cranial morphologies are distinct enough to discriminate between. These have implications for evolutionary studies of the suid family, explaining apparent incongruence between morphological studies and genetics. There are significant implications for archaeological studies, especially those concerned with identifying the origins of domestication where inadequacies in the traditional methodology can be overcome through the application of geometric morphometrics. We also test and reject the traditional hypothesis of heterochrony as the causal mechanism for the development of the domestic morphotype.

Methodologies to test this have recently been developed for geometric morphometrics (Mitteroecker et al., 2005), but had not been applied to stock domesticates before. What is seen in suid ontogeny is not explained by the traditional language of heterochrony, nor are domestic pigs paedomorphic wild pigs. This leaves the cause of morphological changes observed during domestication unexplained, which should be a focus of future work.

1.1.1 Structure of the Thesis

This thesis addresses two main themes – biology and domestication – about which GM techniques provide a greater understanding. The thesis comprises an introduction (Chapter 1) discussing the pig-human relationships and the history and current understanding of the key themes, including taxonomy, form and distribution; and the domestication of pigs - what domestication is and how and why pigs were domesticated. Chapter 2 details the GM techniques used to analyse collection of pig cranial material. Chapters 3-6 are the in-depth applications of geometric morphometric analyses to the pig cranial samples, each representing a manuscript for publication. These are each described more fully below.

The first theme focuses on the biology of suids, examined through studies on the evolution of sub-Saharan African pigs (Chapter 3) and biogeography (Chapter 4) of the suid *Sus scrofa*. The second theme focuses on the domestication of pigs:the quantification of cranial morphology, noting differences between wild and domestic pigs (Chapter 5), and the ontogeny of domesticated pigs compared to wild pigs (Chapter 6). The four manuscripts for publication each have research aims and questions discussed in in detail:

Chapter 3 – **Resolving phylogenetic and phenotypic relationships within Suidae** (Manuscript 1)

Phenotypic trees derived from morphology often differ from independently estimated phylogenetic trees, usually as a result of convergent or parallel evolution. Within the family Suidae, there is marked incongruence between the morphologically and genetically derived relationships between the sub-Saharan African genus *Potamochoerus* and the Eurasian *Sus*. Whereas genetic analyses show the monophyly of the sub-Saharan African pigs, morphological analyses suggest that *Potamochoerus* is more closely related to *Sus* than other sub-Saharan pigs. These conflicting interpretations hamper a resolution of the systematics of the suids and confound efforts to understand their colonisation of the African continent. In order to understand the source of the conflicting topologies, we applied geometric morphometrics and multivariate statistics to 38 unilateral homologous landmarks from 471 African and Eurasian suids. We then reconstructed the ancestral node of Suidae and tested the mode of evolution. *Potamochoerus* is phylogenetically more closely related to African genera but like *Sus*, it possesses a generalist morphology and occupies the same ecological niche. This shared generalist behaviour, a direct consequence of the evolutionary history of *Potamochoerus*, is the principal reason for morphology's failure to alone reveal the monophyly of African suids.

Chapter 4 - **Pigs in space: Biogeographic variation in *Sus scrofa*** (Manuscript 2)

Pigs have one of the widest distributions of any large mammal, endemic throughout the Palaearctic and Indomalaya. Throughout this range there are recognised morphotypes that have traditionally been described as separate species, mainly on the

basis of size and morphological characteristics. These methods are also the basis of investigations into the species history, including studies of domestication. However most of these studies fail to appreciate all the sources of possible variation present within these measurements beyond sexual dimorphism. It has long been recognised that climate, latitude and longitude are linked to shape and size changes in large mammals. The impact that these variables have on suid morphology have not been systematically quantified in suids across their natural range, recent advances in shape analysis, especially in geometric morphometrics (GMM), make this possible. Here we apply GMM to 429 adult suid crania, including most genera, but concentrating on the most wide spread genus, *Sus scrofa*. Our results demonstrate that environmental and climatic variables are major sources of variation in both cranial shape and size in *Sus scrofa*, with precipitation strongly linked to size change in European pigs. The effect of environmental and geographic variables diminishes as wider geography regions and more species are included, the remaining variance increases, representing factors not tested including genetic variation that could be interpreted as speciation.

Chapter 5 - **Quantifying cranial shape differences between wild boar and domestic pigs (*Sus scrofa*) using 3D shape analysis and its application to zooarchaeology** (Manuscript 3)

The phenotypic changes caused by domestication are well known. Zooarchaeologists have attempted to study these changes osteologically in their search for the geographic origins and temporal context of the initial animal domestication during the Late Pleistocene and early Holocene. Traditional biometrical approaches have explored changes in body size over time, but give poor resolution and are adversely

affected by factors such as climate, sex, diet and disease. Here we investigate whether geometric morphometric analyses of cranial shape can be used to provide better resolution between wild and domestic pigs (*Sus scrofa*), as we know that shape is less affected by environmental factors than size. Geometric morphometric methods with traditional multivariate statistics were applied to an adult, modern pig cranial sample of 52 domestic and 142 wild pigs. Analyses were also carried out on morphologically discrete portions of the whole skull to simulate the fragmented nature of archaeological mammal remains. Highly significant discrimination was found between wild and domestic pigs from analyses of the whole skull, the parietal, the basicranium, the angle of the nasal and the zygomatic. Our data shos that geometric morphometric techniques could be successfully applied in zooarchaeology to provide a much better, quantifiable resolution between wild and domestic pigs, even on the basis of partial remains.

Chapter 6 - **Domestication and heterochrony in *Sus scrofa*** (Manuscript 4)

Domestication in animals creates a variety of morphologies and behaviours unique to itself. Traditionally these have been explained through the framework of heterochrony: changes in the rate and timing of development. For example the domestic phenotype is often described as paedomorphic, resembling the juvenile ancestral state, caused by the process of Neoteny – reduction in the rate of growth of shape, relative to growth in size. Recent advances in techniques like geometric morphometrics (GM) allow this hypothesis to be tested in a multivariate framework, which have falsified hypotheses of paedomorphism in dogs (Drake, 2011), as well as wider usage to examine cranial heterochrony in hominines and monkeys. Here we examine the theory that heterochrony is responsible for the development of the

domestic phenotype in pigs (*Sus scrofa*). We applied GM methods to three longitudinal ontogenetic series (one wild, two domestic), calculating the angles between ontogenetic trajectories and comparing morphological distances between the series at different ages. We also tested wild and domestic pigs for evidence of paedomorphism, comparing the adult descendent phenotype (six breeds of domestic pigs) to the juvenile and adult ancestral phenotype (wild pigs). We conclude that heterochrony is not sufficient to explain the domestic morphology of pigs, neither is there evidence of paedomorphism in five of the six domestic breeds tested. Thus the traditional explanation of heterochrony as the causal mechanism for the domestic phenotype is wrong, and a new explanation must be sought.

1.1.2 Pig Exploitation

Humans have a long and complex relationship with pigs, ranging from a simple hunter – prey interaction, to the central focus of a community's economy and ritual life (see 1.1.3). The following section of the thesis details some of the reasons why pigs are important to humans, and gives examples of how pigs have been perceived and relate to different societies.

Pigs are today a valuable economic resource, both as a stock domesticate and a game animal (Scandura et al., 2011), and are increasingly being kept as companion animals (McDonald-Brown, 2009). However, pig exploitation dates from before the Palaeolithic and was focused on hunting (Albarella et al., 2007). Although wild pigs are dangerous prey, capable of protecting themselves and their offspring, they represent a high calorific return on the energy expended hunting them (Rowley-Conwy et al., 2002).

As domestic animals, pigs are raised for their meat. They are fast growing, have large litters (Sack, 1982) and, provided the necessary resources – space, shade, food and water – are met, they are a valuable source of protein, particularly good for expanding populations. Unlike other domesticates, pigs have few secondary products such as milk and wool and they cannot be used for traction to pull carts and agricultural equipment.

There is no archaeological evidence of pigs being kept for companionship like cats or dogs, which is primarily a modern innovation. Evidence shows they were kept as a food resource and that their bones were worked as tools and ornaments (see figure 2

below) (Albarella et al., 2007). Modern ethnographic examples of worked pig bone include the items created by the Dani people of Irian Jaya (Hampton, 1999), who make extensive use of this medium. Pig bone knives are made from the tibia, with the cutting edges created using grindstones. These knives are used to cut or divide tubers. Bones knives are used for this task in preference to stone tools, possibly due to the ubiquity of pig bone in the Dani culture or the ease of working it. The Dani also use boar tusks (the male canine) as a scraping tool. This tool is used to smooth spear, axe and adze hafts, as well as digging sticks and arrows. A cutting tool is also made from pig teeth: the inner edges of the tooth are sharpened with chert flakes to create cutting edges, allowing the tool to be used in a to-and-fro action. The ubiquity of the bones and teeth in a pig rich environment, combined with the ease of creating and maintaining the tool makes pig teeth and bone an adaptable resource.

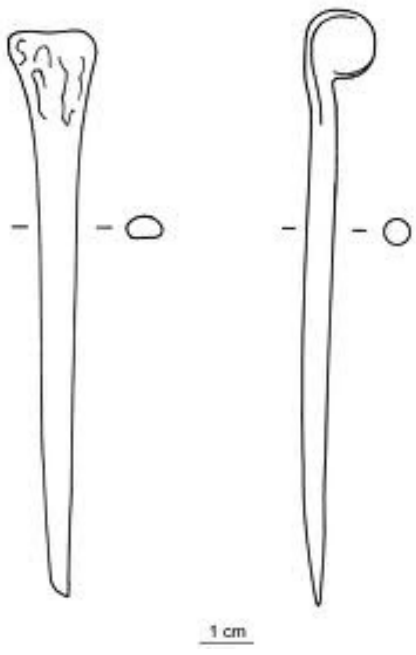


Figure 2: Hair or clothing pins made from pig fibula from medieval Holland (Prummel et al., 2011)

1.1.3 The Extreme Relationships between Pigs and People

Throughout recorded history there have been incidences of extreme human reactions to pigs that are unusual in human-animal relations; these have been termed 'Pig Love' and 'Pig Avoidance' by Marvin Harris (1974). Pig love goes beyond appreciation of the taste and the culinary characteristics of swine flesh: "it is a state of total community between man and pig" (Harris 1974:39). This includes raising pigs as a member of the family, physically and verbally interacting with them, feeding them from the family table and tending to them when sick. This pig love does not preclude ritual slaughter, but raises it to a level of heartfelt sacrifice that separates pig love from the ritual veneration seen in the Hindu relationship with cows. The classic example of pig love is seen in the indigenous peoples of Papua New Guinea, such as the Maring, who operate on a cyclical system of internecine clan warfare. This relationship centres on a ritual known as *kaiko*, which consists of small scale pig offerings preceding a larger ritual sacrifice. In the build up to the *kaiko,* the clans go to war, which is characterised by pig sacrifice to implore the ancestors to intercede in a particular scheme or battle. The result is the almost total eradication of the adult porcine population, which signals the cessation of hostilities and the rebuilding of the pig population until the next *kaiko*. Almost all aspects of the Maring culture is based around pig rearing, providing for them and protecting them, so that the clan is able to start their next *kaiko* richer in pigs than their rivals and thus able to sustain hostilities longer than their opponents (Harris, 1974). This example of pig love is unusual, but indicative of the sometimes high esteem in which pigs can be held.

The opposite case to pig love, pig avoidance, is perhaps better known, in particular the taboo on the consumption of swine flesh upheld by the Jewish and Islamic

religions. This taboo is a total ban not just on eating pork or using pork products, but also on interacting with pigs in any way. Should a member of these religions come into contact with a pig then, according to some doctrines, a complex series of ritual cleansings needs to be followed. In Judaism permissible foods are called Kosher; meat must be from a ruminant which has split hooves. The Torah gives two passages relating to pigs:

> And the swine, though he divide the hoof, and be clovenfooted, yet he cheweth not the cud; he is unclean to you. Of their flesh shall ye not eat, and their carcase shall ye not touch; they are unclean to you (Leviticus 11:7-8)
>
> And the swine, because it divideth the hoof, yet cheweth not the cud, it is unclean unto you: ye shall not eat of their flesh, nor touch their dead carcase (Deuteronomy 14:8)

For followers of Islam, the Quran prohibits the consumption of pork:

> He has made unlawful for you only (carcass) that which dies of itself and blood and the flesh of swine and that on which the name of any other than Allah has been invoked. But he who is driven by necessity, being neither disobedient nor exceeding the limit, then surely, Allah is Most Forgiving, Merciful (16:116).

The reasoning for such religious taboos is not clear. That pigs are non-ruminants without cloven hooves is descriptive, not explanatory; neither religious text states why these animals should be avoided. It is possible that cleanliness is a causal factor: pigs roll around in mud or urine to cool down as they have fewer sweat glands than other large mammals (Hafez, 1968, Sack, 1982). Pigs are also omnivorous and will eat refuse; however, so will chickens, which are not banned, but also do not have pigs' reputation for being dirty animals. Harris (1974) suggests that ecological or

economic reasons explain the pig taboo. Pigs are not well adapted for the Middle East, where the cores of these religions are located. Pigs require a constant water source and shade from direct sun light (Hafez, 1968), occupying woodland in which to forage and root. These needs place them in direct competition with humans for scarce water and land resources. Urban pigs kept by individual families in towns and cities could partially remove the families from the market based taxation system as the pigs could enable them to produce their own meat. It is possible that these factors resulted in a prohibition against pig keeping with the pretence of hygiene as the reason.

1.1.4 Pigs and Social Status

Pigs have often been associated with social status; specifically they are seen as a marker of wealth. The lack of secondary products and the intensive food and land requirements needed to raise them meant that in societies where adequate land for foraging was not available pigs became a status symbol. This situation is evident in the British Iron Age where some areas of Britain were unsuitable for pig rearing, making the presence of pig rearing indicative of conspicuous consumption. In the Scottish Western Islands pigs comprise of between 6-16% of mammal faunal assemblages in wheelhouses and 18-40% in the higher status brochs (Parker-Pearson, 1999), demonstrating that pigs were reared as status symbols, items of power.

1.2 The Biology of Pigs

Pigs are ungulates; they walk on the tips of their hoofed digits, of which they have four: two principal ones (III and IV) and two accessory ones (II and V) (Sack, 1982). As such they are members of the artiodactyls like cows, sheep and goats, although pigs are not ruminants. Their closest relatives are the Tayassuidae (Peccaries) which fill a similar niche to pigs on the American continent. The next closest relative is the Hippopotamidae of Africa (Oliver, 1993).

1.2.1 Current Taxonomy

The family Suidae consists of four sub-families: the Babirusa (*Babyrousa*), the Phacocherinae (*Phacochoerus*), the Suinae and the Porcula (Groves, 2007).

Babyrousa contains three recognised species: *B. celebensis*, *B. togeanensis* and *B. babyrussa* (Meijaard and Groves, 2002b). *Phacochoerus* contains two species (Grubb, 1993b), the common warthog (*Ph. africanus*) and the Cape and Somali warthogs (*Ph. aethiopicus*; now extinct around the Cape). Porcula contains a single genus, *P. Salvania,* the Nepalese pygmy hog that was established as a monotypic genus by (Funk et al., 2007).

The Suinae contains three genera: *Hylochoerus meinertzhageni* (the giant forest hog) which includes three subspecies, *H.m. meinertzhageni*, *H.m. rimator* and *H.m. ivoriensis* (Grubb, 1993b); *Potamochoerus* which contains two recognised species, the African bush pig (*P. larvatus*) and the red river hog (*P. porcus*) (Grubb, 1993b); and *Sus*.

Sus contains seven main species. The most wide spread of these is *Sus scrofa* which is endemic to the majority of Eurasia (Groves, 2007). The remaining species, along with *S. scrofa*, are all found in Island South East Asia (ISEA) and comprise *S. philippensis*, *S. celebensis*, *S. verrucosus*, *S. barbatus*, *S. ahoenobarbus* and *S. cebifrons*. These are split into two main groups: the warty pigs (*S. philippensis*, *S. celebensis* and *S. cebifrons*) and the bearded pigs (*S. verrucosus*, *S. barbatus* and *S. ahoenobarbus*) (Cucchi et al., 2009, Groves, 1981, Groves, 1997). There are two additional minor species that are critically endangered: *S. bucclentus*, the Vietnamese warty pig (Groves and Schaller, 2000); and *S. oliveri* of Mindoro in the Philippines (Groves, 1997).

Sus scrofa consists of 16 subspecies (Groves, 2007) that can be split between Europe and the Near East on the one hand and South East Asia on the other on the basis of genetics (Hongo et al., 2002, Kim et al., 2002, Larson et al., 2005). Morphologically *Sus scrofa* is split into four main groupings (Groves, 1981), although the boundaries between them are not clearly delineated: the 'Western' group of Europe and Near Eurasia (including *S.s. scrofa*, *S.s. attila, S.s. nigripes* and *S.s. meridionalis*) and North Africa and the Middle East (*S.s. algeria* and *S.s. lybicus*); the 'Indian' group from Iran to Thailand (*S.s. cristatus, S.s. davidi* and *S.s affinis* whose taxonomic status is debated); the 'Eastern' group of Mongolia and Russia to China and Vietnam (*S.s. sibiricus, S.s. ussuricus*, *S.s. moupinesis, S.s. leucomystax*, *S.s. riukiuanu and S.s. taevanus*); and the 'Indonesian' group from the Malay peninsula through the Indonesian islands (*S.s. vittatus*) (Groves, 2007, Groves, 1981). This thesis goes on to show the phylogeny and morphology of *Sus* are complementary; the different phylogenetic groups, identified in Larson et al (Larson et al., 2005) map onto the

morphological designations: the differences between Eastern and Western type pigs being far greater than the differences within the Eastern type clades (the Indian, Eastern and Indonesian groupings).

In this thesis only the following genera were studied: *Ph. aethiopicus, P. porcus, P. larvatus, B. celebensis, S. scrofa, S. celebensis, S. cebifrons*, *S. philippensis, S. barbatus* and *S. ahoenobarbus*. This was due to availability of material.

1.2.2 Geography, Ecology and Habitat of the Suids Studied

Of the African pigs, *Ph. aethiopicus* is found in south-eastern Ethiopia, western Somalia, and in central and eastern Kenya where it inhabits open, arid regions from bush and open woodland to sub-desert steppe (d'Hart et al., 2008). Along with its sister species *Ph. africanus* (found throughout the sub-Saharan African savannah) it is adapted to savannah habitat and grazing behaviour. They are omnivores like all suids; eating bark, fungi, berries and carrion but specialising on perennial grasses, bulbs and roots (Estes, 1991). *P. porcus* is widely dispersed through the west and central African rainforest, in habitats ranging from mature and gallery rainforest to dry savannah woodland and cultivated areas (Querouil and Leus, 2008). *P. larvatus* inhabits the southern Sudan, Ethiopia and Eritrea and southwards throughout east Africa, mostly to be found in areas of dense vegetation (Seydack, 2008). Both *Potamochoerus* species are typical suid omnivores, their diet focusing on grasses, water plants, roots, bulbs, fruit, carrion and small animals (Vercammen et al., 1993).

All *Babyrousa* species inhabit the tropical rainforest of Sulawesi, in areas with good access to water and are now confined to more remote inland areas (Groves, 2001,

Meijaard and Groves, 2002a). *B. celebensis* is found on mainland Sulawesi, while *B. togeanensis* and *B. babyrussa* are found on the Togian archipelago and the Sula Islands respectively. Babirusa are all omnivorous, although the absence of the rostral bone suggests that they do not root like other suids (Macdonald, 2010a). They consume a wide variety of fruit, root and animal matter (Macdonald, 2010b, 2010c) though their diet includes a higher proportion of fruit than other pigs.

S. scrofa is the most widely distributed of the wild suids, its natural range extending from Western Europe to Japan, and from Siberia to the Southern Indonesian Islands (Polly and Eronen, 2011) although its range has suffered significant fragmentation. It is found in a wide variety of habitats, from semi-desert to tropical rainforest to the temperate woodland of Eurasia, its adaptability and widely omnivorous diet (ranging from roots to molluscs to small vertebrates) having allowed it to become the most populous of the family Suidae (Oliver and Leus, 2008).

Sus species other than *S. scrofa* are restricted to the islands of South East Asia. *S. celebensis* is found on Sulawesi (Burton and Macdonald, 2010) and *S. cebifrons* (Oliver, 2010b) and *S. philippensis* in the Philippines (Oliver and Heaney, 2010). *S. celebensis* and *S. philippensis* inhabit forests at almost any altitude, whilst *S. cebifrons* prefers forest at lower altitudes. The main bulk of their diets are roots, fallen fruit, leaves and shoots; carrion, vertebrates and invertebrates are consumed as well (Burton and Macdonald, 2010). *Sus barbatus* and its sub species are found mainly on the Malay peninsula (*S.b.oi*), Sumatra and Borneo (*S.b.barbatus*) (Kawanishi et al., 2010, Lucchini et al., 2005) whilst *S. ahoenobarbus* is found on Palawan (Oliver, 2010a). Both types favour tropical forest but *S. barbatus*

demonstrates the capacity of suids to inhabit a wide variety of habitat types, being found from beaches to upper montane cloud forest (Caldecott et al., 1993). They both consume roots, fungi, turtle eggs and a wide variety of plant material, the most important of which is fruit (Caldecott et al., 1993, Kawanishi et al., 2010).

1.2.3 Evolutionary History of Suids

Pigs have a deep evolutionary history. The superfamily Suoidea (which includes extinct suids and *Sus*) is thought to originate from South-East Asia during the Eocene (Orliac et al., 2010). The ISEA region that today has the highest suid diversity, possibly as a result of sea level fluctuations isolating communities on the islands in the early Pliocene (Lucchini et al., 2005). The ancestors of the Babyrousinae and Suinae lineages diverged from their common ancestor in South East Asia. The Suinae then radiated across Asia, with further divergence occurring as the ancestral suid of *Hylochoerus*, *Potamochoerus* and *Phacochoerus* colonised Africa (Gongora et al., 2011), with the ancestral suid of *Sus scrofa* radiating through Eurasia.

The first evidence of *Sus* reaching Europe dates to 1-1.5 million years ago, in the form of fossils from Italy (Rook and Martinez-Navarro, 2010). Divergence between European and Asian wild boar haplotypes occurring sometime around 900,000 years BP (Kijas and Anderson, 2001, Fang and Andersson, 2006). Suids retreated from much of mainland Europe during the last glacial maximum, surviving in refugia in the Iberian Peninsula, Italy and southwest Europe (Sommer and Nadachowski, 2006), although the extent of their range during this period is not fully established. Re-colonisation of mainland Europe occurred soon after the retreat of the glaciers, leaving biogeographic divisions in the animal's mitochrondrial DNA (Fang and

Andersson, 2006, Scandura et al., 2008). Since industrialisation, suids have suffered from overhunting and fragmentation of their habitat, leading to localised extirpation and subsequent reintroduction of neighbouring populations (e.g. Britain) that has led to a recent (post World War II) increase in population. Despite the intensification of farming hybridization between wild and domestic stocks appears to be rare. Certainly the presence of domestic genetic markers is low in modern wild stock (Oliver and Leus, 2008, Scandura et al., 2011), thus any genetic biogeographic signals in wild stocks should still be present, as appears to be the case in the study by (Larson et al., 2005).

1.2.4 Known Biogeographic Variation within *Sus scrofa*

The most widely studied causes of variation in suid morphology and size have been taxonomy (Groves, 1981, Genov, 1999) and domestication (Albarella, 2002, Payne and Bull, 1988, Zeder, 2006a). Variation in form has also been mapped through the Holocene, to reconstruct the history of *Sus* (e.g. retreat into peninsula refugia) and the effect of changing climate on body size though this period (Albarella et al., 2009),

As described above in the suid taxonomy section (1.2.1), morphologically *Sus scrofa* is split into four main groups: the Western group, the Indian, the Eastern and the Indonesian (Groves 2007, Grubb 1993a). These groups fit tolerably well with the known mitochondrial phylogeny of *Sus* (e.g. Larson et al 2005) which shows separate maternal lineages in the geographic regions proposed by studies on morphology (see figure 3 below).

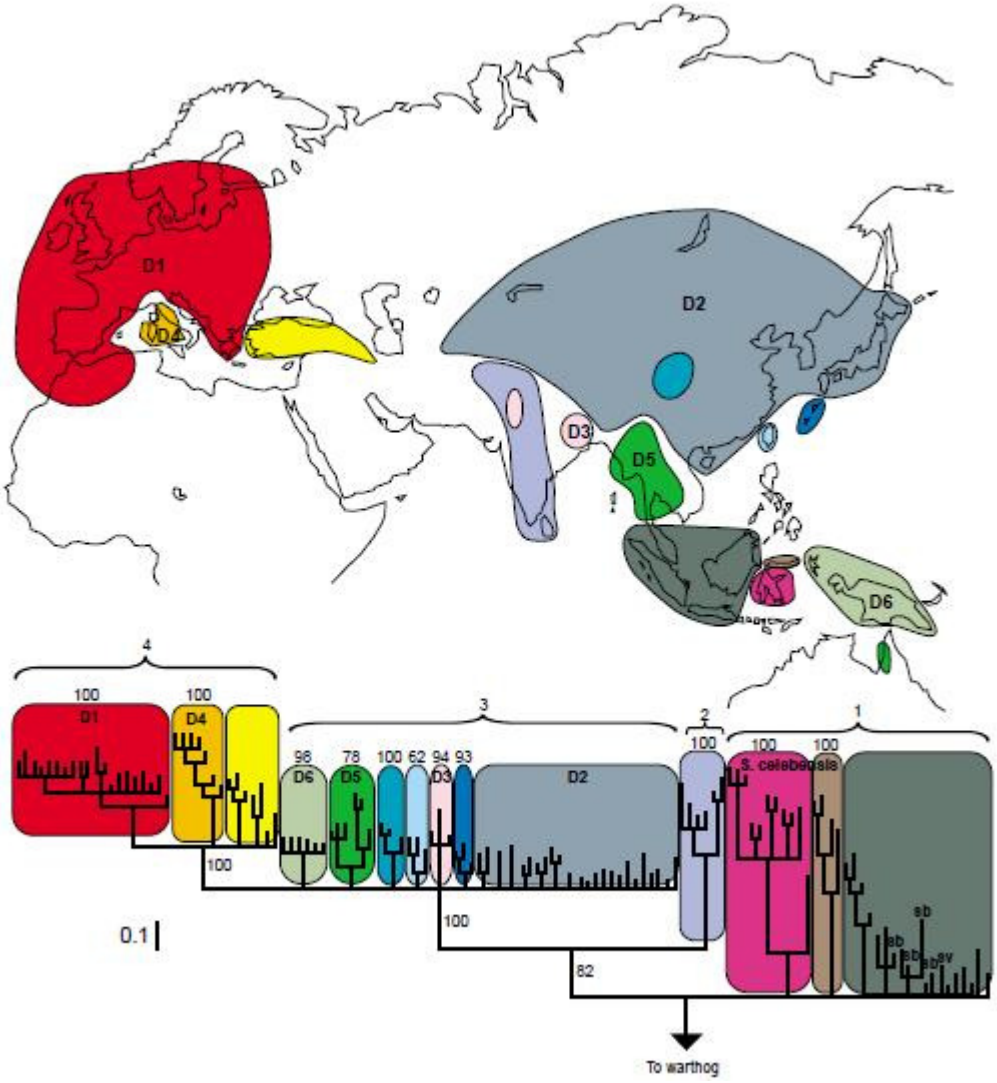


Figure 3: Distribution of *Sus* haplotypes (Larson et al., 2005)

Most known biogeographic variation in pigs is based on differences in size. In Europe, size increases from west to east and south to north (Albarella et al., 2009). Size increases in eastern Europe have been attributed to 'continentality' – harsher winters in the east having an increased bottlenecking effect, reducing intra-specific competition (Weinstock, 2000). The south-north size increase is driven, and explained by, the presence of larger pigs in the Near East, although why pigs should be larger in the Near East is currently unexplained (Albarella et al., 2009).

(Davis, 1981) surveyed extant and past pig populations (amongst other animals such as Aurochs, dogs, foxes, gazelles and goats) in the Levant, noting a negative temperature-size relationship in modern populations, coupled with size decreases in pigs at the end of Pleistocene, and another size decrease associated with domestication. Davis attributes size decreases to Bergman's rule in wild pigs, foxes and dogs, noting that the regression lines of log dental size on temperature are similar in these species. The Pleistocene size reduction (present in all the animals Davis examines) is explained by the changing climate (e.g. lower temperatures) at the end of the late glacial maximum, which occurs at the Pleistocene/Holocene transition.

(Endo et al., 2002) examined wild pig mandibles (*Sus scrofa*) from Japan, Taiwan and Iriomote Island, noting similarities in size between Taiwanese and Japanese pigs from Honshu and the environmental effects of latitude and elevation on shape. Little further work has been conducted on other potential influences on morphological variation in pigs, especially the effects of climatic or geographic variables such as moisture and temperature or latitude and longitude on suid shape and size across the wider extents of the *Sus scrofa* range. In manuscript 2 I attempt to address this gap, analysing pigs from across Eurasia and analysing how cranial variation is affected by climate and geographic variables, and what proportion of variation they explain.

1.2.5 Known Constraints of *Sus scrofa* range

Although *Sus scrofa* is found in a wide variety of habitats it cannot tolerate temperatures above 35°C (95°F) with humidity above 65% without shade and water. This intolerance is known mainly through experiences of the transportation of domestic livestock and is due to a lack of sweat glands and thick layers of

subcutaneous fat (Hafez, 1968). Alleviation of high temperatures in the wild are sought through seeking shade and wallowing in mud or water, thus wild pigs are rarely found far from water and shade (Oliver, 1993) even in semi-arid environments. Frozen ground and deep snow also limit the range of *Sus*, limiting mobility and the ability to acquire food through rooting. Pigs never crossed the 'Bering filter' to reach North America and are only found in Eurasia, Oceania and Africa (Finlayson, 2004).

The main mechanism of population regulation is intra-specific competition for food or space governed by stochastic environmental factors (Uzal and Nores, 2004). This is reflected in the preference of *S. scrofa* to inhabit areas of energy rich foods (Massei and Genov, 2004).

1.2.6 Suids and Insularity

Pigs exhibit the classic response of large mammals to insularity and the 'island rule'– dwarfism (Millien et al., 2006, Meiri et al., 2011). Recent studies of body size extremes have shown that while examples of insularity are not as numerous as once thought, large animals are one group for which the island rule holds true (Meiri et al., 2011). In pigs the effects of the island rule are seen on many of the islands where pigs are found, including Corsica and Sardinia (Albarella et al., 2009), ISEA (e.g. *Sus ahoenobarbus* (Oliver, 2010a) and the islands off-shore from Japan and Taiwan (Endo et al., 2002).

The (Endo et al., 2002) study on pigs from Taiwan, Honshu (Japan) and Okinawa found that the size of the pig was linked to the size of the island. The smallest pigs

were found on Iriomote Island (part of the Okinawa Islands) which is 289 km^2, while pigs were larger on the Islands of Honshu (227,963 km^2) and Taiwan (36,193 km^2). The relationship between island size and pig size is not absolute, as the second smallest pigs are found on Corsica and Sardinia, which are larger than the Japanese islands, and on some larger islands (e.g. Ireland) there is no dwarfing at all (Albarella et al., 2009).

Reasons for dwarfism on some islands and not others may depend on the sland itself, especially its area and isolation, the climate, geology (e.g. whether they are part of the continental shelf, part of a tectonic plate or volcanic) and the biogeographic settings (e.g. realm, ocean) (Meiri et al., 2011). Crockford (2002, 2006) attributes the expression of dwarfism and gigantism to thyroid hormone rhythm in conjunction with stresses unique to islands (e.g. habitat, founder effect and diet). She contends that having stress-tolerant individuals as a large part of the founder population explains the variability of expression of the 'island syndrome' as stress-tolerant phenotypes, with thyroid hormone rhythms and associated growth patterns typically generate early maturation at smaller sizes (Crockford, 2006). Yet the role of thyroid hormone is hard to pinpoint in specific changes, partially because of its complexity, and partially because it is so pervasive in all aspects of development (Dobney and Larson, 2006). As Crockford suggests, further research is needed to establish its role.

Pigs have been introduced to many islands outside of their natural range by humans, including the introduction of pigs to Cyprus in the Epipaleolithic (Vigne et al., 2009), Ireland during the Mesolithic (McCormick and Murray, 2007) and Corsica and Sardinia in the Neolithic (Albarella et al., 2006b). During these introductions pigs

must have been under human supervision during transportation before release as hunting stock, but would still be wild animals. However, in some cases it may be that domesticated animals were transported and released as feral animals, providing an explanation for the situation on Corsica and Sardinia where wild, feral and domestic animals are found as a result of a domestic introduction (Rowley-Conwy, 2011).

These early island introductions also violate the assumption that animals found outside of their natural range must be domestic – the Cypriot and Ireland introductions occur long before the innovations of agriculture or domestication had reached these areas. Thus the establishment of the status (wild or domestic) of original founder populations could be significant to studies of the origins and spread of domestication.

1.3 Domestication

Domestication is a process that facilitated the transition from hunter-gathering to sedentary farming. As such it is one of the crucial developments in the creation of modern society. Domestic plants and animals first appeared in South-West Asia around 12,000 years ago at the start of the Neolithic Revolution, a suite of widely encompassing changes experienced by humans at the end of the last ice age. The Neolithic Revolution describes the change from a hunter-gatherer lifestyle to that of agro-pastoralists, which includes the development of sedentary societies with associated technology such as pottery, specialised food production techniques like irrigation and transhumance, art, architecture and trade (Bellwood, 2005).

The change from hunter-gatherer to agriculturalist is one of the seminal moments of human history. Vigne described neolithisation as follows:

> Characterized by the start of an unprecedented increase in human activity and its subsequent impact on the environment. It is marked by the birth of new types of ecosystems including those strongly impacted by humans (man-modified ecosystems, e.g. exploited forests) and those distinctly artificial (manmade ecosystems, e.g. agrosystem, village, city). (Vigne 2011a:177)

The Neolithic Revolution was first described by Vere Gordon Childe (1925, 1936) who postulated that climate change at the end of the Late Glacial Maximum forced humans and animals together into 'Oasis' of more stable resources. This theory has been superseded. The most common modern hypothesis focuses on climatic amelioration producing warmer, wetter, more favourable climatic conditions that caused hunter-gatherer populations to expand, forcing them to propagate wild plants, which became the ancestors of domesticated plants (e.g. rye, wild lentils). The

subsequent onset of the Younger Dryas and the loss of favourable climatic conditions may have reinforced the reliance on cultivated plants to offset fluctuations in the availability of wild resources (Bellwood, 2005).

One of the hypotheses directly relevant to animal domestication is that of human niche construction (Vigne, 2011a, Rowley-Conwy and Layton, 2011). Human niche construction caused changes in the local environment to enable increased reproduction in wild animals making them a more reliable food source. In a 'disturbed' climate, such as that of the Younger Dryas, niche construction would be an attractive subsistence strategy. The closer relationship between humans and animals started the process of domestication, leading some authors to describe situations either where wild animals and plants adapt to humans in a symbiotic relationship (Rindos, 1980), or where humans begin to manage plants and animals as 'proto-domesticates'. In turn, humans would have been selected (via cultural evolution) or motivated (via rational choice) to modify their behaviour so as to favour the propagation and growth-multiplication of these proto-domesticates (Vigne, 2011a).

There would not have been a straight forward shift from hunting and gathering to food production. (Reading, 2005) explains that the normative paradigm – one of progression, fast or slow and possibly including intermediate steps of cultural control or proto-domestication – does not account for failure or different tactics during the process of neolithisation. He proposes an alternative paradigm whereby there were dead ends and failed experiments and that it may be possible to see these in the archaeological record. Thus the process of neolithisation and/or domestication is one

of faltering steps, often retracing itself or starting again. As such, it is not a simple additional episode in biological evolution but a discontinuity in the evolution of the biosphere (Vigne, 2011a). That is, humans, as a species, became able to modify their surrounding environment using socialized (i.e. flexible) techniques. The main difference between human niche construction and classic biological processes is the element of human intent (Zeder, 2009).

The question of intent, of how much humans deliberately intervened in the lives of animals, has been a central point in the discussion of domestication (Zeder, 2006c, Jarman, 1976a). The 'balance of power' in the domesticate-human relationship is contentious. Some have argued that the emphasis should be placed on the human role as masters of animals, exercising a form of cultural dominance, implying that these creatures are forced to live and multiply in captivity; the animals acquire domestic traits as a result (Gautier, 1990). Others theories have postulated that animals 'chose' domestication or were willing participants in the process, gaining equally from the arrangement. The theories are focused on the mutualistic aspects of domestication; (Rindos, 1980) notably postulated this latter for plants and it has also been suggested for animals (Higgs and Jarman, 1972). Other mechanisms, such as social parasitism (where one community exploits another), have been proposed for relationships with particular animals e.g. the domestication of reindeer (*Rangifer tarandus*) (Zeuner, 1963), but are limited to specific cases. The overarching point is best summed up by (Meadow, 1989) who characterized domestication as a change of focus on the part of humans from the dead to the living animal and, more particularly, from the dead animal to the principal product of the living animal – its progeny.

1.3.1 Defining the Process of Domestication

Domestication has been defined many times, each emphasizing a different component of the human-animal relationship (Arbuckle, 2005). The problem with each definition is the inherent difficulty in assigning static terms to a process involving long-term and continuous changes (Dobney and Larson, 2006). It is difficult to formulate a definition of domestication that is general enough to account for the wide variation observed in different species, in different captive environments, yet specific enough to be meaningful in terms of the biological processes involved (Price, 1984). Thus no single definition of domestication has been adopted by the scientific community studying it, with many papers having to dedicate a section to explain how the authors are approaching the definition of domestication in each case.

Definitions of domestication have fallen into two main categories as defined by the field of lexical semantics (Dobney and Larson, 2006); complementaries and antonyms. Complementaries are mutually exclusive e.g. open/closed. Antonyms are pairs of opposites that are gradable e.g. fast/slow. Both approaches have been used to define wild/domestic, but the antonym approach, that of a scale between wild and domestic has been favoured.

The change in language describing domestication has followed a greater awareness that the process of domestication is generally slow and not fast (Ervynck et al., 2001): that there is no sudden switch from wild to domestic and that it may be graded. (Zeuner, 1963) identifies 5 stages of domestication:

1. Loose contacts, with free breeding;

2. Confinement to human environment, with breeding in captivity;
3. Selective breeding organized by humans, to obtain certain characteristics, and occasional crossing with wild forms;
4. Economic considerations of humans leading to the planned 'development' of breeds with certain desirable properties;
5. Wild ancestors persecuted or exterminated.

These stages emphasise the increasing intensity of domestication through which a species would pass through time.

Although creating another standard accomplishes little more than creating a proliferation of standards[1] it is important to clearly set out domestication is defined for the purposes of this thesis:

Domestication is an *anthropogenic* process whereby humans and animals enter a symbiotic relationship of mutual exploitation and benefit.

The key term here is *anthropogenic*; this is a human orientated and initiated process but is one that has huge benefits for the animals involved. Humans gain a regular and reliable source of food and 'secondary' products such as milk and other dairy products, skins (e.g. leather) and other raw materials such as bone (for tools or glue). Animals gain protection from predators and the environment and a regular and reliable source of food. Although it may seem odd for animals to 'benefit' given many of them end up slaughtered, many individual animals end up living far longer than they would in the wild where illness or old age would leave them vulnerable to predation. As a species, the domesticates range far beyond their natural range (Rowley-Conwy et al., 2012), moving into to new habitats behind natural barriers

[1] http://xkcd.com/927/

beyond their ability to negotiate[2]. While this may be of little solace to slaughtered individuals, it has resulted in species that have become far more successful[3] with human intervention than they would ever have been without.

An advantage of this definition of domestication is that it captures the entire range of domestication, from the first stages of domestication moving beyond the hunter-prey relationship to the 'fully' domesticated, genetically modified modern breeds. The hunter-hunted scenario is not included as part of the domestication process as there is no 'benefit' to the hunted population barring possibly reducing intra-specific competition. One major issue unresolved is where along this continuum animals become 'domestic', the crux of the matter being how to define 'domestic'.

1.3.2 Defining a 'Domestic' Animal

What constitutes a domesticated animal? (Clutton-Brock, 1988:32) defines it as "one that has been bred in captivity for the purposes of economic benefit to a human community that maintains total control over its breeding, organization of territory, and food supply." (Gentry et al., 2004) expands this definition and describes four characteristics of 'developed' (i.e. modern) domestic animals: (1) its breeding is under human control; (2) it provides a product or service useful to humans; (3) it is tame; (4) it has been selected away from the wild type. Yet there is clearly a range of 'domesticated' animals that do not come into this envelope, including tame animals (as individuals or as groups) not providing product or service' feral or semi-feral animals; or a variety of degrees of domestic animals where humans do not have 'total' control of breeding, territory or food supply, but exert enough control to

[2] E.g. the introduction of sheep (*Ovis aries*) and goats (*Capra hircus*) into Europe.
[3] Success is measured here by increase in range, increase of population and the continuation of inherited genetic lineages that may or may not be the purpose of existence.

organise groups of animals. An example of this last is given by (Albarella et al., 2006a) of early 20th century urban pigs in Britain. Allowed to wander freely through townships and forage (and presumably mate) for themselves, they do not fulfil Clutton-Brock's criteria for domestic animals, yet their owners would recognise them as 'domestic' animals. Clearly, defining a domestic animal is problematic.

This is particularly a problem in studies of the earliest domestic animals. There is inevitably a stage where animals are primed for domestication due to their proximity to human settlements, or the early stages of management of localised wild populous in the early stages of human niche construction (Vigne, 2011b) yet where is the threshold where an animal is no long wild and has become domestic? Labels to describe half-way houses have been created' including 'proto-domestic'; yet to an extent these duck the issue (Zeder, 2006c), and perhaps it is better to appreciate that the animal and society is on the way to domesticating animals, rather than to worry about how far along the path they have come.

As such, whatever label is applied, ultimately we are best served by thinking of domestication as a scale, with 'wild' animals that have never seen or come into contact with a human at one end, and 'fully domesticated' animals that are a result of intensive breeding programs and spend their entire lives in captivity at the other (fulfilling (Gentry et al's., 2004) four characteristics defining developed, modern domestics). Feral animals, that is domesticated animals that have escaped or been released, reach beyond the domestic side of the scale, even if they subsequently revert to 'wild' status. An example of this scale is graphically produced below (Figure 4: reproduced from (Vigne, 2011a)). Although the issue of where along the

continuum an animal becomes ‘domestic’ is not resolved, it may be that it is too ‘local’ an issue to apply a global rule, and as such a ‘domestic’ label is applied on a case by case basis.

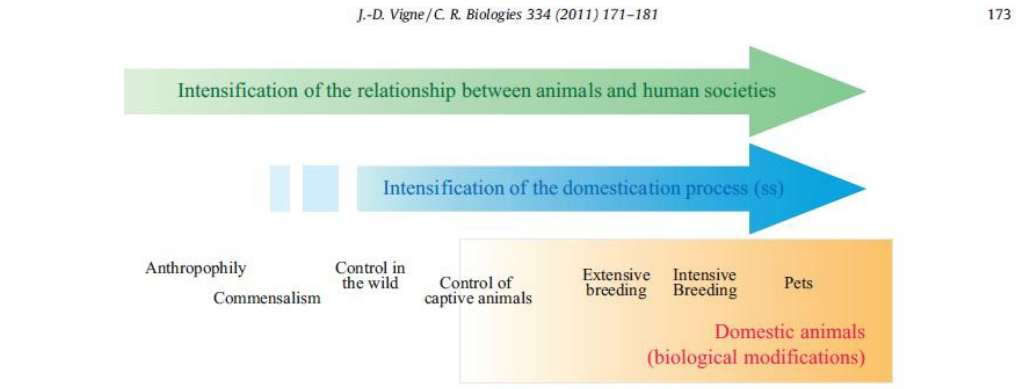


Fig. 1. Domestication can be considered as an ultimate phase of intensification in the relationship between animal or plant sub-populations and human societies. It is comprised of several grades of intensification that, by various means and over varying periods, may end with the emergence of domestic animal as well as plant and microorganism lineages shaped by humans. The control of wild animals is a form of domestication that does not entail any visible morphological modifications, at least from an archaeology point of view.

Figure 4: Representation of the scale of interaction between animals and humans, from (Vigne, 2011a)

The role of tameness is been an important consideration in the process of domestication. Tameness can be achieved by habituation, positive associative conditioning, and it may be attained without any deliberate human effort. In habituation the animal's fear of humans is gradually reduced by repeated exposures in a neutral context; that is human presence has neither positive nor negative reinforcing properties. Positive associative conditioning occurs when the animal's fear of humans is reduced by humans acting as providers of food, water, shelter, and grooming. Humans become secondarily associated with positive stimuli and the threshold for avoiding people is raised (Price, 1984). Thus the initial role of taming could be an important step on the ‘path’ to domestication.

However, Melinda Zeder points out, it is important not to get too focused on the exact demarcation between wild and domestic in any given context:

> To some extent, it remains a matter of personal preference to decide just when a domestic subsection of a plant or animal species has been created. Threshold criteria that require total genetic isolation and emergent speciation or complete dependence on humans for survival set a very high bar that many, if not most, widely accepted domesticates would fail to clear. Even somewhat looser standards that involve a lesser degree of genetic modification in the target plant or animal population, or a certain level of human investment in propagating, nurturing, or owning the resource, run the risk of constructing artificial boundaries along what was really a more seamless incremental process. (Zeder, 2006b:107)

Thus the argument as to at what precise point in time we have actual 'domestic' animals (whatever they are) is distracting from the real focus of study – the process of domestication itself. What sort of evolutionary process is it? And what are the effects? And how and why does it occur?

1.3.3 How do Animals Become Domesticated?

It is quite possible for individual members of a species to become tamed or accustomed to human presence, but for domestication to occur these individuals must breed and their offspring and successive generations become viable breeding animals as well (Price, 1984, 1999).

Six physiological and behavioural conditions have been proposed by (Clutton-Brock, 1999), expanding on work by (Galton, 1865) and (Guppy, 1961), for animals to fulfil if they are to become domesticated. These are:-

1. Hardy; the animals have to adapt to new environments, diets and often conditions which are more conducive to infection than their natural state.
2. Social; in most cases (cats being the most obvious exception) humans become the dominant member of the group, thus creatures that are social by nature are far easier to domesticate.
3. Reduced flight response; or it must be easily suppressible, as animals with a strong flight response (antelope, gazelles and deer) do not eat or breed well if constrained.
4. Useful; the animal must have an obvious primary purpose, be it as food (pigs, sheep, goats and cattle), a hunting aid (dogs), pest control (cats, ferrets) or locomotion (horse).
5. Breed freely; the most important factor for domestication. Captive breeding is tricky even under favourable conditions such as modern zoos, thus if a species does not freely breed the chances of successful domestication is low.
6. Easy to tend, gregarious and placid animals with a varied diet are easier to maintain and herd (and thus protect), thus minimising input.

Given the stringency of these conditions it is not surprising that only a few species have been domesticated. It is known that the ancient Egyptians attempted and failed to domesticate some species like gazelles and hyenas (Zeuner, 1963), and it is probable that similar failed experiments were conducted at many points in human history. But pigs curious, intelligent and gregarious nature; resistance to disease and

general hardiness; quick breeding and high return of meat vs. resource input makes it not surprising that they were one of the first animals domesticated.

1.3.4 Domestication Pathways

It is likely that pigs followed a domestication trajectory closer to that of dogs rather than those of sheep, cattle or goats (Clutton-Brock, 1988, 1999). In the initial relationship each population adjusted to the presence of the other, in the case of pigs they became used to the permanent human camps while humans became used to the local populations of wild boar (Albarella et al., 2006a). Tamer or braver individual pigs would approach the human settlements, perhaps attracted by scavenging opportunities. These may have been hunted or welcomed, treated as pets or accepted into family groups as in the pig loving cultures of Papua New Guinea (Dwyer, 1996). Regardless of the response, physiological and phenotypic changes would already have begun to reshape the local wild populous, but it was not until humans began to purposefully capture and breed animals, and thus enhance selective pressures on that domestic population, that true domestic pigs were created.

This type of pathway has been labelled a commensal pathway, animals that came into contact with humans to scavenge or to prey on the scavengers (Zeder, 2012) and include dogs, cats, mice and chickens as well as pigs. Those animals that proved useful were accepted and encouraged, with people gradually taking a more active role in their breeding habits, seeking to encourage desired traits. Not all commensal animals became domesticated, remaining pests (e.g. mice). The main alternative pathways are directed, or prey, as summarised in figure 5 below.

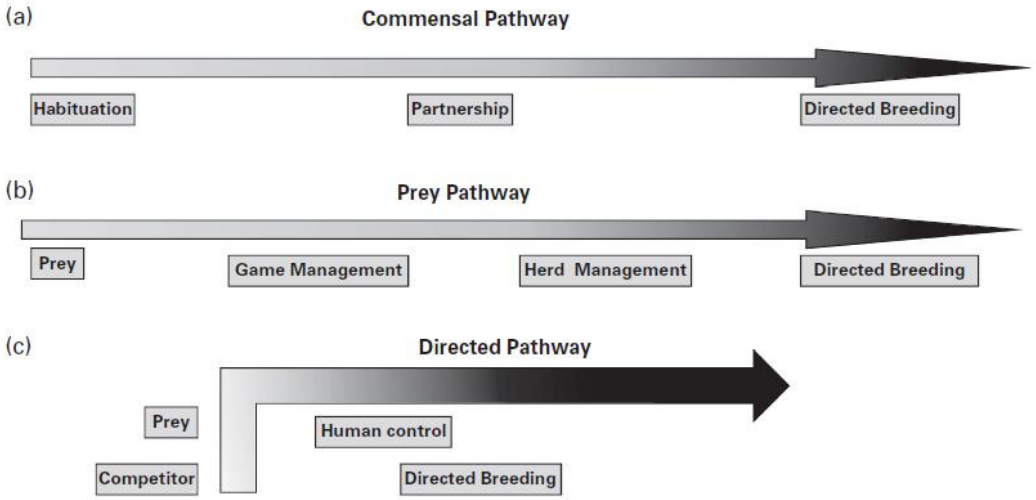


Figure 9.7. Pathways to domestication. (a) Commensal pathway, (b) prey pathway, (c) directed pathway.

Figure 5: Summary of the main types of domestication, from (Zeder, 2012)

Domesticates originally targeted as prey may have become domesticated in response to overhunting, with humans propagating food resources and providing shelter from predators or competitive hunting groups to maintain a stock of food to fall back upon in hard times. Evidence of management of domesticates is seen in the demographic profiles of early Neolithic goat herds of the Zagros (Zeder, 2005, 2006a), with a predominance of young males and mature females suggesting a focus on herd growth, keeping only a few healthy males and focusing on breeding females. Most of the major domesticates would have followed the prey route like cows, sheep, goats, water buffalo, yak, llama and perhaps reindeer.

Animals on the directed pathway may have begun their route to domestication as prey species, but became utilised for other purposes. For example sheep also produce wool and milk, and evidence for exploitation for milk goes deep into the Neolithic (Evershed et al., 2008) suggesting that soon after domestication the potential for

secondary products was quickly realised. Other reasons for directing animals to become domesticates include transportation (e.g. the horse), traction (donkeys/camels) and pelts (e.g. mink). There are potential niche routes, or individual cases that do not fall into individual or multiples of these routes, like elephants which are more like tamed captives (Zeder, 2012), and already mentioned failed experiments in domestication like cheetah, or gazelles and deer, animals in which the flight response is to great to successfully breed out.

1.3.5 Cultural and Biological Processes of Domestication

1.3.5.1 Cultural

The cultural aspects of domestication deal with how human society changed to accommodate domestic animals. In order to be domesticated, animals have to be incorporated into the social structure of a human community and become objects of ownership, inheritance, purchase and exchange (Clutton-Brock, 1999). The relationship is changed from mutualism, where the environment and its resources are shared to one of domination, whereby humans control resources and access to them. It is for this reason that societies where animals are treated as equals and revered (e.g. totemic societies like the North-West American Coast Indians) never developed domestication (Vigne, 2011b, Ingold, 1994).

1.3.5.2 Biological

The biological changes that occur in domestic animals begin when a small number of individuals are separated off from the wild species. If they successfully breed and become used to human company they will form a founder population, which is changed both by *artificial selection* for economic, cultural or aesthetic reasons,

inbreeding, by a *modified form of natural selection* in the human controlled environment, by *genetic drift*, and by *relaxation of natural selection* (Price, 1984, Clutton-Brock, 1999).

Artificial selection is unique to domestication and is the best understood mechanism. Artificial selection may be applied either consciously (intentionally) or unconsciously (inadvertently). Personal biases and preferences often influence the selection of breeding stock and these may be very subtle (Price, 1999).

The 'fox farm experiment' (in Russia) created a new domestic animal (from the wild silver fox) by continuously selecting for tameness. After 40 years of continuous selection in over 45,000 foxes a variety of changes had occurred including piebald colouring, drooping ears, curly tails and shortened snouts (Trut, 1999, Belyaev, 1969, Belyaev, 1979). This demonstrates that selecting for a single trait has wide ranging and unexpected affects on the behavioural and physiological characteristics of an animal (Dobney and Larson, 2006). Even though only a single trait was selected for, it is unlikely that the genes responsible for that specific trait caused the raft of changes observed. As it stands, only a few genes have been found that are responsible for morphological change in domesticates (e.g. MC1R and coat colour (Ludwig et al., 2009) and although it is possible that there is 'master' suit of genes for observed affects of domestication, untangling them is highly problematic (Dobney and Larson, 2006).

Inbreeding can be a problem in small closed populations resulting in a reduction of genotypic variability within a population as well as in "inbreeding depression",

which is the lowering of vigour or fitness brought about by the expression of many deleterious genes previously masked by dominant or epistatic alleles (Price, 1984).

Inbreeding has been practiced (combined with artificial selection) in order to obtain a particular characteristic (e.g., unusual morphological characteristics). Through systematic inbreeding a degree of homogeneity and constancy of characteristics that is normally not seen in wild populations can be achieved (Price, 1984, 1999).The loss of variability as the result of inbreeding is less costly to a population being maintained by humans, who often attempt to preserve variants that would normally not survive in nature. Early adopters of domestic populations must either have continuously 'drip-fed' in new wild animals to keep the genetic variability of their stock healthy, out-bred domestic females with wild males, had a large enough population to avoid the worst effects of inbreeding or had unhealthy animals. Inbreeding may be one major reason for failed domestication events.

Natural selection in captivity encompasses all the selection in captivity not ascribed to artificial selection. This depends on what the captive environment allows for development and expression of species-typical biological characteristics, and the number of generations in captivity (Price, 1999).

Once animals are in a human controlled environment the founder group is subjected to population bottlenecking that can result in intermittent and sometimes significant *genetic drift*. In small populations drift is likely to reduce variability within populations but increase it between populations (Clutton-Brock, 1999, Price, 1984).

Relaxation of natural selection occurs with the transition from the natural environment to the captive one. Behaviours that are strongly selected for in the wild lose their significance once captive e.g. the ability to find food and water. As a result the variability for these traits is likely to increase, reducing the population's fitness for survival in the wild (Price, 1999).

1.3.6 Changes seen in Domesticated Animals

The mechanisms of biological change associated with domestication are expressed through morphological variation and behavioural modification. For example body size reduction has often been noted in the early stages of domestication (Albarella, 2002, Clutton-Brock, 1988, Ervynck et al., 2001, Payne and Bull, 1988) although it is a poor marker of domestication due to the difficulty of determining the contribution of natural taxonomic, environmental and spatial variation to its occurrence (Zeder, 2006c).

One of the best catalogued differences between wild and domestic animals is the proposed paedomorphic changes of the skull. Paedomorphism is the retention of juvenile morphology or behaviour into adulthood, expressed in morphology as snout shortening and concavity of the face where the occipital squama becomes upturned, braincase reduction, hair softening and loss, tooth crowding and tooth length reduction combined with an overall reduction in body size (Bokonyi, 1974, Price, 1999, Zeder, 2012). Behavioural paedomorphism includes tameness, expressed as a lack of fear and increased inquisitiveness and social bonds with reduced aggression (Wayne, 1986, Coppinger et al., 1987, Trut et al., 2009, Hare et al., 2012).

Paedomorphism is caused by heterochronic changes (Price, 1999, Zeder, 2012, Alberch et al., 1979), the evolutionary process that generates diversity via changes in the rate or timing of ontogenetic pathways (Gould, 1977), and which has been directly attributed as the mechanism for the morphological change in dogs (Moray, 1992, Moray, 1994), and other domesticates (Trut, 1999, Zeder, 2012).

(Gould, 1977) described three components of ontogeny - age, size and shape. The evolutionary disassociation of these three components during ontogeny can produce descendent morphology that either resembles the ancestral morphology at a younger stage of development (paedomorphosis) or a continued stage of development (peramorphosis) (Alberch et al., 1979). Paedomorphism can arise from either the mechanisms of neoteny, slowing the growth rate of shape relative to age; progenesis, reducing the period of growth in shape, resulting in early sexual maturity; and post displacement, where shape growth occurs later (Godfrey and Sutherland, 1995). It is neoteny that is often invoked to explain the divergent morphology of domestic animals. However, closer examination of the cranial characteristics of dogs (Drake, 2011) have shown that they do not share the morphological characteristics of adult or juvenile wolves, and that the vast range of phylogenetically novel dog skull shapes does not coincide with the expectations of the heterochronic model. This leaves the model of morphological change uncertain.

An increase in variability of coat colour/change in pelage has been noted in animals around the Mesolithic/Neolithic transition (Clutton-Brock, 1999). Increasing coat colour variability has been linked to the MC1R gene (Anderson, 2007, Ludwig et al., 2009) with the suggestion that different coat colours in domesticates were artificially

selected for. An increase in variety of pelage characters, such as lengthening of the ears, long tails or more useful characteristics such as thicker wool/hair may also have been selectively breed, either for identification (from wild or other breeders stock) or as a desirable, usable characteristic (Clutton-Brock, 1999).

These changes could have appeared fast, slow or not at all according to the type of modification, the species and the strictness of the conditions imposed (Vigne et al., 2005, Vigne, 2011b). Arguments have been made that in many cases the process is slow (Arbuckle, 2005, Ervynck et al., 2001) as the early forms of domestic animals do not exhibit overt morphological change. But domestic animals not closely segregated from wild animals would have experienced continuous gene flow with the local wild populous, and as such were still linked with natural selective pressures whilst simultaneously experiencing reduced pressures from inbreeding and artificial selection. Yet morphological change can also happen extremely quickly, as witnessed in insular mammals (Millien et al., 2006), thus Vigne's suggestion that morphological change is dependent on context is probably correct.

In conclusion, some of the changes of domestication would initially have been an unintended consequence of the evolutionary/developmental mechanisms involved, while others were the result of artificial selection e.g. coat colour. Some of these modifications result from hormonal changes, due to environmental conditions and the stress of captivity, (i.e. without human intent (Arbuckle, 2005) whereas others result from epigenetic/developmental changes (heterochrony) or are purely genetic mutations possibly selected by humans (Vigne, 2011b).

1.3.7 Wild Progenitors

One of the major issues in the study of domestication is the identification of the wild ancestors of domestic species. This question has implications in finding the earliest sites of domestication, as wild animals must be present to be domesticated. Conversely, where animals appear outside their natural range there is a strong case for human interference and possible domestication (Rowley-Conwy 2011).

In the case of pigs it has been proposed that the eastern and western pigs were domesticated separately (Darwin, 1868). The earliest domestication events were in south-west Asia (Ervynck et al., 2001), with later centres in Europe and south-east Asia (Larson et al., 2007b). The European and South-West Asian progenitor is relatively easy to ascertain as only *Sus scrofa* inhabits it, but determining the exact subspecies is harder as *S.s. scrofa, S.s. attila* and *S.s. lybicus* are all present in this region, thus the exact subspecies is not known.

The Asian progenitor is harder to ascertain. Darwin attributed it to *Sus indicus*, which has since been split into various sub-species (Groves, 1981). There were also multiple domestication events in South East Asia (Larson et al., 2005, Larson et al., 2007b, Larson et al., 2010) and it seems probable that several species were domesticated at different times in different events, involving at least *S. scrofa*, *S.s. moupinesis*, *S.s. cristatus* on the continent and *S. scrofa* and *S. celebensis* in Island South East Asia (Groves, 1981, Larson et al., 2007b, Cucchi et al., 2011).

1.3.8 The Domestication of Pigs: When, Where and How Many Times?

When and where species were domesticated is an area of great interest (Vigne, 2011a). Although it is hard to pinpoint the exact moment of domestication due to the inexact nature of the methodologies (see below), and depends on the definition of domestication used, it is accepted that the region that the first domestic animals appear in is the Near East. Excluding dogs (which were domesticated much earlier than other animals) the earliest domesticates were sheep, goats, cows, pigs and cats from approximately the middle of the 11th millennium BP (Vigne, 2011a). Further separate domestication events from local stock also took place in the Zagros with goats at ca 10kyrs BP and cattle domestication in Pakistan (the Indus valley) (ca. 8.5 kyrs BP).

Genetic studies have shown that following the original pig domestication event(s) in the Near East, domestic pigs from there were introduced to Europe (from around 7,500 BP) (Larson et al., 2007a) as part of a proposed 'Neolithic package' (Childe, 1925, Childe, 1936, Vigne, 2011a, Rowley-Conwy, 2011). The suggested routes the introduction followed are around the coastline of the Mediterranean basin (Zeder, 2008) and through the Balkans and into central Europe, a possible route around the Black Sea is also possible. The progression of the Neolithic through Europe is shown below (Figure 6).

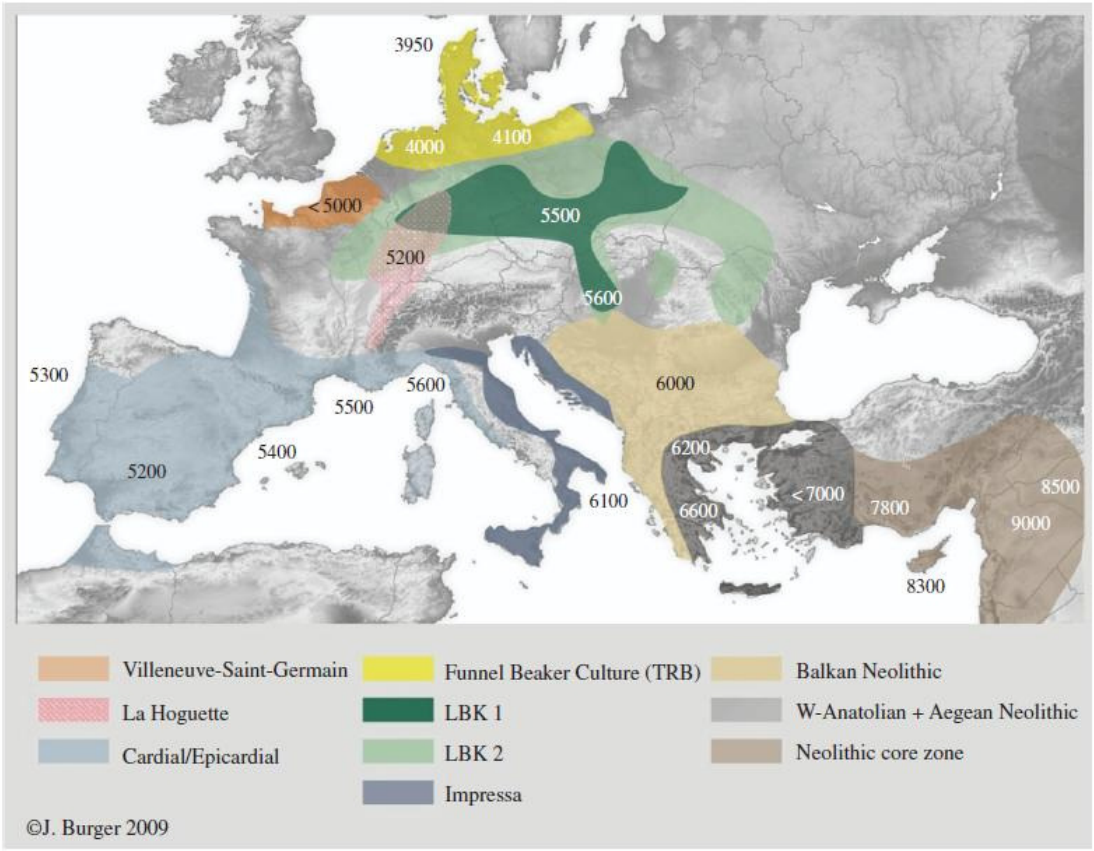


Figure 6: Arrival dates and approximate geographical expansions of defined Early Neolithic cultures from (Burger and Thomas, 2011)

The Near Eastern type pigs disappeared in mainland Europe by the Iron Age (2700 BP) and were replaced by indigenous pigs, suggesting introgression with the local populations (see figure 7). European pigs were subsequently exported back into the Near East. Multiple clades of domestic pigs indigenous to Europe (e.g. the separate Italian and Sardinian clade and the 2 mainland European lineages) provide evidence of additional localised domestication events (Larson *et al* 2007a).

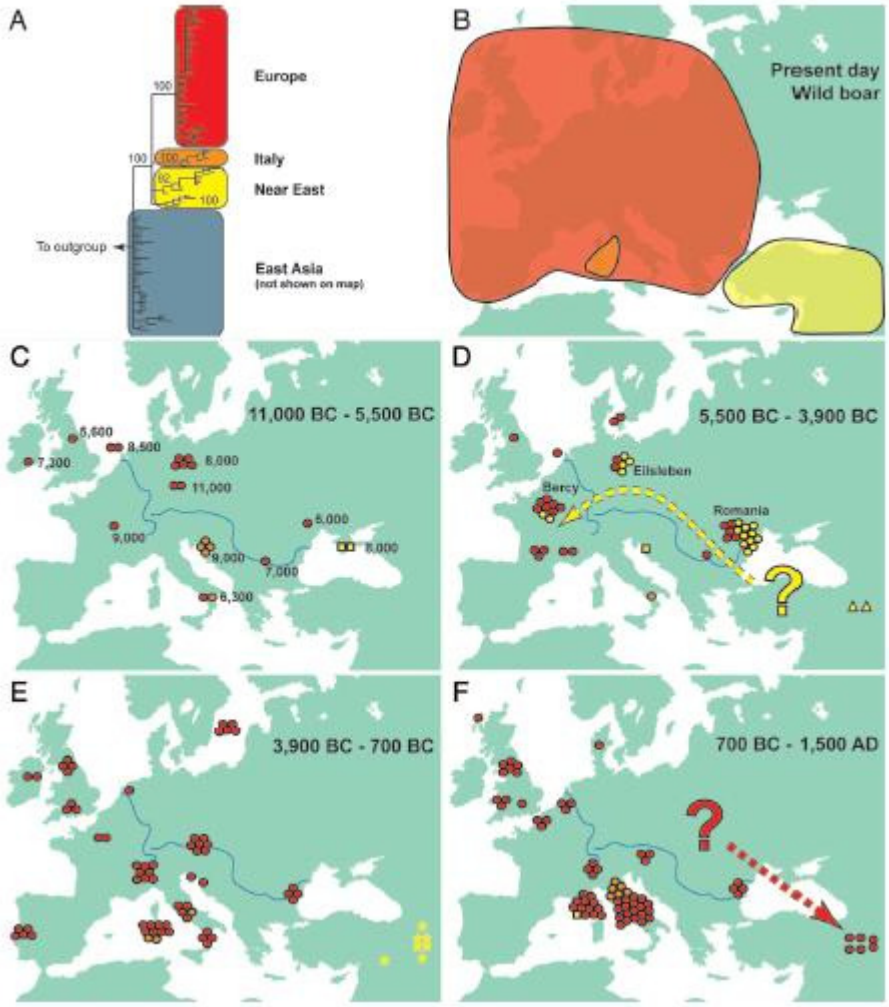


Figure 7: Series of Maps from (Larson et al., 2007b) depicting (A) the mitochrondrial separation of European, Italian, Near Eastern and East Asia pigs, (B) the present distribution of the mitochrondrial haplotypes, (C-F) the introduction and introgression of Near Eastern haplotype pigs into mainland Europe during the Neolithic and Bronze Age, with the following dispersal of European haplotype pigs into the Near East in the Iron Age.

Genetic studies (Larson et al., 2005) of pig mitochondria (thus based on the maternal lineage) initially established that there were at least 7 centres of domestication in the Near and Far East, this number has since been increased by 5, 1 in India, 3 in peninsular Southeast Asia and 1 of the coast of Taiwan (Larson et al., 2010). Domestication was occurring at different times and in different places, the lack of overlap in genetic (mitochrondrial) signatures (Haplogroups) disproves any

suggestion of expansion or migration into these cases (unlike Europe). Thus it can be concluded that domestication was not an isolated or unusual event but was in fact quite a common phenomenon (Dobney and Larson, 2006).

1.3.9 The Study of Pig Domestication

Wild pigs were first formally described by Linnaeus (*Sus scrofa*) in 1758 and domestic pigs by Erxleben (*Sus scrofa domesticus*) in 1777 (Gentry et al., 2004). The effects of Domestication have been studied since Charles Darwin's seminal book 'On the origin of Species' (1859) included a chapter on human induced variation caused by domestication. He followed this up with a two volume work 'The variation of plants and animals under domestication' (1868). These applied his theories of natural selection to the morphological variation and inheritability of characters under the influence of domestication, and included a chapter on domestic pigs. It considered the wild progenitors of domestic pigs and their variability in the wild, including changes in the morphology of the skull and other morphological 'curiosities', convergence of characteristics in eastern and western pig 'races', changes in the length of gestation, shared characteristics in the coat colours of young pigs of all types and feral and cross-bred pigs.

1.3.10 Methods used in the Study of Pig Domestication

The earliest and most commonly used method to distinguish domestic pigs from wild pigs is size, the premise being that the earliest domestic pigs were smaller than their wild progenitors due to changes in diet, restricted range, relaxation of morphological characteristics associated with breeding success in the wild and population bottlenecking (and founder effect) with genetic drift (Zeder, 2006a).

The first formal methodology[4] for detecting domestic pigs was devised by Ludwig Rütimeyer (1860, 1864) focusing on the length of the tooth row and 3rd molars of pigs from an early Swiss Neolithic lakeside site. He concluded that there were 3 types of pigs present, wild, domestic and 'peat' (*Torfschwein*) pigs (*Sus scrofa palustris*) that were postulated to be the domestic descendents of Near Eastern stock pigs. These were separated on size, e.g. his *ferus* (wild) pig 3rd molars he placed in the size bracket 40-53mm long and the *palustris* in the 33-39mm bracket. This was a controversial finding at the time, criticism focusing on a lack of adequate comparative material and the confounding effect of sexual dimorphism (this was successfully rejected on the basis that male and female maxillae were present in both wild and domestic samples). Though the *S.s palustris* sample was later amalgamated with the domestic type pigs[5] (Nehring, 1889, Rowley-Conwy et al., 2012) the definition of wild and domestic based on size differences was established. Since then size differences have been the basis of discrimination between wild and domestic pigs and other animals. Measurements have been formalised and standardised by von den Dreisch (1976) and assemblages made available for general comparative purposes (Albarella and Payne, 2005).

1.3.11 Methodological Issues

One of the obvious problems with size as a basis for determining the status between wild and domestic animals is that animal size varies for reasons other than domestication. Temperature and other environmental factors, diet and individual

[4] Prior to this several Scandinavian naturalists has identified wild pigs through size on an ad-hoc basis, see Rowley-Conwy (2012:3-4).
[5] Thus *S.s. palustris* is not a currently recognised sub-species (Groves 1981)

variation are all contributing factors to size changes (Zeder, 2006a). Climatic variation can be overcome by only comparing samples from similar habitats and temporal sequences (to eliminate climate change over time), but this can be very restrictive in availability of climatic data and suitable comparative material and excludes regional comparisons. Individual variation can be accounted for either by using larger samples, or by conflating measurements of different elements (cranial and post-cranial) using the log ratio method (Payne and Bull, 1988). The effects of diet on size and stature are not well documented but it is thought that teeth will be less affected as they are less plastic than bone (Cucchi et al., 2011).

Ontogenetic (age related) change can be mitigated to some degree by concentrating only on adults, pigs' remains may be aged by epiphyseal fusion, tooth eruption and tooth wear (Silver, 1969). However there are issues with these approaches, some bones continue to grow after fusion, teeth can be reduced in size due to the growth of other teeth e.g. 2^{nd} molars can be worn down by the emergence of 3^{rd} molars (Rowley-Conwy 2011) and the methodologies are based on modern proxy populations (Greenfield and Arnold, 2008).

Sexual dimorphism can be a major issue (Payne and Bull, 1988, Vigne et al., 2005) , especially in goats where the use of body size as a domestic marker has been questioned (Zeder, 2001, Zeder, 2006a) on the basis that the most causal factor of size differentiation is sex and not wild/domestic status. One way around this is by assigning sex to individuals, but this can be problematic in analyses of post-cranial material or for other animals where sexing bones is difficult.

Another major methodological issue is detecting the presence of multiple, distinct populations. For example, in a sexually dimorphic animal assemblage where wild and domestic animals of both sexes are present there could potentially be four separate populations. Alternatively there could be 'semi-domesticated' or indeterminately wild/domestic animals (animals undergoing the domestication process) present (Jarman, 1971, 1976b). There are also potential issues of inter-breeding (deliberate or otherwise) with contemporary wild individuals (Dwyer, 1996). To recognise multiple populations in the archaeological record (Payne and Bull, 1988) suggested using Pearson's co-efficient of variation (the standard deviation of a sample expressed as a percentage of its mean). This is a normalized measure of dispersion of a probability distribution, in this is case the variation within the overall sample. Comparison with other assemblages allows discrimination between samples with only a single population (lower co-efficient of variation) and samples with multiple populations (large co-efficient of variation).

There are important repercussions from husbandry strategy on using size as a domestic marker. If animals were kept under loose supervision and allowed to interbreed with the local wild population the resultant free gene-flow between them would restrict any size change (Rowley-Conwy, 2011). Only if domestic animals were kept under strict segregation from wild animals is any morphological size change likely to occur in the domestic population. Thus size variation is only likely to recognise animals that conform to 'wild' or 'domestic' in the traditional sense, yet size can still be used to document domestication as in the early Euphrates valley, where there is a temporally deep archaeological record and gradual changes over time have been recorded (Peters et al., 2005). Thus traditional biometrical techniques

still have their place (Albarella, 2002) despite the associated issues. To gain a greater resolution other methodologies must be used in addition to size to spot any early transitional domestic animals, or domestic animals that were kept in alternative husbandry strategies.

1.3.12 Alternative Methodologies

Demographic profiling was one of the first non-morphological methods applied to studying domestication (Zeder, 2006b, Zeder, 2006a). This is based on the assumption that the age and sex of animals killed by hunters maximising their return will be different from those killed by herders interested in the long term viability of their herds. Thus domestic animals will be killed younger (with an emphasis on killing young males and keeping older females for breeding) as herders control and manage their slaughter strategies to maximise productivity (Rowley-Conwy et al., 2012).

Sex determination is based either on sexual dimorphism of size or other morphological characteristics. In pigs this is most often the shape of the canine (von den Driesch, 1976). Age at death data is taken from the epiphyseal fusion of post-cranial elements and tooth eruption and wear (Silver, 1969). Assemblages with large numbers of slaughtered young males and older females (typical of a traditional herding strategy) may be indicative of domestication, as suggested by (Zeder, 2001) for the early Zagros.

This method can be problematic in species, such as pigs, where sex determination is difficult, especially in juveniles, and in archaeological assemblages where bones are

often fragmentary. In animals with high natural fecundity (e.g. pigs) there is naturally a higher mortality rate (Oliver, 1993) which can ape the domestic mortality profile. Intensive hunting strategies may also lead to higher mortality of juveniles; thus distinguishing between intensive hunting, close herding or some intermediate stage may be hard (Rowley-Conwy et al., 2012), yet may reveal significant changes in subsistence strategies between periods.

Linear Enamel Hypoplasias (LEHs) are dental defects that are produced during moments of physiological stress in an animal's early life. If stress occurs during tooth development it can result in marked incremental lines and depressions (beyond those that naturally occur) in tooth enamel that are known as LEHs. Once the stress is resolved normal growth resumes, leaving the LEH as a permanent marker of the stress event (Dobney and Ervynck, 2000). As tooth formation is relatively predictable and regular it can be used to give clues as to the health of animals during their formative years. LEH are infrequent in wild and modern domestic populations, yet in early domestic populations LEH are sometimes more common, suggesting incidents of stress in early closely managed populations (Rowley-Conwy et al., 2012). While it can be hard to distinguish between wild and domestic levels of LEH or determine the level of those of pigs not closely supervised/feral/semi-domestic, an increasing proportion of LEHs in a population over time provides additional evidence of domestication.

Stable isotopes and diet can be used to differentiate between wild and domestic pigs, as the feeding of livestock has been described as a pre-condition of domestication (Price, 1984). Diets of tightly controlled domestic pigs should differ from those of

wild pigs, and even the diet of pigs loosely associated with humans should differ from that of wild pigs with little or no contact with humans as pigs scavenge for human dietary discards (Dwyer, 1996). Pigs are omnivorous (see 1.2.2) and can and will eat a highly varied diet; this would have been one of the factors making them attractive to early adopters of agriculture.

One way to determine differences in diet is to compare the δ^{13}Carbon and δ^{15}Nitrogen scores of populations. Stable isotopes show a trophic level effect in which the relative proportions of one isotope change in a systematic way between food source and consumer. This change, called fractionation, depletes or enriches isotopes ratios, which is then compared to look for change (Ambrose, 1993, Reitz and Wing, 1999). High ^{13}C scores indicate the influence of C_4 plants in diets, as different photosynthetic pathways (e.g. C_3 vs. C_4 plants) discriminate differently against ^{13}C. Animals eating root crops, legumes, wheat (*Triticum aestivum*), rice (*Oryza sativa*), wild fruit, nuts and foliage have a $\delta^{13}C$ approaching those of C_3 plants. C_3 plants are more common than C_4 plants and have a lower $^{13}C/^{12}C$ ratio than C_4 plants. Animals eating C_4 plants, which include millet (*Panicum miliaceum*), sorghum (*Sorghum vulgare*) and tropical grasses (C_4 plants are more common in the tropics) have a higher $^{13}C/^{12}C$ ratio. Nitrogen ratios can also differ among plants, legumes fix Nitrogen though symbiotic bacteria, which source nitrogen from a combination of the soil and air. Air has a lower $\delta^{15}N$ value than soil so legumes have a lower $^{15}N/^{14}N$ ratio than plants that receive all their nitrogen from the soil. The marine environment has a higher $\delta^{15}N$ value than the terrestrial environment, and the bone collagen reflects this, with marine vertebrates showing a significantly higher $\delta^{15}N$ value than that of land vertebrates (van der Merwe et al., 1993). Together these

can be used to investigate the proportions of marine and C_4 plants in past population diets. In addition, bioaccumulation of the heavier isotopes through the food chain can be used to investigate trophic level, and the proportion that meat contributes to diet (Reitz and Wing, 1999).

Carbon and nitrogen stable isotopes of pig bones from the sites in Western Asia, Europe, East Asia (China and Japan) confirm that there are significant dietary differences between wild boars and domestic pigs. The δ15N values of domestic pigs from Neolithic sites in Southeast Anatolia, Turkey were lower than those of wild boars because of large quantity of pulse in their diets (Lösch et al., 2006). The domestic pigs in Ryukyu Islands, Japan, had higher δ15N or δ13C values than wild boars in other islands, owing to different feeding patterns by humans (Matsui et al., 2005, Minagawa et al., 2005). In early northern China, Shandong Province, three distinct populations of pigs were found, A group with low δ13C and δ15N values, B group with high δ13C and intermediate δ15N values and C group with low δ13C and high δ15N values. In comparison with the stable isotope values of humans, wild boars and domestic pigs during Yangshao Culture and Longshan Culture, A group was attributed to wild boars while B and C group belonged to domesticated pigs (Hu et al., 2008).

The field of *genetics* has made a huge impact on the studies of domestication. As discussed above one aim has been to identify the origins and numbers of domestication events. Once the identification of the biogeographic distribution of wild animal haplotypes is complete the presence of domestic individuals within them can point to a domestication event. Movement of different haplogroups can be used

as an indication of the spread of domestication, as in (Larson et al., 2007a) study of the spread of domestic pigs in Europe (see section 1.3.8). Issues with this approach remain in species with little biogeographic structure (Hofreiter et al., 2004), such as dogs, and there are issues with ancient DNA preservation (Dobney and Larson, 2006, Campos et al., 2012), but this approach has granted insights to human migrations and early domestication in chickens (Gongora et al., 2008, Storey et al., 2008) and cows (Edwards et al., 2007).

The possibility of discovering genes responsible for the expression of traits associated with domestication has been postulated (Stricklin, 2001) yet finding a complete suite of domestication genes is unlikely due to the complex interactions of genes, and genes the environment (Dobney and Larson, 2006, Anderson, 2007). There has been some success identifying individual genes associated with domestication, such as the MC1R gene that regulates the expression of pelage colouring (Anderson, 2007). An increase in the diversity of colour (especially the emergence of piebald colouring) is associated with domestication in all domestic animals (Darwin, 1868). MC1R has been used to study the domestication of horses (Ludwig et al., 2009), an increase in the diversity of coat colour suggests that horses were domesticated around 4,500BC in Kazakhstan.

Geometric morphometric methods (GMM) have recently gained traction in the field of domestication studies in pigs and horses. Geometric morphometrics is the study of morphology using a suit of powerful statistical tools to examine variation in the morphology of bones or teeth such as those caused by the environment or by human influence (i.e. domestication). The application of this methodology in

zooarchaeology has focused on teeth, as mammalian teeth do not vary much due to environmental factors, instead being genetically controlled. Teeth also survive particularly well in the archaeological record and with GMM most teeth can be analysed. Tooth shape studies have been used to identify some of the earliest domestic pigs in China (Cucchi et al., 2011). Phenetic relationships here revealed clear phenotypic signatures in samples of modern and Neolithic pigs; which provided evidence for pig domestication at the site of Jiahu from at least 6600 BC cal., establishing the Yellow River region as one of the earliest centres of independent Chinese pig domestication. Studies of animals from Island South East Asia (Cucchi et al., 2009) suggested that wild pigs on New Guinea were the descendants of pigs domesticated in mainland South East Asia and introduced by early farmers to ISEA although there was no clear evidence for a Neolithic introduction of domesticated pigs, or for the local domestication of indigenous bearded pigs.

GMM has also been applied to post-cranial material. Analysis of horse metapodials in early human hunting sites in North and South Western Europe during the Late Glacial showed strong regional structuring of horse populations (Bignon et al., 2005), suggesting an absence of long distance migrations and the fragmentation of populations. This is consistent with postulated mosaic landscapes of the "Mammoth-Steppe" biome that occurred during the Late Glacial in Eurasia and confirms the existence of early complex and diversified hunting communities. Analysis of Cervid anatomy associated with locomotion has been applied to palaeo-climatic reconstruction of the plio-pleistocene (Curran, 2012), using adaptations of animals to open or closed environments to determine what climate existed where their remains were recovered.

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Chapter 2 - Methodology

2.1 Material

This section gives details of the material that the thesis is based upon. First is a description of the object of the thesis – the pig cranium. This is followed by the numbers and origins of the samples included, as well as details of the institutions from which they were sampled. Then the particulars of the geographic and environmental covariates, including latitude, longitude, precipitation, temperature and elevation of the samples (used in the analysis of manuscript 2), and the methods used to age individuals of uncertain birth and/or death dates, including discussion of some of the associated issues . Finally, the problems with traditional methodologies that have been used previously to investigate some of the areas addressed by this thesis are detailed.

2.1.1 The suid cranium (from Sack (1982) and Sisson and Grossman (1910))

The head and neck of the pig resemble a cone with the apex at the snout and with the base blending into the body via a short neck. One of the dominant features of the suid cranium is the broad and prominent nuchal crest which is the highest part if the skull (see Figure 8a & c). It forms a part of the occipital bone, which thins laterally and turns downwards to form part of the temporal crest. The temporal crest is posterior to the centre of the nuchal crest, forming a concave depression that is flatter in domestic pigs than wild (Figure 8c). At the base of this depression sits the foramen magnum with two divergent ridges above it (Figure 8a: label A). The paramastoid processes are very long and straight, with the hypoglossal foramen either medial or posterior to the root of paramastoid (8b).

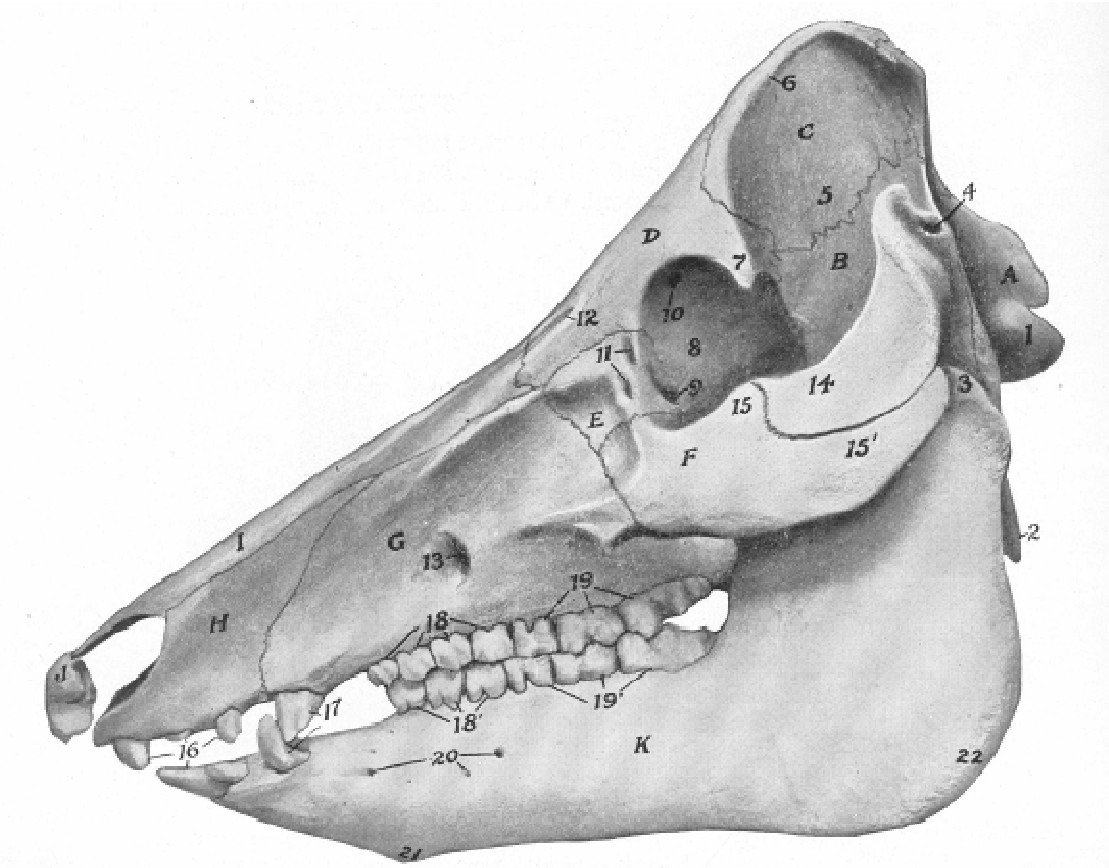

FIG. 177.—SKULL OF PIG; LATERAL VIEW.

A, Occipital bone; *B*, squamous temporal bone; *C*, parietal bone; *D*, frontal bone; *E*, lacrimal bone; *F*, malar bone; *G*, maxilla; *H*, premaxilla; *I*, nasal bone; *J*, os rostri; *K*, mandible; 1, occipital condyle; 2, paramastoid process; 3, condyle of mandible; 4, meatus acusticus externus; 5, temporal fossa; 6, parietal crest; 7, supraorbital process; 8, orbital part of frontal bone; 9, fossa for origin of ventral oblique muscle of eyeball; 10, orbital opening of supraorbital canal; 11, lacrimal foramina; 12, supraorbital foramen and groove; 13, infraorbital foramen; 14, zygomatic process of temporal bone; 15, temporal, and 15′, zygomatic, process of malar bone; 16, incisor teeth; 17, canine teeth; 18, 18′, premolars; 19, 19′, molars; 20, mental foramina; 21, mental prominence; 22, angle of mandible.

Figure 8a: Laterial view of a domestic pig skull (Sisson and Grossman, 1910)

The dorsal part of the skull is concave in domesticates, but flat in wild and feral animals, this concavity is produced by the frontal region becoming more vertical and a shortening of the nasal region. The nasal region consists of the nasal, frontal and parietal bones (8a: I, D, C) that are bounded on either side by the premaxilla, maxilla, the lacrimal and the squamous temporal bone (8a: H, G, C). The zygomatic arch is prominent, yet short, and bends upright at its posterior end (Figure 8a: 14 & 15). It consists of the malar (8a: F) and part of the temporal. At the tip of the snout is the rostral bone (8a: J) which is attached to the incisive part of the premaxilla and nasal. It forms the base of the hyper mobile disc-like movable tip of the snout and is used

extensively in its rooting behaviours. It is through this disc that the very long nasal cavity opens. The orbits are small and the rear of the orbit is open, as the supraorbital process (Figure 8a: 7) does not connect to the zygomatic.

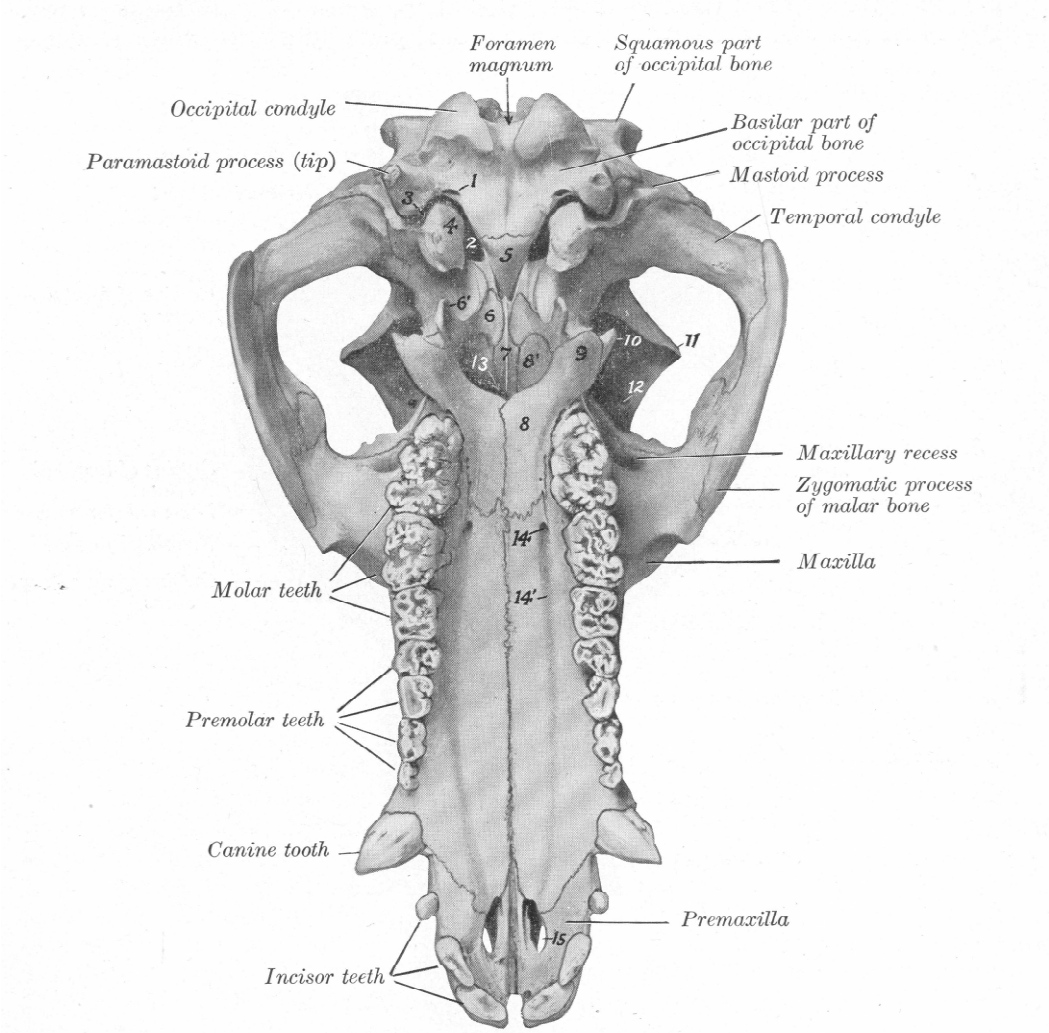

FIG. 178.—SKULL OF PIG; VENTRAL VIEW, WITHOUT MANDIBLE AND HYOID.

1, Hypoglossal foramen; 2, foramen lacerum anterius; 3, foramen lacerum posterius; 4, bulla tympanica; 5, body of sphenoid; 6, pterygoid bone, and 6′, hamulus of same; 7, vomer; 8, horizontal, and 8′, perpendicular, part of palatine bone; 9, pterygoid process of palatine bone; 10, pterygoid process of sphenoid bone; 11, supraorbital process; 12, orbital opening of supraorbital canal; 13, choanæ or posterior nares; 14, 14′, anterior palatine foramen and groove; 15, palatine fissure.

Figure 8b: basicranium of domestic pig crania (Sisson and Grossman, 1910)

The basicranium is split between the palate, containing the teeth, the maxilla and premaxilla (Figure 8b); and the main body of the cranium containing the bulla tympanica (8b:4), the posterior nares of the nasal aperture (8b:13), the palatine bone which includes the pterygoid process (8b:8), the basal part of the occipital (8b: 11 &

12), the root of the paramastoid (8b: 3) and a deep cavity containing the hyoid (8b: 2). The palate consists of the front two thirds of the cranium and is narrower in wild pigs than domestics; it widens at the molars and narrows at both ends. The dental formula of pigs is 3-1-4-3, with long straight lower incisors and curved upper incisors which allow a grasping action. The canines are the only obvious sexually dimorphic characteristic of pigs, and are much larger in males with a grooved channel on the interior surface of the female's lower canine. The canine root does not close and continues to grow throughout the pigs' life, the lower canine rubs against the upper canine, a constant sharpening action that allows the canine to be used in self-defence. The upper canine curves upwards, and in male *Babirusa* has spectacularly rotated through 180 degrees at the alveolus to form one of the most distinctive suid cranial characteristics (Sack, 1982, Sisson and Grossman, 1910, Groves, 1981).

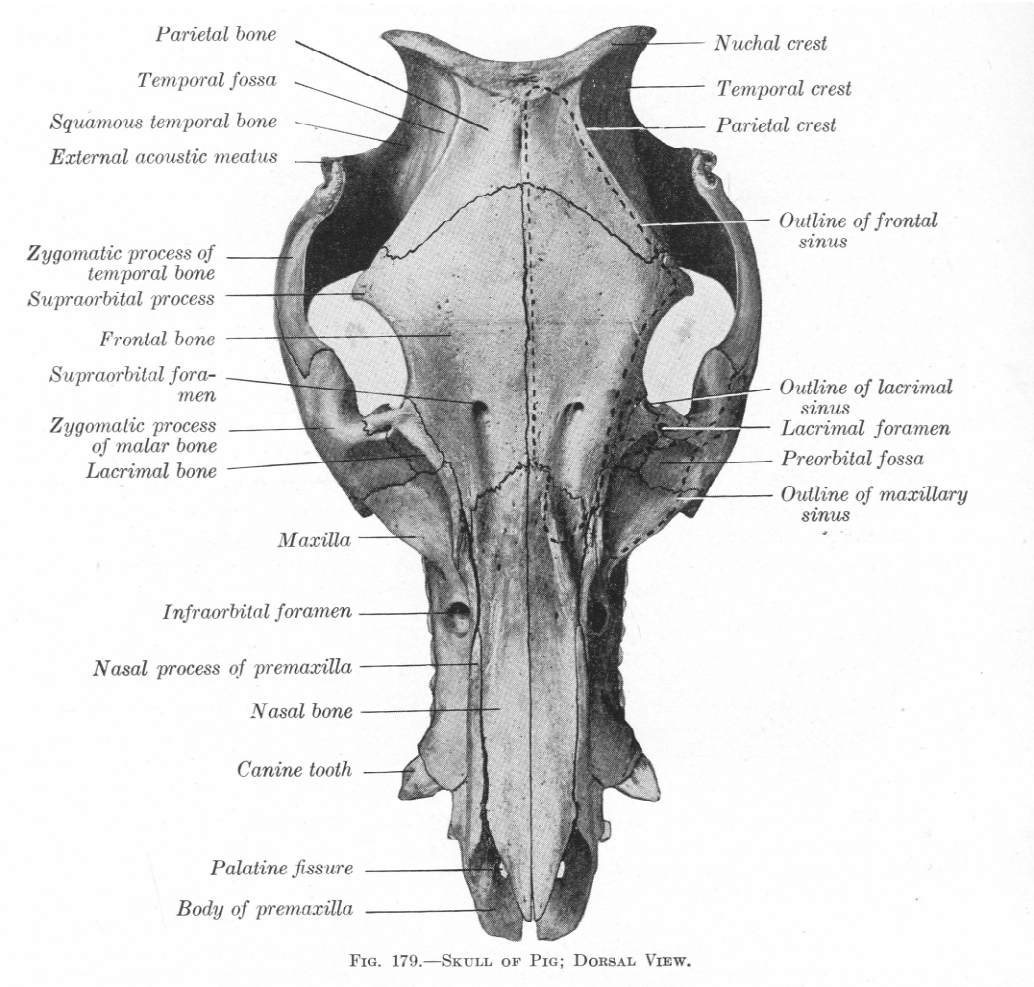

Figure 8c: Dorsal view of a domestic pig crania (Sisson and Grossman, 1910)

2.1.2 Materials

The data for this thesis come from several museum collections: the Museum für Naturkunde Berlin; the Natural History Museum, London; the Muséum National d'Histoire Naturelle, Paris; the Muséum d'Histoire Naturelle de la Ville de Genève; the Museum fur Haustierkunde, Halle; the Field Museum of Natural History, Chicago; the American Museum of Natural History, New York; the Smithsonian National Museum of Natural History, Washington DC and the Royal (Dick) School of Veterinary Studies, Edinburgh.

Three-dimensional landmarks were collected from 1027 pig hemicrania (right side) - including all 3 sub-families of Suinae; the Babyrousini (*Babyrousa*), the Phacocherini (*Phacochoerus*) and especially the Suini (*Sus*), which forms the focus of this thesis.

For the family Phacocherinae 12 individuals of the genus *Ph.aethiopicus* were digitised. In the family Suidae examples from *Babyrousa, Potamochoerus* and *Sus* were digitised. Twenty-eight babirusa (family *Babyrousa*) were collected, mainly *B.celebensis* (22) but also *B.togeanensis* (6). Twenty-four *Potamochoerus*: 15 *P.larvatus* and 9 *P.porcus* were also included (see table 1, Manuscript 1 for details).

The sub-family Suinae is formed of 7 main species (see section 1.2.1) of which 6 are represented in this dataset: *S.barbatus* (32), *S.ahoenobarbus* (6), *S.cebifrons* (14), *S.celebensis* (45), *S.philippensis* (34) and *S.scrofa* (838 including domestics). The only major omission is *Sus verrucosus*, the Javan warty pig, for which no intact crania were available in any of the collections visited (see Table 1, Manuscript 2).

Sus scrofa is the most prolific of the *Sus* species, endemic to most of Eurasia, North-Africa and Island South-East Asia. Examples were collected from a wide variety of this range (see Figure 9), although no groups of a statistically significant size were collected from the Iberian Peninsula, South-East Europe or Central Russia. Future work would make adding these localities a priority. Domestic *Sus scrofa* were collected from the Museum fur Haustierkunde, Halle. The domestic breeds were Berkshire, Cornwall, Tamworth, Veredeltes Landschwein, Hannover-Braunschweig Landschwein and Deutsches Edelschwein, as well as a small sample of first

generation Tamworth-Wild pig hybrids (domestic sows and wild boars). See Manuscripts 3 & 4 for further details.

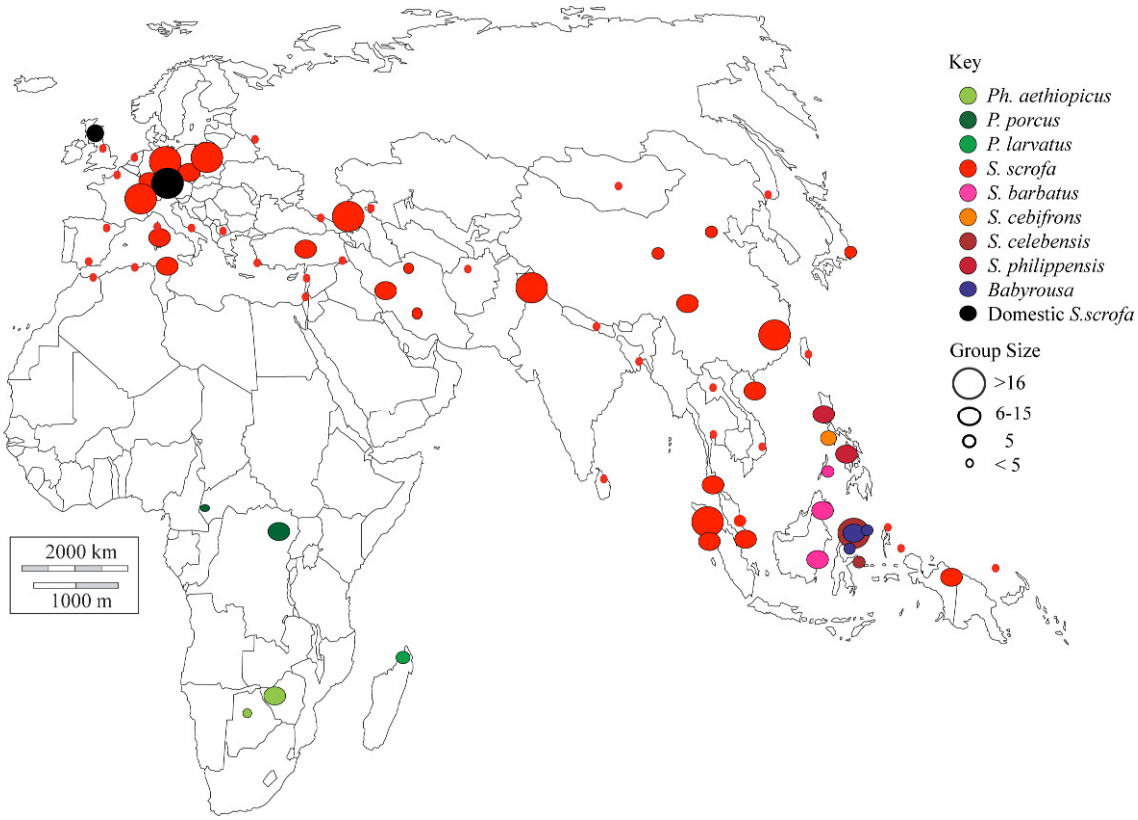

Figure 9: Distribution of samples

2.1.3 Covariates

Geographic covariates were derived from information in museum records; in many cases records were old and/or incomplete as the detail depended on the memory of the hunters or collectors. As a result the exact geographic origins for many of the samples are not known; consequently the data has been collated into geographic regions.

Temperature and precipitation data were extrapolated from the Wilmot and Matsura database (Legates and Willmott, 1990a, 1990b, Willmott and Feddema, 1992,

Willmott and Matsuura, 2001). Values were used for the mean group latitude and longitude. Elevation information for geographic co-ordinates originates from the SRTM3 database, a NASA global survey taken from the GPS visualiser website (Schneider, 2012).

2.1.4 Ageing methods

The majority of domestic individuals are of known age, with specific birth and death dates recorded at the Museum für Haüstierkunde Halle, Germany where they were reared.

It is not possible to assign absolute age of death for archaeological or wild specimens; instead they are assigned to age classes. Wild and domestic individuals of unknown birth or death dates were aged according to Higham (1967). This method is based on dental development, namely tooth eruption with older individuals aged by tooth wear. Tooth wear and eruption are common methods for ageing individuals within archaeological assemblages (Reitz and Wing, 1999) and are based on the premise that tooth eruption is predictable and occurs at the same stage of ontogeny in all individuals.

Problems exist with these methods, mainly a disconnection between proposed tooth eruption and wear classes with the absolute age of death, as variation with e.g. diet can have a profound impact of the rate top tooth wear (Greenfield and Arnold, 2008). There is also debate whether to base the age classes on absolute age of death data based on modern (Payne, 1973) or 19th century (Silver, 1969) pigs. Assessment of these forms of methodology have shown that tooth eruption is more accurate than

tooth wear, but both give broadly accurate estimates (Greenfield and Arnold, 2008, Jones, 2006). These methods are appropriate for this thesis as fine graded distinction is unnecessary between the broad natal, juvenile or adult classes used in manuscript 4.

2.1.5 Biometrics, and issues associated with them

Pigs in an archaeological context are traditionally recorded and compared using weight and size measures, including linear measurements. Traditional biometrics have been used to measure lengths, widths and depths of skeletal elements. Each measurement gives the magnitude of a dimension which is intrinsically size as well as shape based, and it is hard to separate the two components. They also do not give any information on the interior geometry of a shape and each measurement is generally treated individually, rather than as part of a single homologus shape. Additionally, measurements with similar start points are not independent, and if they run in the same direction they may duplicate information (Adams et al., 2004, O'Higgins, 2000, Slice, 2005, Zelditch et al., 2004).

In recent literature discussion has moved on to how biometrical methods may better explore shape. Albarella (2002) suggests that shape is an important tool in classical zooarchaeological studies. Investigations into issues with weight, gender and breed are all more likely to be answered through shape studies rather than size studies. The use of decimal log ratios (introduced into archaeology by Meadow (1981, 1999) and used by Payne and Bull (1988)) where populations of animals can be compared along the same axis (i.e. lengths or widths) to a standard animal form is suggested. This is a step up in complexity but still suffers from the same problems that all biometric

methods do (see above). Subsequently size change has been deemed to be an unsatisfactory method for demonstrating domestication events (Vigne *et al* 2005). As a result there has been a move to alternative research and methodologies, such as Eigenshape outline analysis on teeth – used to distinguish between wild and domestic individuals (Warman, 2005) which drawing from many of the same branches of statistics as geometric morphometrics; genetics (Zeder *et* al 2006), dental defects, such as linear enamel hypoplasia to reconstruct and contrast health of early wild and domestic populations (Dobney and Ervynck (2000); or demographic profiling to show the difference in subsistence strategies between hunter-gatherers and early pastoralists (Zeder, 2006).

2.2 Methods

This section initially explains the theory of Geometric Morphometrics, which underpins all the analyses conducted in this thesis, and is followed by a section containing an overview of the traditional multivariate statistical methods used to analyse the data further.

2.2.1 Geometric morphometrics

Geometric morphometrics is a suite of statistical techniques for the multivariate statistical analysis of Cartesian coordinate data. The data are usually represented by two or three dimensional landmark point locations, through which the information about the relative spatial arrangements of the landmarks is preserved throughout an analysis (Slice et al., 1996). The landmark points create a configuration that represents the biological structure under consideration - in this case, the pig cranium. The landmarks are specifically chosen to be homologous, to be relevant to the scientific questions being posed, and to represent the anatomical shape of the specimens according to set criteria (see 2.2.7). The configurations of landmarks are standardised through a superimposition method called Generalised Procrustes Analysis, from where they may be subjected to traditional multivariate statistics for data exploration and analysis.

2.2.2 Generalised Procrustes Analysis

The superimposition method used in this thesis, and most commonly used in GMM, is called Generalised Procrustes Analysis (GPA). This procedure consists of several steps. First, the configurations are centred on the mean configuration of all landmark co-ordinates, called the centroid (Bookstein, 1996a). Next the configuration is scaled

to the centroid by dividing each co-ordinate of each landmark by the centroid size of the configuration - the centroid size is the square root of the sum of squared distances of a set of landmarks to the centroid (Slice et al., 1996). Finally the configuration is rotated, beginning by aligning all specimens to the first shape of the configuration. This is achieved by minimising the squared distances between corresponding landmarks of the configurations (Gower, 1975). Once all configurations have been aligned to the first, the average shape is determined; all configurations are then rotated to this reference shape. This is repeated until the newly computed average shape ceases to change. Thus the final reference shape is the one that minimises the average distances of all the shapes in the configuration from itself.

After superimposition, shape differences can be described by the differences in coordinates of corresponding landmarks between objects. These differences can also be used as data in multivariate comparisons of shape variation (Bookstein, 1996a).

The process of rotation, translation and scaling creates a shape space where several dimensions are lost. This can be calculated as $pk - k - k(k - 1)/2 - 1$, where p is the number of landmarks and k is the number of dimensions. For three dimensional analysis this works out as $3p - 3 - 3 - 1$ which can be resolved as $3p - 7$ (Slice, 2005). This shape space is known as Kendall's shape space, so called having been first described by him as all the geometric information that remains once location, scale and rotational effects are filtered out from an object (Kendall, 1977, 1984). Thus GPA is the process of moving from a pre-shape space to a shape space – a space where shape is the differential between configurations of points (Zelditch et

al., 2004). GPA fitting was conducted in either Morphologika2 (O'Higgins and Jones, 2006) or MorphoJ (Klingenberg, 2008), and used in all Manuscripts.

2.2.3 Kendall's shape space and tangent space

Kendall's shape space has several properties that have significant implications with regard to geometric morphometrics. The first is that Kendall's shape space describes shape in a curved (non-Euclidean) space (Slice, 2001). Most statistical tools assume analysis is conducted in a Euclidean (linear) space (Mitteroecker and Gunz, 2009, Rohlf, 1998). This problem can be overcome either by working within Kendall's shape space and restricting the suite of useable statistics, or by projecting the co-ordinates from Kendall's shape space into a Euclidean space tangent to Kendall's shape space (Rohlf, 1996). This is an orthogonal projection from the GPA to a linear space tangent at the sample mean (Bookstein, 1996b) that preserves the distances between specimens within the two spaces (Slice, 2005). All GMM analysis in this thesis is conducted in such a tangent (Euclidean) space. The software tpsSmall (Rohlf, 1997) can be used to assess the accuracy of the approximation of the tangent space. In the case of this thesis, the approximation is good, and errors due to the differences in shape space should therefore be negligible.

The second relevant property is that independent isotropic distributions (invariant with respect to direction) of landmarks result in isotropic distributions of points in the shape space (O'Higgins, 2000). Conversely non-isotropic landmark variation will result in non-isotropic variation in shape space. It is this variation that is interesting from a biological standpoint, as this non-isotropic variation is often the result of

climate, sex, age etc. Put simply, variation in shape of the object studied will be reflected in configurations of points in shape space.

It is this construction that underpins geometric morphometric theory, as each point in Kendall's shape space (curved) is represented by a configuration of points in Euclidean (linear) space, irrespective of scale, location or rotation (Adams et al., 2004).

2.2.4 Size

It is important to note that although GPA scales landmark formations, a measure of size is retained in the form of 'centroid size', although this is separate from the product of the GPA. As size is often biologically meaningful, it can be reintroduced as a variable to analyses as the natural logarithm of centroid size (Mitteroecker and Gunz, 2009). Natural log transformation is used in order to scale centroid size relative to the mean configuration (Dryden and Mardia, 1998).

2.2.5 Procrustes distances

The Procrustes distance between individual specimens, or group means, is a measure of the fit between specimens or groups. This is approximately the square root of the sum of squared differences between the positions of the landmarks after GPA and is related to the distance between specimens or groups in Kendall's shape space (Slice et al., 1996). Procrustes distances were calculated in MorphoJ (Klingenberg, 2008) and used in Manuscript 4.

2.2.6 Visualisation Techniques

One of the advantages of GMM is that the morphological differences measured may be visualised, allowing easy dissemination of results to even non-specialist audiences. The visualisation of morphological change is based on the 'deformation' of form. This originated with the use of transformation grids (Thompson, 1917) – inferring the shape change between points by their relative movement, illustrating how the shape of one part of an organism my be described as a distortion of the same part of another (Mitteroecker and Gunz, 2009, O'Higgins, 2000, Zelditch et al., 2004). With regard to GMM, deformation can be expressed between landmarks of the original and reference shapes using homology functions (matching points in the vicinity of one form to that of the other).

One of the problems with deformation and landmark based GMM analysis is that data between the landmarks is lost. To combat this the *thin plate spline* (TPS) interpolation is used (Bookstein, 1989, 1991) which computes a mapping function between two point configurations while the space in-between is smoothly interpolated by minimising the bending energy of the deformation, and results in only localised bending of the deformed surface (Dryden and Mardia, 1998).

For the images in this thesis a surface scan was taken of an adult domestic pig from the Anthropology Department Durham University teaching collection using a Konica Minolta V1-910 non-contact 3D digitiser. This scan was then morphed to represent different groups of pigs as required using the EVAN toolbox (2010). Images generated were used for visualisations in all four manuscripts.

2.2.7 Landmarks

Landmarks form the basis of most geometric morphometric methods. A landmark is a single point on an object, described by Cartesian co-ordinates, that it is biologically, evolutionarily homologous or mathematically equivalent between all specimens and samples under analysis. Homology has several meanings; in evolutionary studies it may be matching parts between organisms – as the structures share an evolutionary background they are therefore homologous (O'Higgins, 2000). In developmental studies physical structures maybe be matched through ontogenetic time, even though these structures may have re-modelled or moved, they are homologous through the continuity of the information they contain (Van Valen, 1982). Mathematical equivalence is concerned with the actual anatomical loci themselves (Zelditch *et al* 2004) rather than the structures they are associated with. When taken as a whole, a collection of landmarks should provide comprehensive coverage of the morphology of an object so that its whole form may be analysed, as landmarks are not considered individually, but as a formation. The information between landmarks is only infered, meaning that inferences regarding form must be made on a general level, not a local one (O'Higgins and Jones, 1998). However, assuming the landmarks are placed on a structure so as to adequately describe its form, when the whole formation of points is analysed change in the shape of the points infers change in shape in the spaces between the points. This is true when visually modelling deformation e.g. using a thin-plate spline (Bookstein, 1991).

To aid the choice of homologous landmarks, Bookstein (1991) devised a series of categories to define landmarks, so that the investigator may determine how reliable

they are. There are 3 categories, Types 1, 2 and 3. Type 1 landmarks are considered optimal, Type 2 less so, and Type 3 landmarks are to be avoided if possible.

Type 1 landmarks are those defined with respect to discrete juxtapositions of tissues, such as triple points of suture intersections, they may be precisely identified and any forces that alter or move them may also be described. Type 2 landmarks lack such information in at least one direction, so forces that affect their position or form cannot easily be determined. Type 2 landmarks include extremities such as the tips of teeth or wings or the ends of bony processes. Type 3 landmarks are defined in juxtaposition to structures, like the endpoints of maximum length, breadth, etc., defined with respect to some distant structure. Landmarks that are derived from traditional metric measurements often fall into this category, being end points of measurements rather than morphologically derived points. Of these, the two- or three-dimensional locations of Types 1 and 2 are most often fully defined with respect to local morphology, and all dimensions are more-or-less biologically informative. Type 3 landmarks, however, are "deficient" in that they contain meaningful information only relative to the remote defining structure and are not defined in all directions (Bookstein, 1991, Slice, 2005, Zelditch et al., 2004).

Further to this classification, Zelditch *et al* (2004) derived five criteria to provide a guide to choosing landmarks for a shape study. They should be (1) homologous anatomical loci that (2) remain in their topological positions relative to other landmarks, (3) provide adequate coverage of the morphology, (4) can be found repeatedly and reliably, and (5) lie within the same plane.

From these descriptions it is obvious that as many type 1 landmarks should be included as possible and that type 3 landmarks should be avoided. However, in order to fulfil Zelditch *et al*'s (2004) third criterion (adequate coverage) this is often not possible, and type 3 landmarks must be used.

2.2.8 Data Collection

Each specimen is represented by a configuration of 44 three-dimensional cranial landmarks. Only unilateral data (the right side of the skull) were recorded. This decision was made to maximise data given the time constraints on data collection, and to reduce redundant variability. The data were collected using a 3-D Microscribe G2 digitiser (Immersion Corporation) by a single person (J.Owen) in order to eliminate inter-observer error. The skull was placed on its side, and supported so that there could be no movement when digitising was taking place.

2.2.9 Landmarks used and explanation for choice

The choice of landmarks was mainly based on the anatomy of the pig skull and the developmental biology behind its formation (Sack, 1982, Sisson and Grossman, 1910). It has also drawn upon classic zooarchaeological biometric practice (von den Driesch, 1976). The 44 landmarks used in this investigation are listed below with the land mark type (1, 2 or 3) given in brackets. The position of the landmarks is visualised in figures 10a and b.

1 Most anterior midline point on nasals (2).

2 Anterior join in nasal and pre maxilliar suture (2).

3 Anterior point of nasal (2).

4 Suture at the meeting point of the premaxillar, maxillar and nasal (1).

5 Most posterior point of superorbital foramen and groove (2).

6 Most lateral point of the Nuchal Crest (3).

7 Most anterior point of Nuchal Crest - on the midline of the paretial (3).

8 Most superior point of zygomatic process of temporal (2).

9 Most posterior point of zygomatic process of malar (2).

10 Superior point of the temporal process of malar (2).

11 Most inferior point of the malar (zygomatic arch) (3).

12 Anterior most point of the process emerging of the malar (zygomatic arch) (2).

13 Most posterior point of infraorbital foramen (2).

14 Most anterior point of infraorbital foramen (2).

15 Most superior point of the lower lacrimal formina (2).

16 Most superior point of the occipital (3).

17 Most inferior point of the occipital (3).

18 Base of supraorbital process (2).

19 Anterior point of incisive foramen/palatine fissure (2).

20 Most posterior point of incisive foramen/palatine fissure (2).

21 Most anterior point of canine alveolus (2).

22 Most posterior point of canaine alveolus (2).

23 Anterior point of the alveolar margin of the tooth row (2).

24-27 Contact points between M3/M2, projected labially (buccally) onto alveolar margin (2).

28 Most posterior point of the alveolar margin of the tooth row (2).

29-32 Contact points between M3/M2, projected lingually onto alveolar margin (2).

33 Most anterior point of the pterygoid process of the palatine (2).

34 Most lateral point of the pterygoid process of the palatine (2).

35 Most posterior point of the pterygoid process of the palatine (2).

36 Suture of the nasal and palatine bones (on the midline) (1).

37 Tip of posterior nasal spine (2).

38 Meeting point between the basisphenoid and basioccipital along midline, posterior of the vomer (1).

39 Anterior most point of the bulla tympanica (3).

40 Most anterior point of the paramastoid process (2).

41 Most anterior point on the margin of the Hypoglossal canal (2).

42 Lowest point on the orobasal border of foramen magnum (2).

43 Most posterior tip of occipital condyle (2).

44 Most superior point on the border of foramen magnum (2).

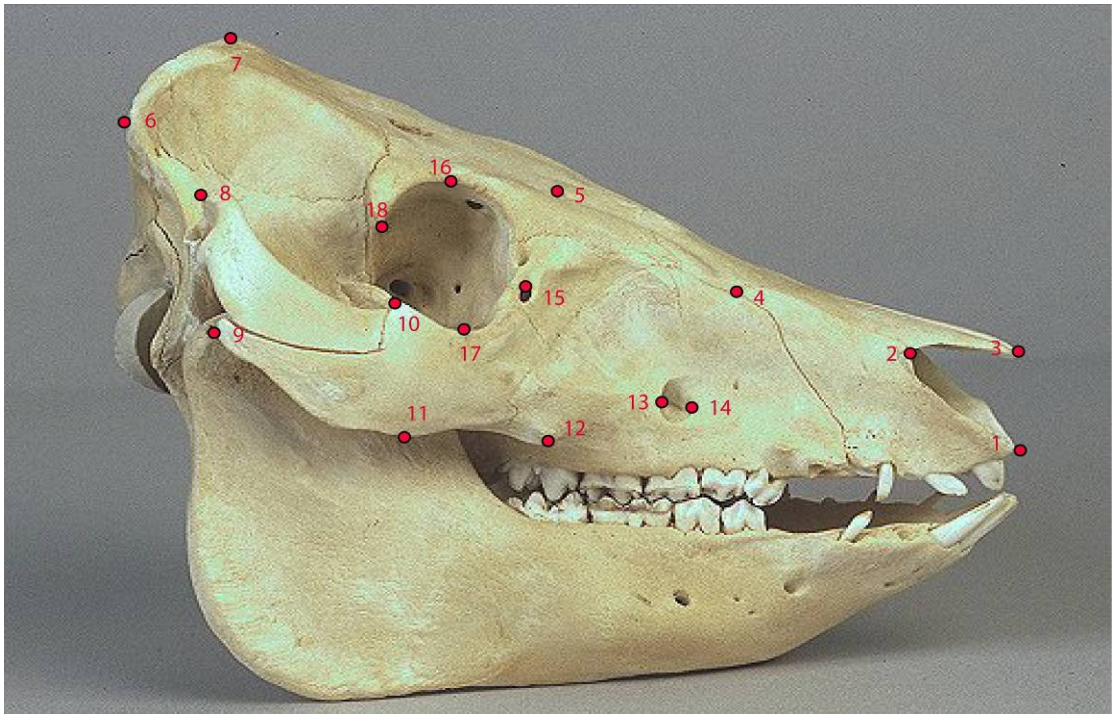

Figure 10a: Position of landmarks on the crania

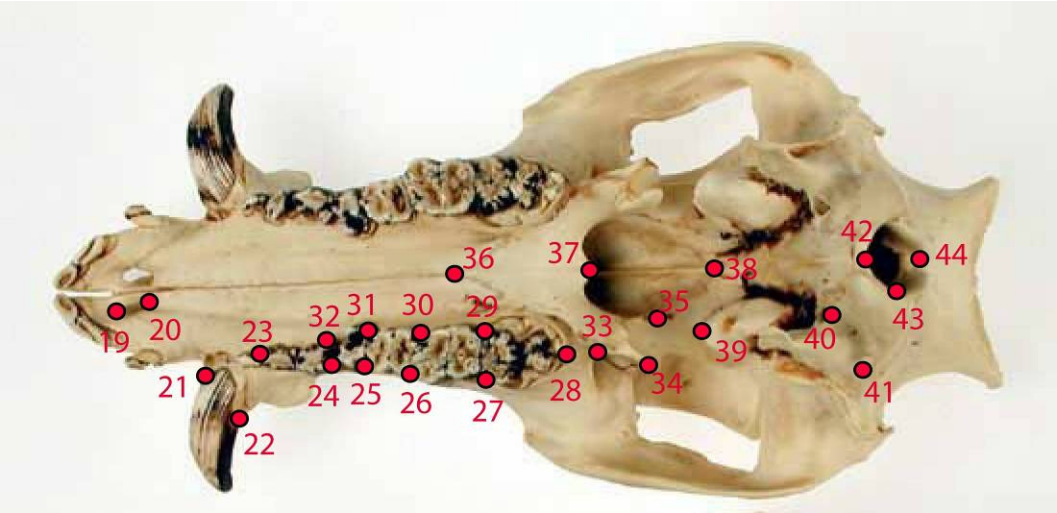

Figure 10b: position of landmarks on the basicranium

Of these 44 landmarks two are Type 1, thirty-six are Type 2 and six are Type 3. The majority of the landmarks are type 1 and 2 and suggest that the methodology should be adequate and not suffer from inherent bias. The 6 Type 3 landmarks (the top and bottom of the occipital and parietal and the tympanic bulla) have been chosen to represent areas of interest in anatomical regions where there are no Type 1 or 2 landmarks. Several obvious suture joints (such as between the frontal, nasal and maxilla) have not been included as these joins are not reliably observed on older animals, even though they appear on many younger individuals, due to continued bony growth and obliteration of the sutures.

In young individuals and Warthogs (*Phacochoerus africanus*) with their different dental formula, landmarks along the tooth row (24-27 and 29-32) are dropped, resulting in a configuration of 38 landmarks. This is noted where relevant in the papers of the results chapter.

2.2.10 Estimating intra-observer error

Method reliability and intra-observer error was assessed following the method proposed by O'Higgins and Jones (O'Higgins and Jones, 1998). A single cranium was digitised 10 times on separate days and compared with an unrelated reference collection (kindly provided by Dr Alastair McDonald from the Division of Veterinary Biomedical Sciences in Edinburgh University Royal (Dick) School of Veterinary Studies). GPA (see 2.2.2) and PCA (see 2.3.1) were then carried out on the data. The results are shown in Figure 13 (below), it shows the results of the PCA, depicting the first two PCs. All the repeats of the cranium used for reliability clusters at the negative end of PC1 (52% total variance) and the positive end of PC2 (16% total variance). The repeats are clustered tightly together, with several of the repeats plotting directly on top of each other. This indicates that errors of precision are small compared to sample variability, and that the landmarks chosen do not induce great amounts of random variation.

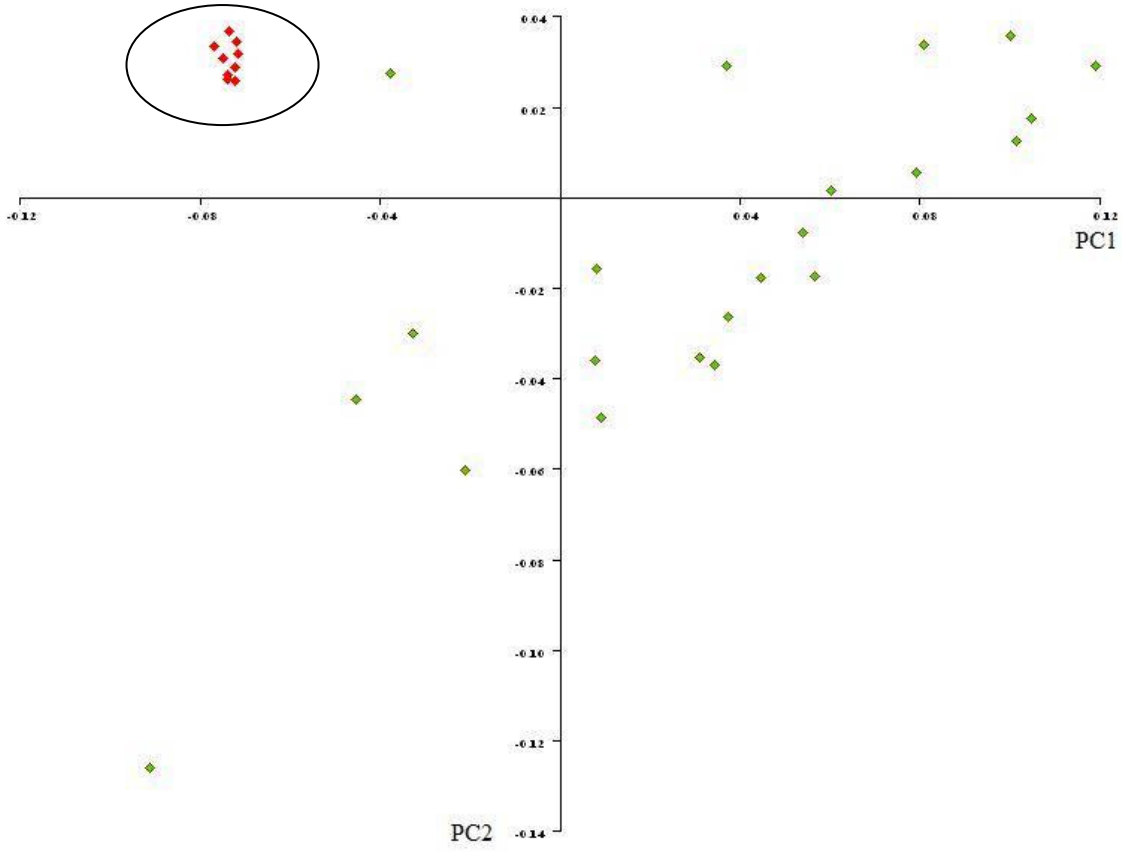

Figure 11: PCA showing 10 repeats of a single specimen in red, compared against a reference collection in green. Note the tight cluster of repeats in the top left hand corner (circled).

2.2.11 Sexual Dimorphism

Sus scrofa are notoriously difficult to sex on the basis of skeletal morphology (von den Driesch, 1976, Payne and Bull, 1988). The major difference between males and females is the form of the canine, which is larger and more curved in males, and in females has a channel running along the anterior side of the tooth (von den Driesch, 1976).

Size is frequently used for discrimination between the sexes. Males are held to be larger than females, but this is difficult to quantify in mixed wild-domestic

populations, as differences in size are also very notable between those groups. In early assemblages the wild pigs are larger, while in modern assemblages, where domestic pigs have received 'improved' or intensive breeding programs, domestic pigs are larger. These size differences are often greater than those due to sexual dimorphism and can easily override any sex related signal (Vigne et al., 2005).

No shape related sexual dimorphism has been catalogued in pigs using traditional biometric techniques. To test if there are any morphological differences solely attributable to sex that might influence the results of these investigations several tests were applied (Gonzalez et al., 2009). ANOVA was used to test size differences between the sexes, and MANOVA to test shape differences between the sexes. Two samples were used to test for sexual dimorphism, one of wild pigs from a single geographic region (Poland) to remove possible effects of climate or geographic variability, and a sample of domestic pigs (Deutsches Edelschwein - from East Germany) were also tested for sexual dimorphism.

Sexual dimorphism was found to be non-significant in wild pigs, 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 $p=<0.001$, $df=125$, $F=2.5$). For a 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 ($p=<0.001$, $df=125$, $F=5.07$). Due to the small sample sizes available we conflated the males and females into a single sample - being aware that sexual dimorphism in the wild sample could potentially be a source of bias. However, mixing the male and females groups replicates conditions

found when analysing archaeological material, as it is difficult assess the sex of pigs, especially in the absence of canines (von den Driesch 1976, Payne and Bull 1988).

2.2.12 Allometry

Allometry describes the relationship between body size and shape. In GMM it is the linear or linearised characterisation of the dependence of shape on size. This relationship is often the focus of studies, especially when describing shape change during ontogeny e.g. in primates (Mitteroecker et al., 2005), hippos (Weston, 2003) and marmots (Cardini and O'Higgins, 2005).

Allometry between adult specimens may be investigated using multivariate regression with log centroid size as the independent variable and PC scores as the multidimensional variables of shape. The correlation of shape, size and age is assessed and the significance of the angle of ontogenetic trajectories of pairs of populations tested using re-sampling and permutation tests (Viðarsdóttir et al., 2002, Mitteroecker et al., 2005). To remove the effects of allometry from a study, log size is regressed against shape and further analysis is then conducted on the regression residuals.

2.3 Methods of analysis

Detailed in this section are some of the common statistical methods used to analyse data in this thesis.

2.3.1 Principal Components Analysis (PCA)

Principal components analysis is widely used in morphometrics to simplify the exploration of shape variability by reducing the dimensionality of the data. It ranks co-variance factors (in the form of new variables or principal components) and gives each a score (as an eigenvalue) to describe what proportion of variance is described by each principal component.

The first step of PCA is to determine the direction of greatest variance; a vector which minimises the sum of squared distances between itself and the data points. This is the first principal component. Each subsequent principal component is computed the same way as the first, except that all correlation with preceding principal components has been removed, thus making each principal component independent. In effect, the first principal component describes the largest proportion of variance in the dataset, the second component describes the second largest proportion of variance and so on. This allows the majority of variance to be explained by a small number of principal components (typically the first few PCs summarise the majority of variance within the data), simplifying interpretations without the loss of much information (Rao, 1964).

Principal components can also be used as variables in their own right, replacing Procrustes fitted landmark scores. This is especially useful in datasets with high

degrees of dimensionality, as it can simplify analysis. By using only the scores on the first few principal components which typically contain most of the variation within the dataset, rather than all principal components, a summary of multidimensional data is created (Klingenberg and McIntyre, 1998). A degree of caution should be exercised when selecting PCs, so as not to remove potentially biologically meaningful variability and affecting the outcomes of further statistical tests.

Principal components scores can be used to identify clusters of data. It is useful to note that because PCA in this case is being computed from shape variables; visual references of variation can be generated by multiplying the original shape variables by the PC coefficients and summing them (Legendre and Legendre, 1998, Zelditch et al., 2004). PCAs were created in Morphologika2 (O'Higgins and Jones, 2006), MorphoJ (Klingenberg, 2008), the EVAN Toolbox (EVAN Toolbox, 2010) or SPSS (© Microsoft Corporation) and used in all four Manuscripts.

2.3.2 Canonical Variates Analysis (CVA)

Canonical variates analysis (CVA) is a method used to find the shape features that best distinguish multiple groups of specimens that have been defined prior to analysis (Slice et al., 1996). It is frequently used in an exploratory style to visually assess the separation of groups, and the presence of areas of high or low data density (Mitteroecker and Bookstein, 2011). It is designed to simplify descriptions of differences between groups that are mutually exclusive (i.e. they vary by a categorical variable), which can include traits such as sex and species, these are sometimes known as ‘qualitative traits’ or ‘grouping variables’. Generally these traits should be discontinuous but sometimes continuous variation can be graded and

classified like discontinuous variation (for example where information is limited or occurs along a graded scale). Where this occurs such continuous traits are treated as separate groupings for the purpose of the analysis, but limits the inferences that may be drawn from the conclusions (Zelditch et al., 2004).

CVA finds linear transformations of the data which maximize the among group variation relative to the pooled within-group variation. The canonical variates may then be displayed as an ordination to show the group centroids and scatter within groups. This gives a new co-ordinate system by which the position of each group may be described. This may be thought of as a 'data reduction' method in the sense that one wants to describe among group differences in few dimensions. The vectors of coefficients are orthogonal as in Principal Component Analysis, although the canonical variates are uncorrelated with each other (Drydan and Mardia, 1998; Slice et al., 1996). CVs are not a complete description of the differences between groups, they represent the part of the difference between groups that is most useful discriminating between them, the part that has the least variation within groups relative to the difference between them (Zelditch et al., 2004).

CVA produces results that look quite different to those produced by PCA for two reasons. Firstly, CVA maximises differences between groups, and this is often different to how individuals differ. Secondly, CVA re-scales to axes that optimise between group variation relative to within group variation. This difference between PCA and CVA can be useful to illustrate which shape vectors are causing shape change. CVA can represent dissimilarity between groups of specimens in a two dimensional scatter plot as it has maximised the differences between them on a single

CV (Mitteroecker and Bookstein, 2011), where as PCA may spread the differences between groups on multiple vectors (PCs), making it hard to illustrate the difference between groups in two dimensional plots, although the differences on individual PCs may point to potential sources of biologically meaningful variation between samples that would be harder to spot on a CVA. CVAs were created in MorphoJ (Klingenberg, 2008) and used in Manuscripts 1 and 2.

2.3.3 Permutation Tests

Permutation tests resample groups without replacing them, in this thesis they are used to assess the reliability of CVAs (2.3.2) and regression analysis (2.3.8). Groups are randomly re-assigned, or permuted, a set number of times and pair-wise differences in the means of the permuted sets are calculated. The proportion of times in which the difference between the means of the permuted sets exceed that of the original groups is taken as the probability that the observed value could have arisen by a random splitting of the underlying distribution (Zelditch et al., 2004). Permutation tests were computed in MorphoJ (Klingenberg, 2008) and SAS, in manuscripts 1, 2 and 4.

2.3.4 Discriminant Functions (DFA)

Discriminant function analysis (DFA) examines the separation between two or more groups known prior to analysis, testing the hypothesis that members of these groups are distinguishable. DFA determines whether group means differ and then predicts group affiliation on the basis of discriminant functions (Sneath and Sokal, 1973). These are derived by building linear combinations of the original variables that maximize between to within-group variance. The groups are clustered around the

mean discriminant score (the centroid) for each group, for each function. Classification is based on each case's proximity to the groups' centroid, and probabilities are calculated to express the likelihood that the case belongs to each of the groups. The smallest distance and highest probability determines the case's group assignment (Kovarovic et al., 2011).

This can be conducted between multiple groups so that they are analysed within the same shape space, which will produce distances (Mahalanobis' or Procrustes distances) between pairs of groups (Zelditch et al., 2004). As the multivariate space is scaled by the inverse of the pooled within group variation, distances within this transformed space are independent of the scale of measurement and differences are expressed in units of standard deviations. The result is that even though discriminant axes can be visualized as shape deformations, they should not be interpreted as meaningful biological factors due to this rescaling (Bookstein, 1991, Mitteroecker and Bookstein, 2011). Therefore, DFA is most useful for comparisons of specific groups, whereas CVA may be more useful for general analysis of group structure in a dataset (Klingenberg and Monteiro, 2005). The reliability of DFA in discriminating between groups is tested with leave-one-out-cross-validation (see below) (Zelditch et al., 2004). DFA was used in manuscripts 1 and 3, they were conducted in MorphoJ (Klingenberg, 2008) and R (R Development Core Team, 2008).

2.3.5 Cross Validation

Discriminant functions and CVA frequently over fit data. DFA must provide group assignment for each individual and it maximises differences between groups which can result in a higher rate of correct assignment than chance alone would allow, even

in datasets that have fictional relationships (Kovarovic et al., 2011). To avoid the effects of such over fitting re-sampling techniques are employed. Two types were used in this thesis, leave-one-out cross-validation with discriminant functions, and permutation tests (see 2.3.3) with CVA and regressions.

Cross validation assesses how accurately a predictive model will perform in practice. Data are partitioned into complementary datasets, performing analysis on one subset (called the *training set*), and validating the analysis on the other subset (called the *validation set*). Multiple rounds are performed using different subsets and the results averaged. Leave-one-out-cross-validation partitions a single observation as the validation set, and uses the remaining dataset as the training set. This is repeated so that each observation is used once as the validation set, producing k numbers of cross-validations, where k is the number of observations in the dataset (Lauchenbruch, 1967). Cross validations were conducted in MorphoJ (Klingenberg, 2008) and R (R Development Core Team, 2008).

2.3.6 Student's and Hotelling's *t*-tests

t-Tests are used to compute the significance of differences between group means. A *t*-test evaluates the probability that two samples with means differing by an observed amount could be explained by random sampling from a single population within the overall variance.

Student's *t*-test compares the means of two groups of univariate data (e.g. size) in order to test the hypothesis of equality between the means. It determines whether any difference is due to random variation or is statistically significant (Legendre and

Legendre, 1998). Hotelling's *t*-test is a generalisation of students *t* statistic (Hotelling, 1931) used with multivariate data. It compares multiple means at the same time by computing the mean vector between two groups, testing the hypothesis that two groups originate from populations with the same centroid (e.g. shape) (Legendre and Legendre, 1998). *t*-Tests were conducted in Excel and SPSS (© Microsoft Corporation).

2.3.7 ANOVA and MANOVA

Significance between groups can be assessed without computing group means using ANOVA. ANOVA stands for *analysis of variance*, where by the variance explained by a categorical variable is compared the variance it does not explain. This ratio (explained variance divided by the unexplained variance) is given as the *F* statistic. The *F*-value is the probability of an equal or larger *F*-ratio for two samples drawn randomly from the same distribution (Legendre and Legendre, 1998).

ANOVA compares variation within groups to variation between groups. As such it can be used to examine differences between multiple groups, and multiple categorical variables. In this thesis ANOVA is used mainly to examine differences in size between groups.

Differences in shape are assessed using either Hotelling's T^2 test (to test for differences between two group means (see 2.3.6) or MANOVA where there are more than two groups. MANOVA stands for *multivariate analysis of variance* and like ANOVA it compares means between groups, but does it for means in multivariate data, like shape. Shape is a single, complex trait described by several continuous

components, to analyse it a multivariate version of the *F*-statistic is needed, one that is also a function of the within-group and between-group variance. A common statistic to fulfil this is Wilks-Lambda, which is a product of the non-zero eigenvalues of the variance-covariance matrices of the groups in question (Legendre and Legendre, 1998, Zelditch et al., 2004). These were computed in MorphoJ (Klingenberg, 2008), and in Excel and SPSS (© Microsoft Corporation), they were used in all four Manuscripts.

2.3.8 Regression

Regression is used to estimate and describe the relationship between a dependent (generally a random) variable (*y*) and a set of independent (explanatory) variables (*x*), to predict the values of *y* for given values of *x* (Legendre and Legendre, 1998). In geometric morphometrics it is often used to test the relationship between size and shape (Meloro et al., 2008, Mitteroecker et al., 2005), or size or shape against other continuously valued factors such as latitude, longitude or climate (Cardini et al., 2007).

In a simple linear regression there is a single *x* and *y* variable. The regression here attempts to draw an optimised straight line (hence the name linear) through a scatter of points for which *x* and *y* are known. Resolution of the regression allows an estimation of *y* for any value of *x* (Legendre and Legendre, 1998).

To investigate shape, which is a multidimensional variable, multivariate regression is required. This is the regression of several dependent variables (e.g. multidimensional shape) onto a single independent variable (e.g. size or temperature). The coefficients

obtained by multivariate regression are the same as those estimated by bivariate regression but the tests of significance used are Wilks' Lambda, or in the case of regression of shape and size Goodall's *F*-statistic (Zelditch et al., 2004). Rather than run regression on Procrustes fitted co-ordinates, principal components scores are used as they have the correct degrees of freedom ($3k$-7 – where k is the number of landmarks – see section 2.2.2). This also allows a reduced data set to be run, in cases where there is high dimensionality that may not be biologically meaningful (Zelditch et al., 2004).

Multiple linear regressions can be either multivariate or bivariate, and are used with one (bivariate) or more (multivariate) dependent variables and two or more independent variables. The relationship between the dependent variables (y) and the independent variables (x) is still scalar, in the same manner as a simple multiple regression (Legendre and Legendre, 1998). Multiple multivariate regressions can be used to explore wider relationships of shape and size, e.g. with climate - including permutations of temperature and precipitation (Cardini and Elton, 2009).

Regressions were computed in Excel and SPSS (© Microsoft Corporation), MorphoJ (Klingenberg, 2008) and Morphologika2 (O'Higgins and Jones, 2006). Linear and multiple multivariate regressions were used in Manuscript 2 and in Manuscript 4.

2.3.9 Cluster Analysis and Neighbour Joining Trees

Cluster analysis is a hierarchical method of summarising a multivariate distance matrix between specimens in a single diagram (Slice et al., 1996). The diagram can either be a tree like, called a dendrogram, or a network. Cluster analysis assigns a set

of objects into groups (called clusters) so that the objects in the same cluster are more similar to each other than to those in other clusters. There are many different types of algorithms used, but in GMM a widely used method is neighbour joining (NJ) (Saitou and Nei, 1987) which builds phonetic trees (phenograms) or networks.

Neighbour joining takes as input a distance matrix specifying the distance between each pair of individuals, taxa or groups. In this thesis Procrustes distances were used. NJ determines which pair has the lowest value (smallest distance) and joins these neighbouring groups to the tree or network with a node, which is then fixed in place. The distance matrix is then recalculated, replacing the pair of joined neighbours with the node, determining the distance from each of the groups to the node. This process is iterative, until till all the groups are joined. NJ is a simple model as makes no assumptions of the data (Legendre and Legendre, 1998). NJ trees were computed in NTsys 2.1 (Rohlf, 2008) and used in Manuscripts 1 and 2.

2.3.10 Mode of evolution

In manuscript 1 the mode of evolution of Suids was investigated to elucidate the evolutionary history of the African genus *Potamochoerus*. This was first assessed by studying the scaling relationship of shape divergence and time since common ancestry. Here morphological (Procrustes) distances are used for shape divergence and genetic distances stand proxy for evolutionary time (Gomez-Robles and Polly, 2012). This reveals whether the mode of evolution in the family Suidae results from long-term directional, stabilizing, or randomly varying selection (Polly, 2004, 2008, Gomez-Robles and Polly, 2012).

Distances between pairs of species were plotted on a scatter graph with genetic distances on the x axis and Procrustes on the y. The mode of evolution was determined by assessing whether the scaling of morphological divergence is linear with respect to the genetic distances (directional or diversifying divergence); curvilinear as the square-root of genetic distance (Brownian motion); or flat (stabilizing selection or stasis), using Maximum Likelihood (Gomez-Robles and Polly, 2012) to estimate the evolutionary mode coefficient from the following equation:

$$P = t \wedge a$$

where P is morphological divergence, t is time since common ancestry (genetic distance serves as the proxy for this), and a is the mode coefficient ranging from 0.0 to 1.0. In a random walk process phenotypes diverge with the square root of time (0.5); in a directional process divergence is linear with time (1.0); and in perfect stasis there is no divergence with time (0.0) (Polly, 2008, Polly, 2004, Gomez-Robles and Polly, 2012). The number of independently evolving variables refers to the number of significant principal components contributing towards the Procrustes distance score.

To determine the mode of evolution responsible for the previously observed incongruence between *Potamochoerus* and *Sus*, the phylogenetic tree was projected into suid morphospace (Polly, 2004, 2008, Gomez-Robles and Polly, 2012, Rohlf, 2002). Cranial shape scores for species were reconstructed at the ancestral nodes of the phylogenetic tree (Gongora et al., 2011) following the methodology of Martins and Hanson (see equations 4 and 5) (Martins and Hansen, 1997), and projected into morphospace with a linear extrapolation along the branches (Polly, 2008). The

projections were constructed by plotting PC scores for each node and genus. The nodes were connected in order of last common ancestor and the genera to the nearest ancestral node. This generalised linear model method assumes a Brownian Motion mode of evolution and is inherently conservative. This model was used to reveal the relationship between morphology and genetic ancestry in suids. Mode of evolution analysis was conducted in Mathematica 8.

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Chapter 3

Manuscript 1

Resolving genetic and morphological phylogenies within Suidae

Title: Resolving genetic and morphological phylogenies within Suidae

Running head: Resolving genetic and morphological incongruence in pigs

Joseph Owen[1,2], P. David Polly[3], Keith Dobney[4], Allowen Evin[4,5], Helgi Gunnarsson[6], Greger Larson[7] and Una Strand Vidarsdottir[2]*

[1]*Department of Archaeology, Durham University, South Road, DH1 3LE, UK*

[2]*Department of Anthropology, Durham University, South Road, DH1 3LE, UK*

[3]*Departments of Geological Sciences, Biology, Anthropology, Indiana University Bloomington, 1001 E. 3rd St. Jordan Hall 142 Bloomington, IN, 47405-7005 USA*

[4]*Department of Archaeology, University of Aberdeen, St Mary's Building, Elphinstone Road, AB24 3UF, UK*

[5]*Centre National de la Researche Scientifique, 3 Rue Michel-Ange, 75794 Paris, France*

[6]*EVAN Society, University of Vienna, Althanstraße 14, A-1090 Wien, Austria*

[7]*Durham Evolution and Ancient DNA, Department of Archaeology, Durham University, South Road, DH1 3LE, UK*

**Corresponding author: una.vidarsdottir@durham.ac.uk*

Abstract

Phenetic trees derived from morphology often differ from independently estimated phylogenetic trees, usually as a result of convergent or parallel evolution. Within the family Suidae, there is marked incongruence between the morphological and genetically derived relationships between the sub-Saharan African genus *Potamochoerus* and the Eurasian *Sus*. Genetic studies place sub-Saharan African pigs in a monophyletic clade but morphological analyses suggest that *Potamochoerus* is more closely related to *Sus* than to other sub-Saharan pigs. These conflicting interpretations hamper a resolution of the systematics of this group and confound efforts to understand whether suid colonisation of the African continent occurred once or multiple times. In order to understand the source of the conflicting topologies, we applied geometric morphometrics and multivariate statistics to 38 unilateral homologous landmarks from 471 African and Eurasian suids. We then

reconstructed the ancestral node of Suidae and tested the mode of evolution. *Potamochoerous* is genetically more closely related to African genera but like *Sus*, it possesses a generalist morphology and occupies the same ecological niche. This shared generalist behaviour, a direct consequence of the evolutionary history of *Potamochoerous*, is the principal reason why morphology alone fails to reveal the monophyly of African suids.

Introduction

The family Suidae is one of the most geographically widespread of extant terrestrial mammals. Suids inhabit six continents as a result of both natural dispersal and human-mediated introductions [1]. Despite their abundance, our understanding of their evolutionary history and dispersal [2, 3], the monophyletic status of some genera, and the phylogenetic relationships within the genus *Sus* [4], remains incomplete. More specifically, there is marked disparity between the position of sub-Saharan *Potamochoerus* and Eurasian *Sus* on trees constructed using genetic and morphological data. While genetic data [3] reveal a deep split between these genera, morphological studies show striking similarities in cranial shape [3, 5, 6]. Explanations for this disparity include: retention of ancestral traits [3, 7], parallel evolution in response to dietary pressures [3, 7], and convergence due to inhabiting similar ecological niches [5].

Combining and contrasting information from morphology and genetics is rapidly becoming an important area of taxonomic research [8]. Morphological studies have quantified the integration and modularity of phylogenetic signals within structures [9] and assessed the strength of phylogenetic signals in the phenotype by quantifying the congruence between phylogenetic and phenetic trees [10]. Alternative approaches project the phylogenetic signal within morphological space, in order to visualise the phylogenetic history of phenotype [11, 12], while genetic studies have investigated the effect of genes on morphological diversity [13] through multivariate quantitative genetics [14].

Using morphometric data to estimate evolutionary relationships remains controversial [9, 10], since the topologies of phylogenetic trees derived from phenotypes rarely match those derived from genotypes [15]. This incongruence

results from phenotypic history including both adaptive and non-adaptive genetic components in conjunction with non-genetic environmental factors. As a result, morphometric data always possesses both phylogenetic and non-phylogenetic signals [10]. Phenotypic change is also complicated because it involves both quantitative changes in existing morphological structures, transformations which may not have a linear relationship with the underlying genetic changes [8], and the addition of 'novel' structures (i.e. structures that are not homologous to those found in the ancestral morphology) [16]. Furthermore, phylogenetic signal is weakened by parallel evolution and convergence [15]. Methods used to map shape variation onto independent phylogenies have been well tested and can now account for the mode of evolution and explain incongruence between morphology and genetics [8, 17].

An integrated application of genetic and morphological taxonomic approaches has the potential to provide alternative and deeper insights into species' developmental history, especially when there are marked topological differences in the evolutionary trees they generate. Perhaps the best-documented example can be found in the order Cetartiodactyla, where both the sister taxon of Cetacea and the monophyly of specific clades are uncertain. Genetic studies place Cetacea with Hippopotamidae [18, 19], whereas studies of morphology place Cetacea with the extinct family Raoellidae and Hippopotamidae with Suina [20, 21]. A reconciliation has been suggested by studies combining topologies from trees generated by genetics and morphology [22, 23], studies combining Hippopotamidae molecular and fossil data [24, 25] and a re-evaluation of earlier morphological work in light of the genetic discoveries [26, 27]. All of these approaches support the existence of a separate Cetancodonta clade (Hippopotamidae + Cetacea).

Both genetics [3, 28, 29] and morphology [4-6, 30, 31] have been used to study suid systematics, but have only been combined in one regional study of *Sus* species in Island South East Asia (ISEA) [32]. Here, we present the results of a large-scale study of the family Suidae undertaken to resolve the incongruence between *Potamochoerus* and *Sus*. In doing so, we established the details of the incongruence between the genetic and morphological trees of 10 suid taxa studied, and compared phenotypic relationships with known phylogenetic relationships. We then modelled the overall mode of evolution of suids and compared the individual genera with this

overall mode to determine whether their evolution was directed or constrained. Finally, we generated the ancestral shape scores of suids by projecting the genetic tree into morphospace to map the evolution of each genus. This provided an explanation for the apparent incongruence in the genetic and morphological relationships and revealed the evolutionary history of the African branch of the suid family.

Materials and Methods

We analysed 471 adult museum specimens (Fig 1, Table 1) representing four of the six extant genera of suids (Table 1): *Babyrousa* from ISEA, *Phacochoerus* and *Potamochoerus* from sub-Saharan Africa and *Sus,* from Eurasia, North Africa and ISEA. The dataset was tested for effects of sexual dimorphism but no significant variation in shape was found, so both sexes were amalgamated in all analyses.

Thirty-eight unilateral three-dimensional coordinates (Supporting Table S1) were digitised from the right side of the cranium, using a Microscribe® GLS (EMicroscribe Inc), by the first author. Specimens were standardised using Generalised Procrustes Analysis (GPA) [33] and morphological relationships explored using Principal Component Analyses (PCA) and Canonical Variance Analyses (CVA). Significance of differences in shape between groups was assessed using Multivariate Analysis of Variance (MANOVA) as well as discriminant functions with leave-one-out cross-validation. A Neighbour-Joining (NJ) tree (Fig 2) depicting the phenotypic proximity of groups was constructed from Procrustes distances between group means (Supporting Table S2). A second NJ for the same genera was generated from genetic distances derived from Gongora *et al*.'s [3] Maximum Likelihood tree based on 2 concatenated nuclear and 8 mitochrondrial sequences. Analyses were conducted using MorphoJ [34], Morphologika2 [35, 36], NTSys [37], the EVAN Tool Box [38], R (version 2.13.0 R Development Core Team), and the *Morphometrics for Mathematica* package [39].

The mode of evolution in the family Suidae (i.e. the pattern of divergence resulting from long-term directional, stabilizing, or randomly varying selection [40-42]) was assessed through comparison of genetic and morphological (Procrustes) distances [40]. Distances between pairs of species were plotted on a scatter graph with genetic

distances on the x axis and Procrustes on the y. The mode of evolution was determined by assessing whether the scaling of morphological divergence is linear with respect to the genetic distances (directional or diversifying divergence); curvilinear as the square-root of genetic distance (Brownian motion); or flat (stabilizing selection or stasis), using Maximum Likelihood [42] to estimate the evolutionary mode coefficient from the following equation:

$$P = t \wedge a$$

where P is morphological divergence, t is time since common ancestry (genetic distance serves as the proxy for this), and a is the mode coefficient ranging from 0.0 to 1.0. In a random walk process phenotypes diverge with the square root of time (0.5); in a directional process divergence is linear with time (1.0); and in perfect stasis there is no divergence with time (0.0) [40-42]. The number of independently evolving variables refers to the number of significant principal components contributing towards the Procrustes distance score.

To determine the mode of evolution responsible for the previously observed incongruence between *Potamochoerus* and *Sus*, the phylogenetic tree was projected into suid morphospace [40-43]. Cranial shape scores for species were reconstructed at the ancestral nodes of the phylogenetic tree [3] following the methodology of Martins and Hanson (see equations 4 and 5) [44], and projected into morphospace with a linear extrapolation along the branches [40]. The projections were constructed by plotting PC scores for each node and genus. The nodes were connected in order of last common ancestor and the genera to the nearest ancestral node. This generalised linear model method assumes a Brownian Motion mode of evolution and is inherently conservative.

Results – Variation in Suid Cranial Morphology

An assessment of large-scale variability in suid cranial shape using PCA (Fig 3a) revealed a morphological separation between *Phacochoerus* and *Babyrousa* at either extreme of the first principal component. Further separation of groups did not occur on any other single PC but a MANOVA based on all PC scores revealed statistically significant morphological distances between all samples in Figures 3a and 3b (Fig 3a p=<0.0001 df=4280 F=2202.09; Fig 3b p=<0.0001 df=3852 F=1089.98). The morphological distinctiveness of each species was further supported by discriminant

functions with cross-validation (Supporting Table S3), which correctly assigned a high percentage of specimens to the correct taxon - >85%, with the exception of *S. cebifrons* (75%) and *P. larvatus* (40% - all mismatches assigned to *P. porcus*).

The relative relationships within the main cluster of *Sus* and *Potamochoerus* (Fig 3a) were illustrated using CVA (Fig 3b). CV1 separated *S. scrofa* and *Potamochoerus* from *S. celebensis, S. philippensis* and *S. cebifrons*, while CV2 separated *S. barbatus* and *S. ahenobarbus* from the other *Sus* species.

Phylogenetic and Phenetic Relationships within Suids

Fundamental differences were evident in the topologies of the NJ trees derived from the genetic and morphological datasets. The genetic tree (Fig 2 left) contained two monophyletic clades: the African genera *Phacochoerus* and *Potamochoerus*; and *Sus* and *Babyrousa*, where *Babyrousa* was a sister taxon to *Sus*. In the morphological tree (Fig 2 right) *Ph. aethiopicus* was the most morphologically distinct suid genus followed by *Babyrousa. Potamochoerus* grouped with *S celebensis* within the *Sus* cluster. Though African pigs were genetically monophyletic, morphologically they were paraphyletic.

Mode of Evolution and Ancestral Nodes Reconstruction

Figure 4a shows the results of the Maximum Likelihood estimation of the mode and tempo of evolution. Points were plotted as distances between species pairs, with the Procrustes distance on the y-axis and the genetic distance on the x-axis. Pairs above the mode line diverged faster - given their genetic distance - than expected (i.e., there is greater directional selection to make them more different), and pairs that lie below the line diverged more slowly (i.e., there is greater stabilizing selection to keep them from diverging). Taxon 3 (*Ph. aethiopicus*) is more divergent from all the taxa than expected, signifying that directional selection has been involved sometime during its evolutionary history. Taxa 1+2 and 4+5+6 (*Potamochoerus* and *Sus*) were less divergent from each other than expected, suggesting that they have been influenced by stabilizing selection or homoplasy.

Despite its morphological distinctiveness, taxon 7 (*Babyrousa*), was no more different from any taxon (other than *Phacochoerus*) than expected given its genetic

distance, meaning that no special claim for directional selection was necessary. The estimated mode for suids was 0.575, slightly more directional than random. The rate of evolution was 0.342 Procrustes units per genetic unit (0.1), with three independently evolving variables.

Figure 4b depicts the ancestral node reconstructions. Here, *Ph. aethiopicus* and *Babyrousa* moved away from two clusters of *Sus* and *Potamochoerus*. *Sus* only moved a short distance from the basal node, while *Potamochoerus* converged on *Sus* as the nodes connecting them have wandered apart before moving closer.

Discussion

Our results demonstrate that although there is a marked discrepancy between phenotypic and genotypic relationships in the Suidae, the combined signals from both patterns of variability inform the evolutionary history of this group to a greater degree than either dataset can demonstrate on its own.

A clear genetic monophyly was evident in the African suids (Fig 2a). This topology was not recovered using phenotypic data (Fig 2b), which instead revealed a closer relationship between *Potamochoerus* and *Sus* than with other sub-Saharan suid taxa. Modelling the mode of evolution (Fig 4a) revealed that *Potamochoerus* cranial shape was severely constrained, causing it to be less divergent from *Sus* than the model would have predicted. The cause for this constraint was shown in the ancestral node shape reconstruction (Fig 4b), which demonstrated that *Potamochoerus* was convergent with *Sus,* thereby explaining the incongruence in the topology between the genetic and morphological trees.

The similarity of form in teeth [45] and crania [5] between *Potamochoerus* and *Sus* has previously been observed [3, 5], and alternatively explained as either convergence[5], stasis [7], or parallel evolution [3]. The results of our ancestral node reconstructions implied that *Potamochoerus* was convergent with *Sus*, and that homoplasy is responsible for their morphological similarity. Since the divergence of the subfamilies Phacocherinae and Suinae took place at least 7 million years ago [3], the continued morphological resemblance of *Potamochoerus* and *Sus* is remarkable,

given their genetic differentiation, and could be indicative of similar environmental adaptations.

Suids are omnivorous generalists [6], occupying a wide variety of ecosystems and habitats and having a varied and flexible diet [6]. Within this family *Phacochoerus* and *Babyrousa* evolved distinct cranial morphologies as a result of niche specialisation [31, 46]. *Phacochoerus* are Savannah specialists with an increased reliance on grazing perennial grasses over the typical suid rooting behaviour [47]. They have hypsodont dentition adapted towards herbivory, broad flat faces and more superiorly positioned orbits [5]. Our results indicate that these specialisations evolved subsequent to the last common ancestor of the African suids examined here. *Babyrousa* evolved a distinct cranial morphology as a result of their extended evolutionary separation and genetic isolation from other suid genera [3]. Despite their unique maxillary canines (that previous studies have struggled to explain [5]), our results demonstrated that the morphological divergence was no greater than expected given their genetic distance from other suids.

Sus and *Potamochoerus* are typical suid generalists. Both genera occupy vast geographic areas with highly varied habitats, and have an adaptable omnivorous diet that has facilitated their success throughout their range. Our ancestral node reconstruction (Fig 4b) revealed that the morphological similarity between these genetically distinct genera is due to selection for the same generalist traits. Initially, African suids diverged from the ancestral morphology. Despite the genetic and geographic differences between *Sus* and *Potamochoerus*, the shared generalist omnivorous behaviour led to a convergence in their cranial morphology despite their distinct evolutionary histories.

These results resolve the incongruence between the genetics and morphology of African suids. African suids are genetically monophyletic, but with a marked homoplasy in cranial shape between *Potamochoerus* and *Sus.*

Conclusion

This study has demonstrated that genetic and morphological variation in suids each reveal a distinct component of the evolutionary history of the family, a complete

understanding of which can only be achieved through an analysis of both. African and Eurasian suids are both genetically monophyletic. Suid morphology, however, appears paraphyletic and suggests that the sub-Saharan *Potamochoerus* is similar to Eurasian *Sus*. Cranial shape characteristics of individual genera reflect signatures derived from both their evolutionary and behavioural ancestry. Incongruence between the morphological and genetic signals can therefore reveal a more detailed appreciation of their large-scale evolutionary history. The approaches employed in this study, enabled by the recent advances in both genetic and morphological analyses, may also be used to resolve a range of similar issues in other taxonomic groups, such as the Family Rhinocerotidae [48] and the tribe Papionini [49].

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Genus	Species	Common Name	Range	Sample Size
Porcula	P. salvania	Pygmy hog	Assam, India	*
Phacochoerus	*P. africanus*	Warthog	Sub-Saharan Africa	11
Potamochoerus	*P. larvatus*	Bushpig	Sub-Saharan Africa	6
Potamochoerus	*P. porcus*	Red River Hog	Sub-Saharan Africa	11
Hylochoerus	*H. meinertzhageni*	Forest Hog	Africa	*
Babyrousa	*B. celebensis*	Babirusa	North Sulawesi	20
Sus	*S. barbatus*	Bornean bearded pig	Borneo	19
Sus	*S. ahonebarbus*	Palawan bearded pig	Palawan	4
Sus	*S. cebifrons*	Visayan Warty Pig	Negros, Philippines	6
Sus	*S. philippensis*	Philippine Warty Pig	Philippines	26
Sus	*S. scrofa*	Wild Boar	Eurasia	329
Sus	*S. verrucosus*	Javan Warty Pig	Java	*
Sus	*S. celebensis*	Celebes Warty Pig	Sulawesi	39

Table 1: List of currently recognised suid taxa[4], those marked* are not represented in the analysis. Sample size refers to numbers of individuals of each genus (total 471) used in this study.

Figure 1:

Map showing distribution of samples. Circle size on the map corresponds to sample size. Colours correspond to species.

Figure 2:

Genetic (left) and morphological (right) NJ trees. Colours correspond those in Figure 1. The red boxes highlight the position of *Sus* and the green boxes the position of the African suids. Further information about group size and location can be found in Figure 1 and Table 1.

Figure 3:

Figure 3a: PCA: PC1 vs PC2 Figure 3b: CVA: CV1 vs CV2 of the *Sus* and *Potamochoerus* group with representations of the average morphology of the main species analysed.
Colours correspond to those in the map in Figure 1.

Figure 4:

Maximum Likelihood estimate of the tempo and mode of evolution in suids (4a) and ancestral node reconstructions of PC1 and PC2 (4b). Ancestral node scores are shown in green, with the basal node in black, the position of genus is shown in red. For further explanation see text.

Figure 1

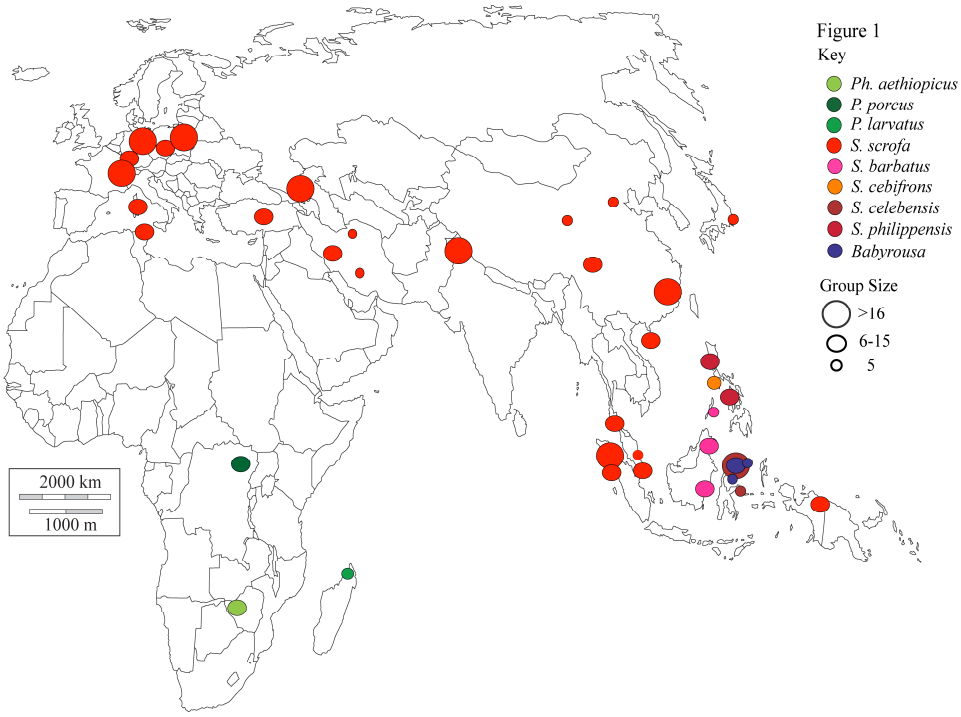

Figure 2

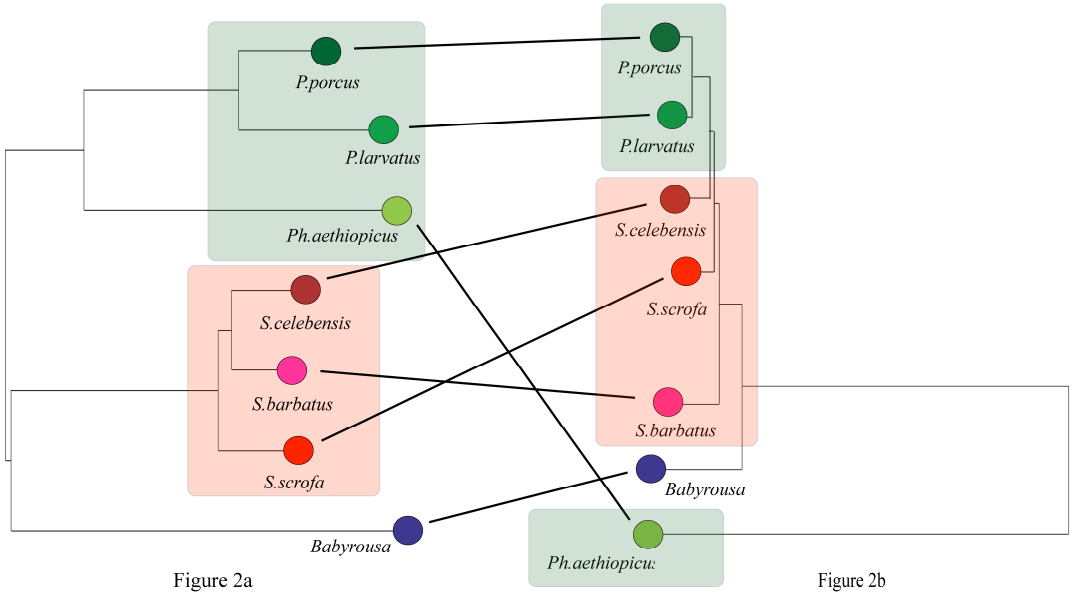

Figure 2a

Figure 2b

Figure 3

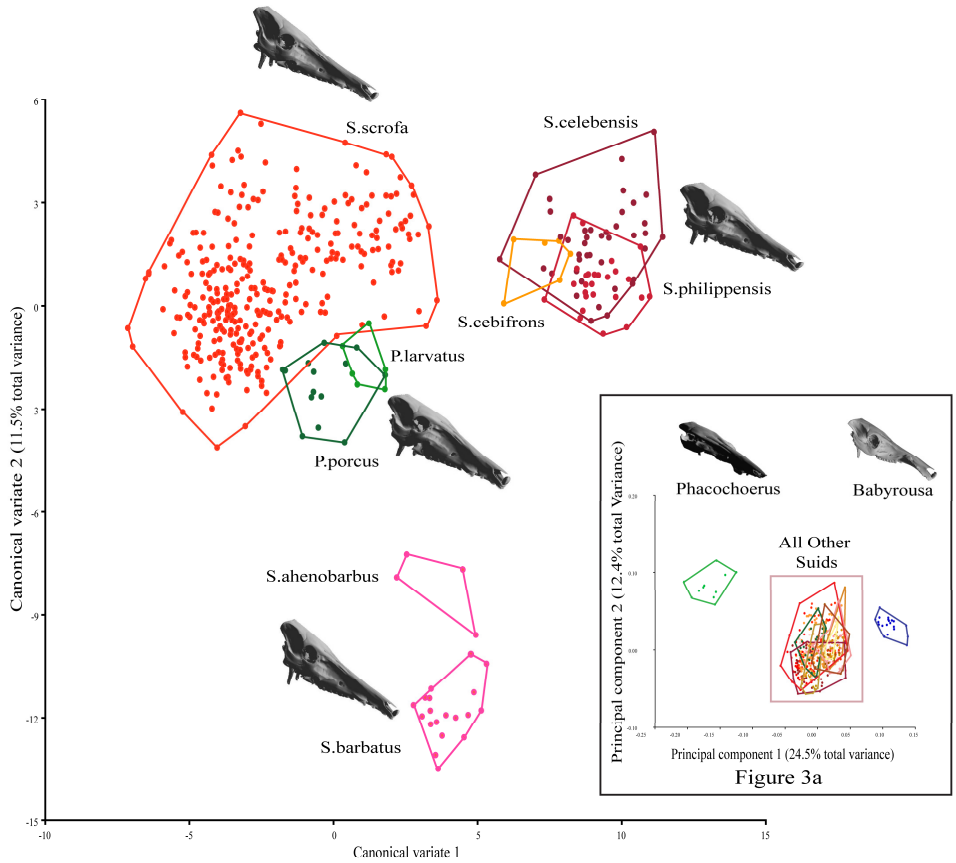

Figure 3b (29.9% total variance)

499 **Figure 4**

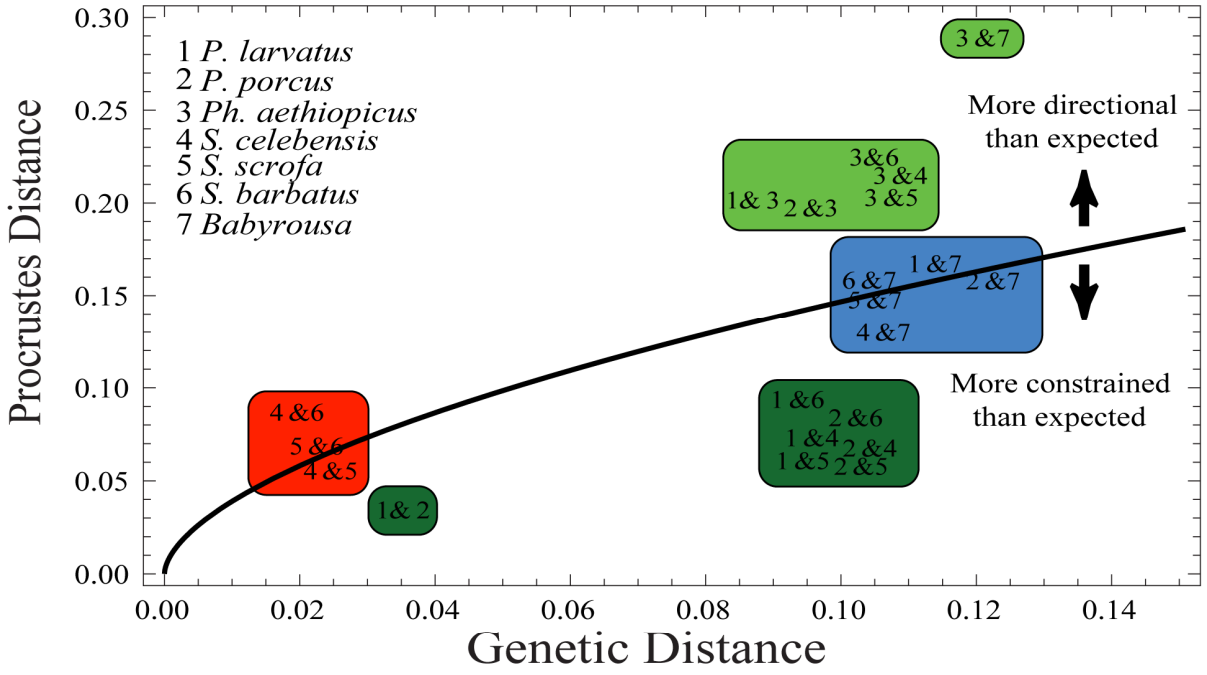

Figure 4a

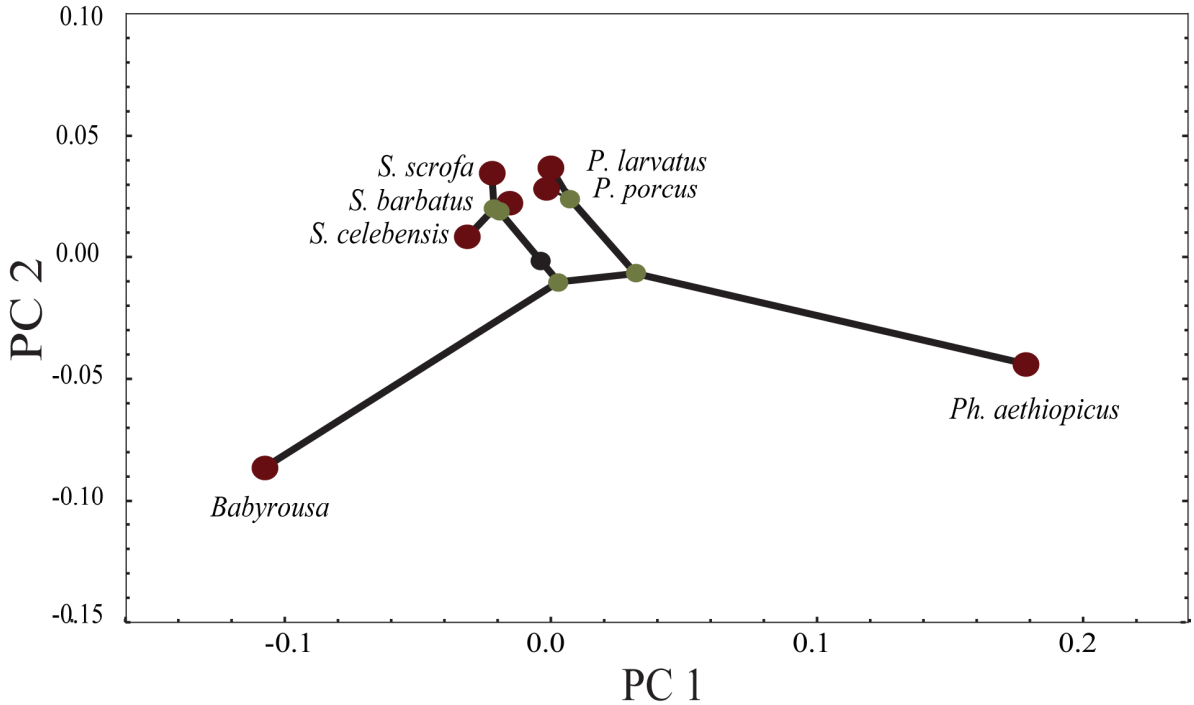

Figure 4b

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S1: List of Landmarks

1	Most anterior midline point on nasals
2	Anterior join in nasal and pre maxilliar suture
3	Anterior point of nasal
4	Suture at the meeting point of the premaxillar, maxillar and nasal
5	Most posterior point of superorbital foramen and groove
6	Most laterial point of the Nuchal Crest
7	Most anterior point of Nuchal Crest - on the midline of the paretial
8	Most superior point of zygomatic process of temporal
9	Most posterior point of zygomatic process of malar
10	Superior point of the temporal process of malar
11	Most inferior point of the malar (zygomatic arch)
12	Anterior most point of the process emerging of the malar (zygomatic arch)
13	Most posterior point of infraorbital foramen
14	Most anterior point of infraorbital foramen
15	Most superior point of the lower lacrimal formina
16	Most superior point of the occipital
17	Most inferior point of the occipital
18	Base of supraorbital process
19	Anterior point of incisive foramen/palatine fissure
20	Posteriormost point of incisive foramen/palatine fissure
21	Most anterior point of canine alveolus
22	Most posterior point of canaine alveolus
23	Anterior point of the alveolar margin of the tooth row
24	Contact points between M3/M2, projected labially (buccially) onto alveolar margin
25	Most posterior point of the alveolar margin of the tooth row
26	Contact points between M3/M2, projected lingually onto alveolar margin
27	Most anterior point of the pterygoid process of the palatine
28	Most lateral point of the pterygoid process of the palatine
29	Most posterior point of the pterygoid process of the palatine
30	Suture of the nasal and palatine bones (on the midline)
31	Tip of posterior nasal spine
32	Meeting point between the basisphenoid and basioccipital along midline, posterior of the vomer
33	Anterior most point of the bulla tympanica
34	Most anterior point of the paramastoid process
35	Most anterior point on the margin of the Hypoglossal canal
36	Lowest point on the orobasal border of foramen magnum
37	Most posterior tip of occipital condyle
38	Most superior point on the border of foramen magnum

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Table S2
Distance Matrix of procrustes distances between taxa in Figure 2b

	S.scrofa	*S.celebensis*	*Babyrousa*	*Phacochoerus*	*P.larvatus*	*P.porcus*	*S.barbatus*
S.scrofa	0						
S.celebensis	0.0617	0					
Babyrousa	0.1497	0.1304	0				
Phacochoerus	0.8473	0.8667	0.8797	0			
P.larvatus	0.0747	0.0754	0.1658	0.8602	0		
P.porcus	0.0617	0.0601	0.1564	0.8591	0.0346	0	
S.barbatus	0.0684	0.0893	0.1596	0.8544	0.0949	0.0853	0

Table S3
Discrimant function cross validation scores - % of species correctly assigned

Species	% Correctly Assigned	
S.scrofa	99.10%	
Babirusa	100.00%	
S.ahonebarbus	75.00%	Mismatch assigned to *S.barbatus*
S.cebifrons	66.67%	
S.celebensis	89.74%	
S.philippensis	85.19%	
S.barbatus	94.74%	
Phacochoerus	100.00%	
P.porcus	85.71%	
P.larvatus	50.00%	Note - all mismatches assigned to *P.porcus*

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Chapter 4

Manuscript 2

Pigs in Space: Biogeographic variation in *Sus scrofa*

Pigs in Space: Biogeographic variation in *Sus scrofa*

Target Journal: Journal of Biogeography

Joseph OWEN[a,b], Allowen EVIN[c,d], Keith DOBNEY[c], Thomas CUCCHI[c,d], Peter ROWLEY-CONWY[a], Greger LARSON[a] and Una STRAND VIDARSDOTTIR[b].

[a]Department of Archaeology, University of Durham, South Road, Durham DH1 3LE, United Kingdom. J.t.d.owen@durham.ac.uk; p.a.rowley-conwy@durham.ac.uk; greger.larson@durham.ac.uk.

[d]Department of Anthropology, University of Durham, South Road, Durham DH1 3LE, United Kingdom. una.vidarsdottir@durham.ac.uk

[c]Department of Archaeology, University of Aberdeen, St.Mary's Building, Elphinstone Road, United Kingdom. a.evin@abdn.ac.uk; keith.dobney@abdn.ac.uk .

[d]CNRS-Muséum National d'Histoire Naturelle, UMR 7209, Archéozoologie, histoire des sociétés humaines et de peuplements animaux, 55 rue Buffon, 75005 Paris, France. evin@mnhn.fr; cucchi@mnhn.fr.

Abstract

Pigs have one of the widest distributions of any large mammal, endemic throughout the Palaearctic and Indomalaya. Throughout this range there are recognised morphotypes that have traditionally been described as separate species, mainly on the basis of size and morphological characteristics. These methods are also the basis of investigations into the species history, including studies of domestication. However most of these studies fail to appreciate all the sources of possible variation present within these measurements beyond sexual diamorphism. It has long been recognised

that climate, latitude and longitude cause shape and size changes in large mammals. The impact that these variables have on suid morphology have not been systematically quantified in suids across their natural range, recent advances in shape analysis, especially in geometric morphometrics (GMM), make this possible. Here we apply GMM to 429 adult suid crania, including most genera, but concentrating on the most wide spread genus, *Sus scrofa*. Our results demonstrate that environmental and climatic variables are major sources of variation in both cranial shape and size in *Sus scrofa*, with precipitation strongly linked to size change in European pigs. The effect of environmental and geographic variables diminishes as wider geography regions and more species are included, the remaining variance increases, representing factors not tested including genetic variation that could be interpreted as speciation.

Introduction

The wild boar (*Sus scrofa* L.1758) occurs naturally throughout the Palaearctic and Indomalaya including Island South East Asia (ISEA), and is present but non-native to the Americas and Australasia (Murray, 1978). As such it has one of the largest ranges of any extant large mammals, occupying a generalised omnivorous niche in many varied and differing habitats (Oliver and Leus, 2008). The pig is important to humans as a food source, both in its domesticated form (Oliver and Leus, 2008) and in its wild state as a game animal (Scandura et al., 2011) and has been intensively studied, focusing both on its history and interaction with humans (e.g. the origins and processes of domestication (Albarella et al., 2007, Rowley-Conwy et al., 2012), and speciation (Groves, 1981, Genov, 1999) .The pig is unusual both in the breadth of its natural range (Oliver and Leus, 2008) and its strong phylogeographic structure

(Larson et al., 2005). The implications of natural variation across its range are rarely factored into research, yet greater understanding of morphological variation in the wild could have an important impact on the understanding of morphological variation caused by domestication or speciation. This paper considers the role that natural variation, due to geography or environmental factors, plays in cranial morphological variation of *Sus scrofa* and other *Sus* species.

Geography, climate and other causes of shape change

The relationship between environment and geography on the one hand, and phenotypic variability on the other is well established in other mammal species with extensive distributions such as Reindeer (*Rangifer tarandus*) and Dogs (*Canis lupus familiaris*) (Cardini et al., 2007, Millien et al., 2006, Albarella et al., 2009, Weinstock, 2000). Size is known to be strongly correlated with temperature under what is known as 'Bergman's Rule' where organisms have larger body size under colder climatic conditions (Meiri and Dayan, 2003). This is often interpreted as latitudinal variation within species, as temperature is highly correlated with latitude (thus latitude is then used as a proxy for temperature) and a positive correlation with latitude and body size has been documented among most endotherms (Meiri and Dayan, 2003). Indeed, Bergman's rule holds true for 62%-83% of vertebrate species excluding squamates and fish (where it is closer to ~30% of species) (Millien et al., 2006). The most widely given explanation of Bergman's rule is thermal regulation, where there is a selective advantage to a higher body surface-to-volume ratio in warm regions and a lower surface-to-volume ratio in colder areas (Mayr, 1954). This has been questioned as there are more efficient methods of body temperature control (e.g. fur insulation (Scholander, 1955, 1956), and body size often correlates better or

more strongly in combination with other environmental factors such as moisture availability (Millien et al., 2006).

Moisture (or precipitation) also influences size and morphology, as moisture is often a limiting factor of primary productivity, especially in arid and semi-arid environments (Yom-Tov and Geffen, 2006). Primary productivity has been linked to mammalian body size (Millien et al., 2006); it is also an important factor in diet (Birkhofer and Wolters, 2012) which in turn has an impact on morphology. The effect of diet on cranial morphology has been studied through biomechanics (Herring et al., 2001, van Cakenberghe et al., 2002) which in pigs has focused on the muscles associated with mastication in wild and domestic *Sus scrofa* (Dinu, 2009, Herring et al., 2001). Mastication is a forceful cranial activity that produces strain loads on craniofacial bone; the coarser the diet, the greater the work load associated with breaking it down and the larger the muscles required to do so. In response to this, and in accordance with Wolff's law (Wolff, 1986) which generally states, bone remodels to become more robust in response to increased strain loads. *Sus scrofa* inhabits a large variety of habitats and has a very broad diet (Oliver and Leus, 2008) which could have an obvious impact on cranial shape. Pigs are also noted for their rooting behaviour, digging with their snouts for roots, tubers and truffles (Massei and Genov, 2004). Animals that undertake a greater proportion of rooting as a food gathering activity will have greater developed muscles around the nasal bone, impacting on the shape of the front of the cranio-facial area (Sack, 1982).

Body size and insularity, or the 'island rule', dictates that among mammals and birds small animals get larger and larger animals get smaller (Meiri et al., 2011). Reasons

for this can include absence/reduction of predators and competitors, as well as resource and space limitations (Millien et al., 2006). It has been suggested that the "island rule" corresponds to a clade-specific response to insularity instead of a size related phenomenon (Meiri et al., 2006, Meiri, 2008).As with any rule there are exceptions, e.g. carnivores are more dependent on prey availability than influenced by insularity (Meiri et al., 2005). Although insularity has recently been shown to occur less often than previously been thought (Meiri et al., 2011) it does hold true (in the form of dwarfism) in large species.

There have been few studies into the effect of environmental pressure on cranial morphological variation outside humans (Cardini & Elton 2007), and little in pigs to date (Fuller, 1965, Larsson et al., 2005). Those that have been carried out have mainly focused on primates (Cardini et al., 2007, Viguier, 2002) with only a few studies on other animals such as the Tammar Wallaby (*Macropus eugenii*) (Hadley et al., 2009), these have shown that cranio-facial variation is strongly linked to environmental and geographic factors. The interactions between climatic factors such as moisture and temperature are difficult to untangle, as these factors tend to co-vary, although several studies have done so through differing approaches based on regression (Cardini et al., 2007, Yom-Tov and Geffen, 2006).

Known constraints on *Sus scrofa* range

Although *Sus scrofa* is found in a wide variety of habitats it cannot tolerate sustained temperatures above 35°C (95°F) with humidity above 65% without adequate water or shade, this intolerance is known mainly through transportation of domestic livestock and is due to a lack of sweat glands and thick layers of subcutaneous fat (Hafez,

1968). Alleviation of high temperatures in the wild is achieved through seeking shade and wallowing in mud or water, thus wild pigs are rarely found far from water and shade (Oliver, 1993) even in semi-arid environments. The main mechanism of population regulation is intra-specific competition for food or space governed by stochastic environmental factors (Uzal and Nores, 2004). This is reflected in the preference of *S.scrofa* to inhabit areas of energy rich foods (Massei and Genov, 2004). In this investigation we will use rainfall (or moisture) as a proxy for primary productivity (and thus diet) to investigate its potential impact on cranial morphology.

Known biogeographic variation within *Sus scrofa*

Across the extensive natural range of *S.scrofa* there are various morphologies that have been split into 4 main groupings; the 'Western races' of Europe, North Africa and the Middle East; the 'Indian races' from Eastern Iran to Thailand; the 'Eastern races' of Mongolia and Russia to China and Vietnam; and the 'Indonesian races' from the Malay peninsula through the Indonesian islands (Groves, 1981, Groves, 2007, Grubb, 1993). These racial groupings fit tolerably well with the known mitochondrial phylogeny of *Sus* (e.g. Larson et al. (2005)) which shows separate maternal lineages in the geographic regions proposed by studies on morphology (Reproduced in figure 1).

Known variation across Eurasia includes size increases from West to East and South to North, with larger individuals in Eastern Europe and the Near East, and smaller pigs in Western and Southern Europe (Albarella et al., 2009). There are also incidences of insular dwarfism e.g. on Corsica and Sardinia (Albarella et al., 2009) as well as in ISEA (e.g. *Sus ahonobarbus,* (Oliver, 2010). Size increases in Eastern

Eurasia have been attributed to 'continentality' i.e. harsher winters in the East having an increased bottlenecking effect reducing intraspecific competition. The South-North size increase is driven, and explained by, the presence of large boar in the Near East (Albarella et al., 2009, Weinstock, 2000), leading Albarella et al. (2009) to conclude that pigs exhibit an inverse relationship of body size and temperature.

Davis (1981) surveyed extent and past pig populations (amongst other animals such as aurochs, dogs, foxes, gazelles and goats) in the Levant, discovering a negative temperature-size relationship in modern populations coupled with size decreases in pigs at the end of Pleistocene and another size decrease associated with domestication. Davis attributed size decreases to Bergman's rule in wild pigs, foxes and dogs, noting that the regression lines of log dental size on temperature are similar in these species. The Pleistocene size reduction (present in all the animals Davis examined) is explained by the end of the last glacial maximum with occured at the Pleistocene/Holocene transition.

Studies of pig cranial morphology that do exist are limited either by approach (e.g. to speciation studies e.g. (Groves, 1981, 2007, Genov, 1999, Lucchini et al., 2005) or to specific geographic areas (Albarella et al., 2009, Endo et al., 2002, Alves et al., 2010). Genetic studies of Suid populations have been more encompassing, with several family-wide phylogenies published (e.g. (Gongora et al., 2011, Mona et al., 2007), but only Larson et al., (2005) examined the phylogeography of *Sus*, by conducting a global investigation into the structure of mitochrondrial DNA whilst looking for evidence of centres of domestication. They showed that pigs, and

187 especially *Sus scrofa*, have a strong geographic basis of genetic partition (see Figure
188 1).
189
190 We propose to investigate biogeographic signals in *Sus scrofa* cranial morphology
191 using a Geometric Morphometric approach. *Sus scrofa* was chosen as the focus of
192 the investigation as it is the most widely spread species of suid and the only one that
193 inhabits multiple habitat types. We first test the long standing hypothesis that *Sus* and
194 *Sus scrofa* cranial morphology co-varies with geography or climate, and if it does –
195 to what degree climate and geography explains suid cranial variation. We also
196 examine our data for any affects of insularity. Finally we compare phylogeography to
197 phenotypic variation, investigating whether the traditional taxonomy is congruent
198 with the mitochrondrial distribution map of *Sus*.
199
200 **Materials**
201 The sample analysed consists of 334 modern *Sus scrofa* crania from museum
202 collections; representing a large part of the geographic distribution of the species.
203 The composition of the sample and the geographic and environmental covariates
204 used in analysis can be found in Table 1. For comparative analysis with the wider
205 genus *Sus* we added 95 specimens from other genera, which are also listed in Table
206 1.
207
208 Geographic and environmental covariates used were latitude, longitude, elevation (in
209 metres above sea level), mean average annual temperature (degrees Celsius) and its
210 standard deviation (SD), mean annual precipitation (millimetres) with associated
211 standard deviation and the Shannon index of precipitation, a diversity index

212 reflecting seasonal variation in precipitation (Bronikowski and Webb, 1996).
213 Geographic co-ordinates for latitude and longitude were extrapolated from museum
214 data, specimens were grouped (see table 1) according to location as many samples
215 had insufficient data to pin-point exact individual origins. These groups were
216 collated into regions to assess possible wider bio-geographic structuring: Europe, the
217 Near East, Mainland Asia and Island South East Asia (ISEA), as based on prior
218 studies of biogeographic structuring in *S.scrofa* (Groves 1981). Elevation
219 information for geographic co-ordinates originates from the SRTM3 database, a
220 NASA global survey taken from the GPS visualizer website (Schneider 2010).
221 Temperature and precipitation data were extrapolated from the Willmott and
222 Matsuura data base (Legates & Willmott, 1990a,b; Willmott & Feddema, 1992;
223 Willmott & Matsuura, 2001). Environmental data were generated for the geographic
224 group mean latitude and longitude rather than individual samples; thus analyses
225 conducted using geographic or environmental covariates are based on variables
226 generated for the mean group location (given in table 1).
227

Group Name (*)	Locality	Group Size	Mean Centroid Size	DF %	Longitude (°)	Latitude (°)	Elevation (m)	Mean Temperature (Celsius)	SD of temp	Monthly Rainfall (mm)	SD of monthly rainfall	Shannon Index
S.s.Geneva (E)	Region from Saillenard, France to Geneva, Switzerland	33	608.72	72.73	5.37	46.70	200	11.02	6.46	938	10.93953	0.996342
S.s.SWGermany (E)	Heilbronn	13	593.1	53.85	9.19	49.19	188	9.33	6.71	745.8	8.557559	0.996498
S.s.Sardinia (E)	San Nicolò Gerrei	16	513.02	100	9.32	39.53	387	14.68	6.47	753.6	34.19213	0.933188
S.s.Tunis (E)	Tunis, Tunisia	10	657.59	60	10.11	36.48	240	20.99	1.32	1707.9	136.7352	0.810651
S.s.Berlin (E)	Zoological gardens, Berlin	32	660.3	46.8	12.79	52.57	37	8.82	6.95	510.6	8.361546	0.992621
S.s.SWPoland (E)	Zabkowice	16	600.65	37.50	16.93	50.68	268	7.89	7.05	693.4	20.68701	0.976625
S.s.EPoland (E)	Nowa Wieś, N. Warsaw	28	634.43	67.86	21.11	52.53	82	7.97	7.93	518.3	17.36525	0.971867
S.s.WRussia (E)	Dubroŭna, Belarus	6	647.34	16.67	30.77	54.44	215	5.28	9.05	545.3	19.55907	0.968689
S.s.Turkey (NE)	Cihanbeyli	8	687.41	37.5	32.68	38.77	1138	9.90	7.97	412.9	15.78281	0.952314
S.s.Caucasus (NE)	Dagestan	20	762.7367	60	46.60	43.10	514	11.87	9.47	397.9	10.29046	0.982501
S.s.IraqIran (NE)	Sedeh Lenjan, Iran	9	718.19	55.56	51.26	32.20	2158	21.87	8.93	266.8	24.8564	0.747114
S.s.NEIran (NE)	Estakhr Sar (Nr. Parvar Protected area)	7	677.12	60	53.38	36.18	985	13.59	7.14	712.1	24.63562	0.964516
S.s.SIran (NE)	Rafsanjan, Iran	5	661.42	20	55.71	30.64	1408	17.64	9.23	79.6	6.8488	0.791566

S.s.Fukien (Asia)	China - Fukien	13	578.34	61.54	119.3	26.07	9	17.09	6.66	1409.9	62.41051	0.944027
S.s.Szechuan (Asia)	China - Szechuan	10	605.81	30	103	30	593	16.43	6.86	1464.2	115.1128	0.843593
S.s.Hainan (Asia)	China - Hainan	3	473.6	0	109.95	19.17	262	24.08	3.67	1409.3	83.06781	0.901374
S.s.Shanxi (Asia)	China - Shanxi	7	615.99	57.14	112	38	1165	5.30	11.03	432.6	41.99508	0.784594
S.s.Gansu (Asia)	China - Gansu	4	545.35	25	102.3	38	1938	5.49	10.34	303.3	24.76137	0.808421
S.s.Burma (Asia)	Tenasserim	13	554.52	53.85	98.75	13	3625	25.25	1.11	3209.9	285.5248	0.771156
S.s.India (Asia)	Kashmir	18	624.32	55.56	76	34.5	4092	-3.30	10.87	494.7	28.74386	0.914863
S.s.Japan (Asia)	Tokyo	6	627.74	100	139.715	35.42	241	15.69	7.88	1706.8	58.33831	0.969076
S.s.Malaysia (ISEA)	Johor	7	584.33	57.14	103.5	1.49	13	26.77	0.40	2834.4	49.77332	0.991811
S.s.Papua (ISEA)	South Eastern Irian Jaya	9	528.35	88.89	140.71	-2.53	178	28.23	0.21	2384.9	66.48296	0.980097
S.s.Nsumatra ISEA)	North Sumatra Prov.	23	513.06	69.57	99.00	2.00	1024	19.28	0.17	2338.9	54.3692	0.984596
S.s.Ligga Is. (ISEA)	Lingga archipelagos (Sumatra)	7	519.82	42.86	104.00	1.04	17	26.28	0.35	2897.9	50.76103	0.99205
S.s.Nias Is. (ISEA)	Nias (Sumatra)	6	499.12	66.67	97.53	1.10	82	26.73	0.39	3452.7	78.47157	0.986677
S.ahonebarbus	Palawan	4	542.03		118.40	9.53	264	22.23	0.48	1868	78.00795	0.945146
S.b.Borneo	Borneo	12	719.79		116.83	-1.36	0	26.92	0.27	2371.3	30.35093	0.995525
S.b.Malay	Malaysia	7	685.84		117.54	4.42	14	26.40	0.29	1875.6	33.80863	0.990953
S.ceb	Negros	6	455.98		123.00	10.00	710	26.74	0.69	2115.7	67.00471	0.970456
S.cel.Peleng	Peleng Island	6	462.5		123.17	-1.40	11	25.33	0.33	1812.4	66.04734	0.966151
S.cel.Lembeh	Lembeh (N.Sul)	5	422.48		125.23	1.43	172	27.55	0.34	2455.5	67.76733	0.978

S.cel.Bumbulan	Bumbulan (N.Sul)	28	460.19		121.94	0.47	19	21.84	0.25	2429.7	41.63954	0.992479
S.p.Mindanao	Mindanao	12	508.5		125.00	8.00	664	24.63	0.51	2807.9	85.55993	0.973708
S.p.Luzon	Luzon	14	511.04		121.00	16.00	413	21.44	1.24	2122.2	101.0302	0.936081

Table 1: Group information and covariates: Data was collected from Museum für Naturkunde (Berlin, Germany), London Natural History Museum (UK), Muséum d'histoire naturelle de la Ville de Genève (Switzerland), Museum fur Haustierkunde, (Halle, Germany), Field Museum of Natural History (Chicago, USA), American Museum of Natural History (NY, USA), Smithsonian MSC (Washington DC, USA).

DF% = percent of group correctly assigned in discriminant function analysis with leave-one-out cross validation. SD = Standard Deviation

* Addition in brackets shows which of the wider regional groupings (*Sus scrofa* only) the sample originates from

E=Europe, NE=Near East, Asia=Mainland Asia, ISEA=Island South East Asia

Groups of differing species are denoted as follows. *S.ahonebarbus* (as is), S.b – *Sus barbatus*, S.ceb – *Sus cebifrons*, S.cel – *Sus celebensis*, S.p – *Sus philippensis*

207 **Methodology**

208 44 homologous, unilateral (right sided), three-dimensional landmarks from the
209 crania of 429 adult (>18 months) *Sus* were digitised using a Microscribe^{tm} GLS
210 by J.Owen. Details of the position of the landmarks digitised can be found in the
211 supporting data (table S1). Landmark and observer error was assessed following
212 O'Higgins and Jones (1998) and found to be negligible.

213

214 The base methodology follows standard Geometric Morphometric Methods
215 (GMM) (Zelditch et al., 2004) with landmark co-ordinates superimposed using
216 Generalised Procrustes Analysis (GPA) prior to further analysis. This removes
217 the effect of rotation, scale and location leaving only true shape differences
218 between samples. A measure of size is retained in centroid size, the squared root
219 of the sum of the squared distances between each landmark and the centroid.
220 Centroid size was compared between groups (see table 1) using ANOVA and
221 visualised in a box plot. Overall shape variation was visualized using Principal
222 Components Analysis (PCA). Differences in overall shape between groups were
223 tested using MANOVA and Canonical Variates Analysis (CVA) with
224 permutation tests using Morphoj (Klingenberg, 2008). The morphological
225 differences between group means was described and visualised using a 3D
226 surface scan morphed to different landmark configurations using the EVAN
227 Toolbox (2010). The surface scan was obtained from a wild adult male *S.scrofa*
228 specimen held in the Durham University collections, using a non-contact Konica
229 Minolta Digitiser (v-910).

230

231 Phenotypic relationships were summarised using a dendrogram based on
232 Procrustes distances between group means, and calculated using an unweighted
233 neighbour joining tree (NJ) in NTsys (Rohlf, 2008). The significance of
234 differences between groups was analysed using MANOVA and discriminant
235 function analysis with leave-one-out cross validation in the R statistical
236 environment (See table 2). To analyse wider biogeographic structuring the results
237 of the phenogram were compared with an established genetic phylogeny (Larson
238 et al., 2005) and a traditional biogeographic structure, based on biometric
239 measurements (Groves, 1981, 2007). The phylogeny of Larson et al. (2005) was
240 chosen as it provides the greatest detail of *Sus scrofa*, although several other
241 phylogenies have been published subsequently (Gongora et al., 2011, Mona et
242 al., 2007, Scandura et al., 2011) they concentrate more on family wide overviews
243 (e.g. (Gongora et al., 2011) or on specific regional areas (Scandura et al., 2011)
244 rather than *Sus scrofa* specifically, and do not provide us with a detailed
245 phylogeographic map as Larson et al. (2005) does.
246
247 The relationships between *Sus scrofa* cranial shape and size, and environmental
248 and geographic variables (see table 1), were investigated using multiple linear
249 regression on size (univariate regression) and shape (multivariate regression)
250 following Legendre and Legendre, (1998). Analyses were conducted using the
251 following software packages: Excel (© Microsoft Corporation), Morphologika 2
252 (O'Higgins and Jones, 2006), MorphoJ (Klingenberg, 2008), NTSYS (Rohlf,
253 2008), SPSS 20 (© Microsoft Corporation), R (R Development Core Team,
254 2008), and the EVAN Toolbox, (2010).
255

Results

Significant differences in size were found between geographic groupings of *Sus scrofa* ($p<0.0001$, $F=7.12$, $df=25$) and are visually represented in a box plot in figure 2. *S.scrofa* from Europe and the Near East are generally larger than pigs from Asia, and within Europe and the Near East there is a West to East size increase. Pigs from some island samples exhibit the insular dwarfism, specifically the smaller size pigs from Sardinia and Hainan, and in general for *S.scrofa* from ISEA, other *Sus* species in ISEA vary in size from the large *S. barbatus* to the small dwarf *S. ahonobarbus*.

Significant shape differences are evident between groups ($p=<0.0001$ $F=774.25$, $df=3125$), although the most pronounced differences exist between *S. scrofa* from Europe and the Near East and *S.scrofa* from Asia (as shown in the CVA in figure 3). PCA of individual specimens shows the overlap and similarity of morphologies in *Sus scrofa*. This is especially true on PC1 (21.18% of total variance), where no discernable geographic discrimination is apparent. On PC2 (13.46% of total variance) European and Near Eastern pigs score more highly than pigs from Asia and ISEA, with little overlap between them and the Near Eastern and ISEA pigs. CVA illustrates the differences between groups more clearly. Individuals from Europe and the Near East cluster at the negative end of CV1 (28.272% of variance), individuals from Asia and ISEA at the positive end, with ISEA pigs scoring highest. CV2 (9.487% of variance) splits pigs from the Near East (lower scores) from Europe (higher scores), whist *S.scrofa* from Asia generally have higher scores on CV2 than *S.scrofa* from ISEA.

281 Morphological differences represented by the CVA are visualised in figure 3.
282 CV1 represents variability around the orbit, with Asian pigs having relatively
283 larger eyes and more robust zygomatics than European and Near Eastern pigs.
284 CV2 represents a relative increase in height of the parietal and the nuchal crest,
285 pigs from Europe and ISEA having higher and wider parietals than pigs from the
286 Near East or mainland Asia.
287

Original	**% Assigned**			
	Middle East	Europe	Asia	ISEA
Middle East	**79.66**	13.56	6.78	0.00
Europe	8.05	**89.26**	2.01	0.67
Asia	5.41	2.70	**82.43**	9.46
ISEA	0.00	0.00	7.7	**92.30**

288 **Table 2:** Results of the discriminant function with leave-one-out cross validation
289 analysis between the wider regional groupings. Values in bold show the
290 percentage correctly assigned to group, the non-bold values show where the
291 misclassified results have been assigned. The table reads left to right for correct
292 interpretation.
293
294 Discriminant functions with cross validation (Table 2) show the strength of the
295 morphological identity of the regional groups, both for individual samples and
296 the four larger regional groupings. The results for individual samples (see
297 supporting table S2) are, with some exceptions (Sardinia, Japan, Papua and
298 Geneva), poor, suggesting the morphologies are very similar across species,
299 which is represented by the results of the individual groups, showing that most of
300 the incorrect classifications remain within regional groups. The larger regional

groupings give far better results; as the CVA plots and the larger clusters on the neighbour joining tree in figure 1 suggest, *Sus scrofa* falls into 4 main bio-geographic groupings supported by high (~80%) or very high (~90%) cross validation scores. Thus between regions there are strongly marked morphological differences but within them it is more difficult to distinguish samples based on morphology alone.

Relationships between groups in *Sus scrofa*

The neighbour-joining tree in figure 1 shows the morphological relationships within *S.scrofa* in table 1. There are 4 main groups; Europe, the Near East, Asia, and ISEA.

Starting from the base of the tree the first bifurcation splits pigs from the Caucasus and Berlin from the other pigs. These form a sub-group next to the main European cluster. This cluster contains branches from East Poland and Geneva, then the Island pigs of Sardinia, and finally pigs from South West Poland and South West Germany. This is followed by the Near Eastern group, split into two, first the North African pigs from Tunis and those from Turkey, and then the three Iranian pig groups.

The next series of bifurcations contains the Asian pigs, first a series of bifurcations spliting the mainland Asian pigs. There is a separate group of the Chinese Island of Hainan and the pigs of Papua, separated from the Asian cluster as they have distinctive cranial morphologies, Hainan as an Island group and Papua as it geographically remote from the other groups. The following

bifurcations then split off pigs from South East Asia, Burma, then Malaysia before a final group of pigs from Sumatra.

Comparison with previously established biogeographic structure

The map in figure 1 shows the biogeographic distribution of *S.scrofa* according to the phylogeny of Larson et al. (2005). This splits *S.scrofa* (and smaller samples of *Sus celebensis, Sus barbatus* and *Sus verrucosus*) into 14 haplotypes. Two represent suids from Sulawesi and one included *S.scrofa* and *S.barbatus* and *S.verrusosus*, the remainder represent various geographic groupings of *S.scrofa*. Europe contains two haplotypes, one found only in Italy and Sardinia, and the other in the rest of Europe. The Near East contains a separate haplotype and the remainder are found in Asia, with several on the mainland and the others in ISEA. This phylogeographic ordering broadly corresponds to the traditional morphometric assignment of 4 main groups; the 'Western' group of Europe, North Africa and the Middle East; the 'Indian' group from Eastern Iran to Thailand; the 'Eastern' group from Mongolia and Russia to China and Vietnam; and the 'Indonesian' group from the Malay peninsula through the Indonesian islands (Groves, 2007).

Our results mirror those generated from genetic data more closely than those from traditional morphological studies. The tree in figure 1 shows European, Near Eastern, Mainland Asian and ISEA groupings. It splits the Western race into Europe and the Near East (with the small African sample falling in the Near Eastern group); the Indian and Eastern races are merged, although there are few Indian samples so this result must be treated with caution. The Indonesian race of

ISEA is supported as a separate entity, as it is both the genetic and traditional morphometric studies.

The effect of climate and geography on *Sus* cranial shape and size

Multiple linear regression of size against the geographic and environmental co-variates show that size is positively correlated with them ($r=0.652$, $r^2=0.425$, adjusted $r^2=0.248$, $F=2.398$, $p=0.044$). Examination of the significant individual predictors against size show that longitude ($r=-0.49$, $p<0.001$), temperature ($r=-0.426$, $p=0.005$), rainfall ($r=-0.566$, $p<0.001$) and the SD of rainfall ($r=0.341$, $p=0.023$) are negatively correlated; while latitude ($r=0.547$, $p<0.001$) and the SD of temperature ($r=0.559$, $p<0.001$) are positively correlated. Neither elevation ($R=0.148$, $p=0.198$) or the Shannon index ($r=-0.179$, $p=0.152$) were significant.

Multiple multivariate linear regression of shape against the geographic and environmental co-variates show that longitude ($r^2=0.972$, $F=24.258$, $p<0.001$), latitude ($r^2=0.972$, $F=10.51$, $p<0.001$), temperature ($r^2=0.816$, $F=3.113$, $p=0.017$), SD of temperature ($r^2=0.906$, $F=6.723$, $p<0.001$) and rainfall ($r^2=0.925$, $F=8.606$, $p=<0.001$) are significant predictors. Elevation ($r^2=0.642$, $F=1.257$, $p=0.335$), SD of monthly rainfall ($r^2=0.479$, $F=0.643$, $p=0.821$) or the Shannon index ($r^2=0.731$, $F=1.905$, $p=0.11$) were significant.

Neither the Shannon index or elevation are significantly correlated to size or shape, while the SD of monthly rainfall correlates with size but not shape. Latitude, longitude, temperature, the SD of temperature and rainfall all have an effect on size and shape of the suid skull.

Discussion

Biogeography

Sus scrofa shows clear biogeographic ordering, with regional groupings of Europe, the Near East, Asia and ISEA. The GM results give a clearer resolution than do traditional biometrics, splitting the European and Near Eastern *S.scrofa* groups apart, concurrent with the genetics, where as the traditional biometrics conflates them.

The GM results split the Papua group from the rest of the ISEA samples, following Larson et al. (2005); the *Sus* from eastern ISEA are different from *Sus* from Malaysia and Sumatra. The Sardinian group in the European cluster are separate, in concordance with genetic evidence that they are a separate haplotype and perhaps even a separate subspecies (*S.scrofa meridionalis* (Groves, 1981). Japanese pigs are separated by morphology using both GM and traditional biometrics (as *S.scrofa leucomystax*) but not by genetics where they form part of the mainland Asia clade, thus the morphology maybe reflecting some form of insularity. One problem with the GM results is that they amalgamate the mainland Asia pigs into a single unit whereas the genetic results show that there are several haplotypes present, and the traditional biometrics suggest two groupings (Eastern and Indian races). This is likely due to a paucity of data from this region and future analysis may grant better resolution.

Effects of climate and geography on shape and size

Both skull size and shape in wild *Sus scrofa* is highly variable across Eurasia, showing significant correlation to longitude, latitude, temperature and rainfall variables for both size and shape.

That geography contributes to shape variation is of particular interest as it affirms what several genetic studies have suggested, that at localised levels wild boar are split into different populations (Ferreira et al., 2009, Nikolov et al., 2009), although topological features could not completely explain their presence (Scandura et al., 2011).

Mean annual precipitation was a significant predictor of shape and its standard deviation a significant predictor of shape and size. That annual precipitation (and SD of annual precipitation) suggests that shape and size change in *Sus* in Europe and the Near East are effected by diet and habitat as well as thermo regulation and Bergman's rule, precipitation being used here as a rough proxy for habitat productivity influencing size by food availability (Cardini et al., 2007).

There is also a strong longitudinal west – east size increase across Europe present in our data (see box plot in figure 2) which has been noted before in both *Sus scrofa* (Albarella et al., 2009, Genov, 1999) and reindeer (Weinstock, 2000) and is linked to the harsh winters of Eastern Europe bottlenecking the population, reducing population density and competition for resources allowing individuals to grow larger (Weinstock, 2000). As such European *S.scrofa* does not conform to Bergman's rule which links size to latitudinal gradients (contra (Davis, 1981),

confirming that factors other than temperature are significant in size and shape variability.

Sus scrofa responds to insularity though dwarfism. Pigs from Sardinia and Hainan are smaller than pigs from the nearby mainland, and pigs from ISEA are in general smaller than those from mainland Asia. The exception to this are pigs from Japan, which show no sign of size reduction, possibly as Japan is an island large enough not to trigger a dwarfing effect.

Conclusion

Sus scrofa is a species that shows strong biogeographic structuring, reflecting its large range throughout Eurasia and North Africa (Gongora et al., 2011, Lucchini et al., 2005, Scandura et al., 2011). This can be traced through both its genetics and morphology; although using a GMM approach on cranial morphology gives greater depth of resolution than do traditional biometrics, confirming that this approach has great scope for use in biogeographic studies (Cardini et al., 2007, Cardini and Elton, 2009). This is important where subspecies have been ascribed largely on the basis of cranial characteristics (Groves, 1981, 2007, Genov, 1999), which often rely on order of magnitude measurements (and are thus more limited in the amount of shape variation they contain); it is possible that they may need re-assessing in the light of recent phylogenetic and morphometric methodological advances.

These results are also significant with regard to studies of determination of status as wild or domestic, these too are mainly based on size differences (Payne and

448 Bull, 1988, Mayer et al., 1998). These investigations are based on the assumption
449 that wild and domestic individuals are morphologically different from each other
450 and that this difference is significant, be it in cranial characteristics, tooth size or
451 overall body size. However, these characteristics are strongly affected by
452 climate, diet, habitat and geography, making the individuals a product of their
453 surroundings. Studies investigating domestic status of suids must therefore take
454 into account possible dietary changes or environmental shifts. This will mainly
455 affect regional or wide temporal studies which should include baseline
456 comparisons with wild animals and other domestics to check for possible
457 climatic shifts.
458
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472
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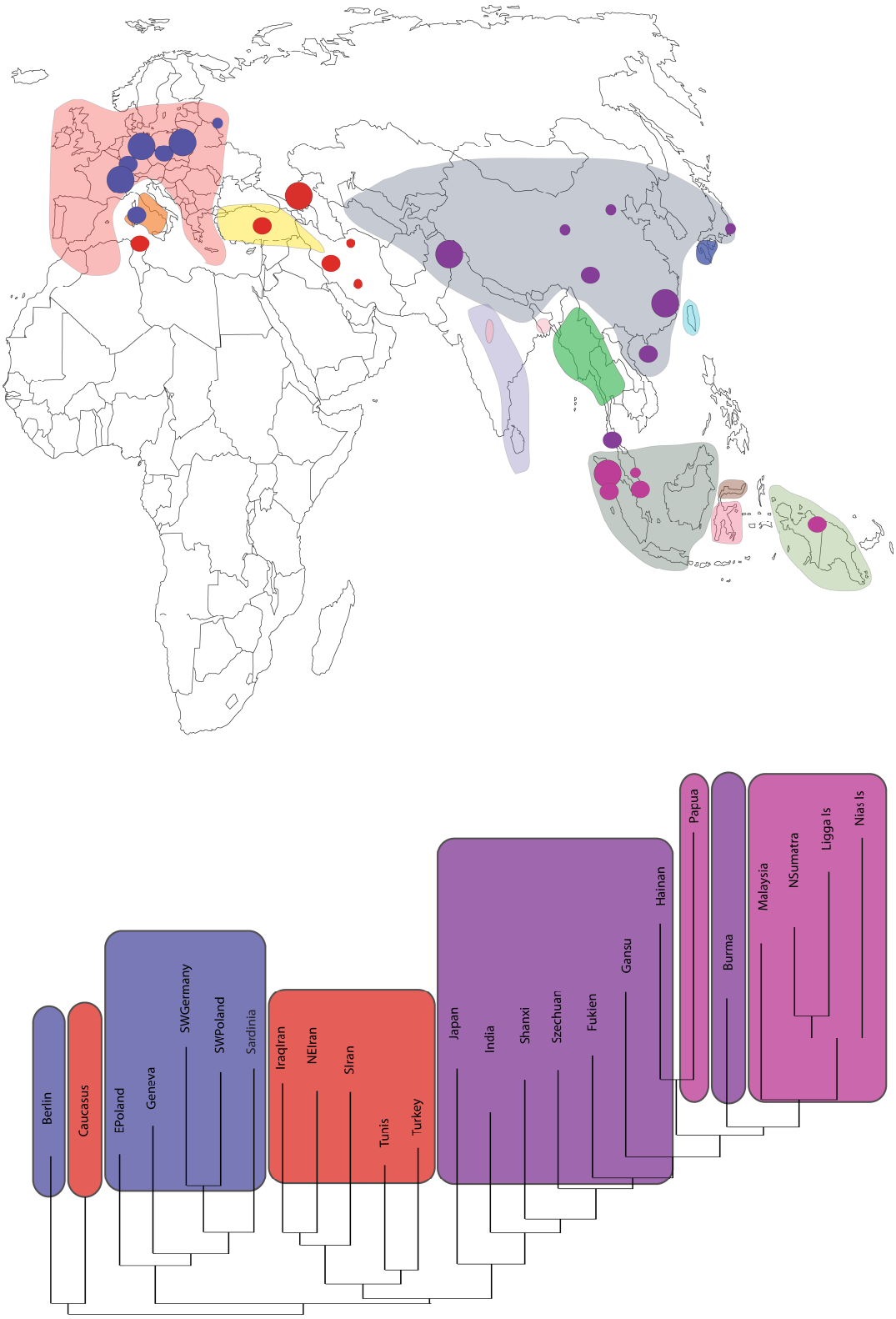
Figure 1: Map of samples over laid on a map of mtDNA groups from Larson et al. (2005), with accompanying Neighbour Joining tree showing the phonetic relationships between samples. Dots represent samples from this study, shaded areas follow Larson et al. Blue = European *S.scrofa*, Red = Near Eastern, Dark Purple Asian, Light Purple = ISEA.

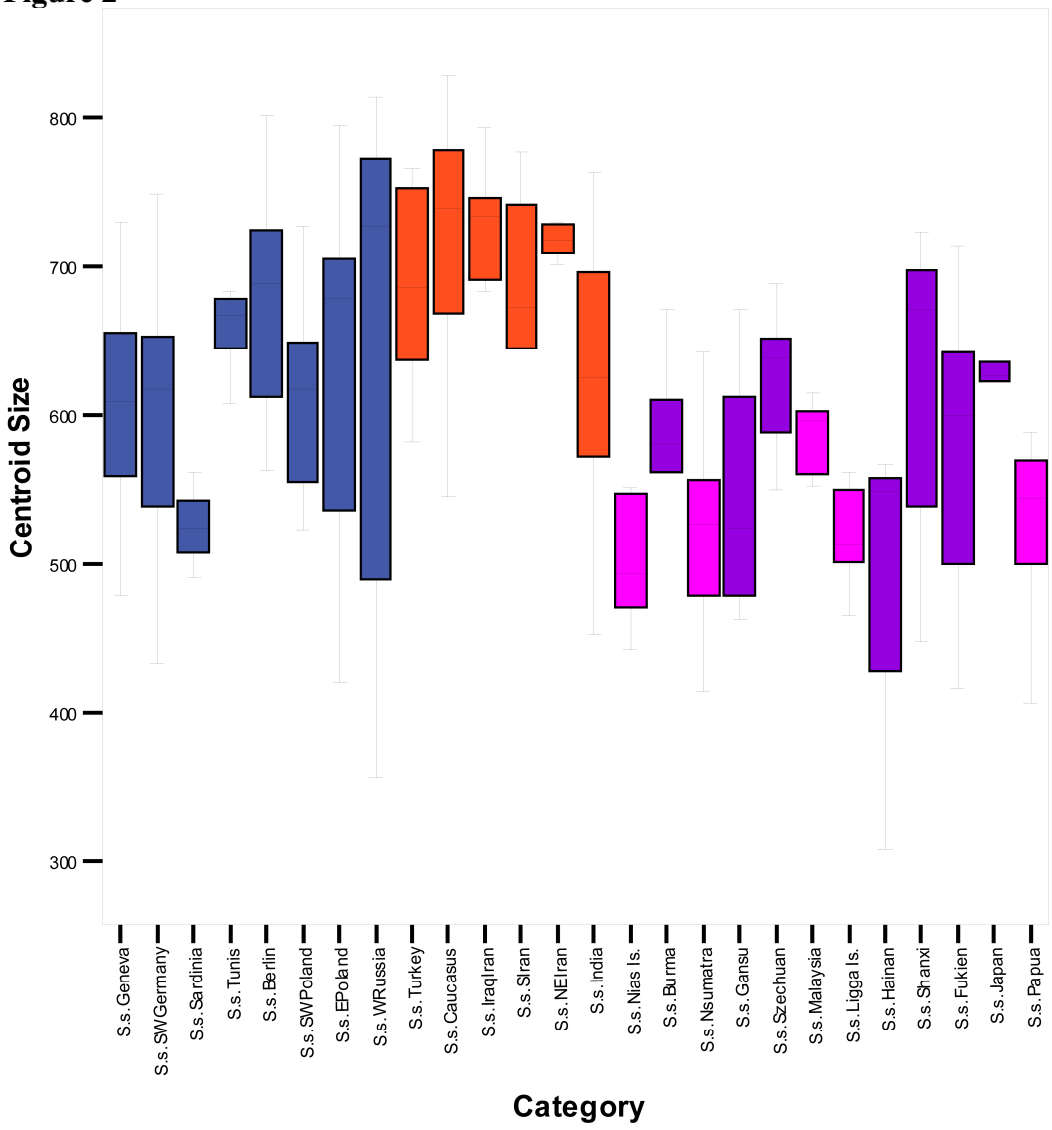
Figure 2: Box plot of centroid sizes, colours follow that of figure 1.

Figure 3: PCA (top) and CVA (bottom) of *Sus scrofa* samples, colours follow that of figure 1.

Figure 1


Berlin
Caucasus
EPoland
Geneva
SWGermany
SWPoland
Sardinia
IraqIran
NEIran
SIran
Tunis
Turkey
Japan
India
Shanxi
Szechuan
Fukien
Gansu
Hainan
Papua
Burma
Malaysia
NSumatra
Ligga Is
Nias Is

662 **Figure 2**



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665 **Figure 3**
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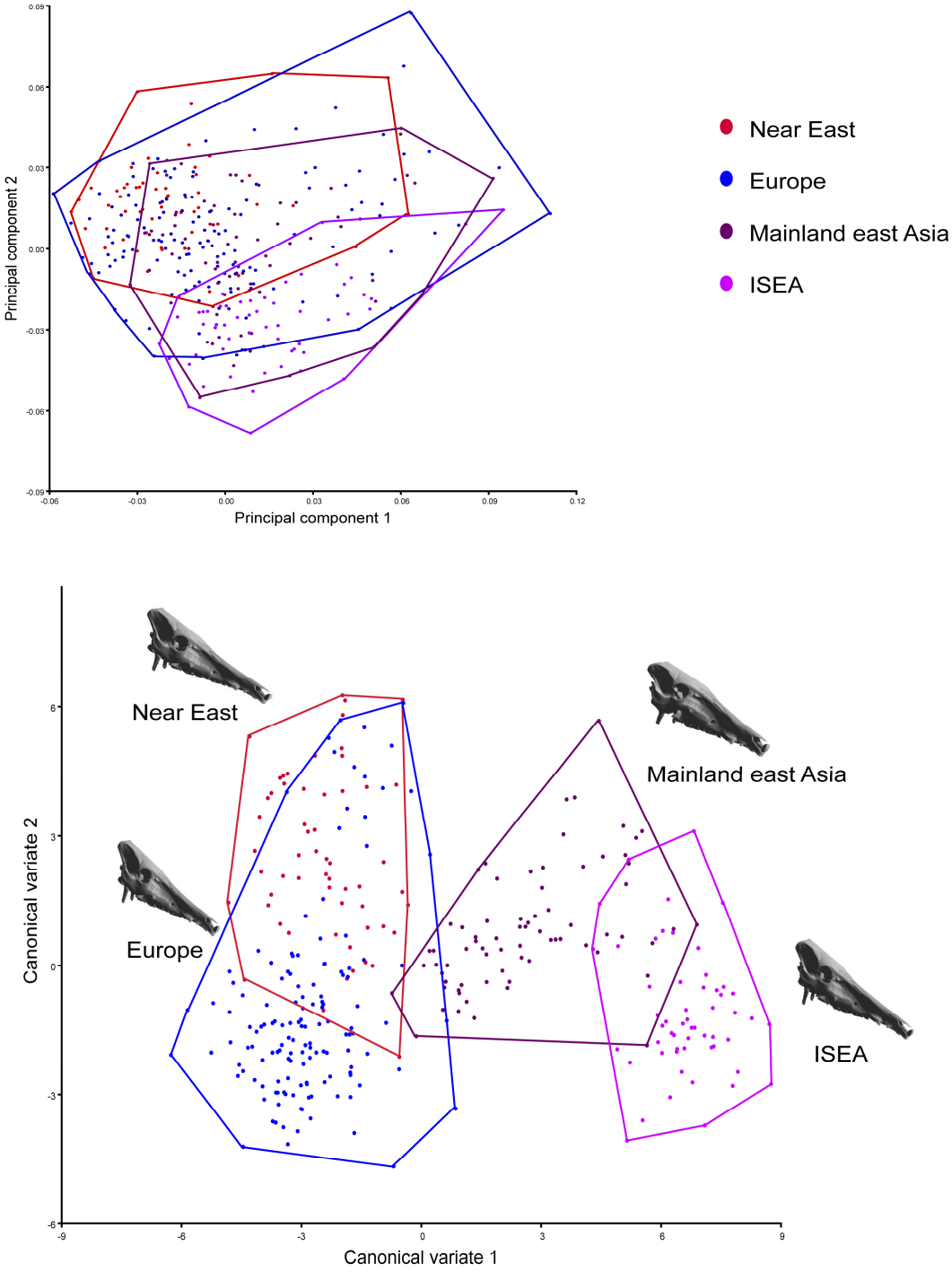

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Chapter 5

Manuscript 3

Quantifying cranial shape differences between wild boar and domestic pigs (*Sus scrofa*) using 3D geometric morphometrics and its application to zooarchaeology

Quantifying cranial shape differences between wild boar and domestic pigs (*Sus scrofa*) using 3D geometric morphometrics and its application to zooarchaeology

Joseph OWEN[a,b], Keith DOBNEY[c], Allowen EVIN[c,d] Thomas CUCCHI[c,d], Peter ROWLEY-CONWY[a], Greger LARSON[a] and Una STRAND VIDARSDOTTIR[b].

[a]Department of Archaeology, University of Durham, South Road, Durham DH1 3LE, United Kingdom. J.t.d.owen@durham.ac.uk; p.a.rowley-conwy@durham.ac.uk; greger.larson@durham.ac.uk.

[d]Department of Anthropology, University of Durham, South Road, Durham DH1 3LE, United Kingdom. una.vidarsdottir@durham.ac.uk

[c]Department of Archaeology, University of Aberdeen, St.Mary's Building, Elphinstone Road, United Kingdom. a.evin@abdn.ac.uk; keith.dobney@abdn.ac.uk .

[d]CNRS-Muséum National d'Histoire Naturelle, UMR 7209, Archéoozoologie, histoire des sociétés humaines et de peuplements animaux, 55 rue Buffon, 75005 Paris, France. evin@mnhn.fr; cucchi@mnhn.fr.

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 origins and temporal context of the initial animal domestication during the early Holocene. Traditional biometrical approaches have explored changes in body size over time, but given poor resolution and been adversely affected by confounding factors such as climate, sex, diet and disease. Here we investigate whether geometric morphometric analyses of cranial shape can be used to provide better resolution between wild and domestic pigs (*Sus scrofa*), as we know that shape is less affected by epigenetic factors than is size. Geometric morphometric methods with traditional multivariate statistics were applied to 52 modern domestic (6 breeds) and 142 wild adult pig crania. Further analyses were carried out on morphologically discrete portions of the whole skull to simulate the fragmented nature of archaeological mammal remains. Highly significant discrimination was found between wild and domestic pigs from analyses of the whole skull, the parietal, the basicranium, the angle of the nasal and the zygomatic. It is also possible to discriminate between crania from different domestic breeds. Our

data shows that geometric morphometric techniques could successfully be applied in zooarchaeology to provide a much better, quantifiable resolution between wild and domestic pigs, even on the basis of partial cranial remains.

Introduction

The domestication of plants and animals was a key part of the transition of human subsistence strategies from hunter-gatherers to sedentary farmers, during the early Neolithic. Studies of this transition include those locating and analysing the origins and methodologies of animal domestication (Rowley-Conwy et al., 2012), which require the ability to distinguish between wild and domestic animals.

The morphological determination of wild and domestic animals relies upon the presence of derived or altered characters in the domestic forms compared to their wild ancestor. The traditional methodology of wild-domestic assignation in the archaeozoological record is largely based on size reduction of either teeth (Mayer et al., 1998) or bone (Albarella, 2002, Ervynck et al., 2001, Payne and Bull, 1988, von den Driesch, 1976) in early domesticated animals. Yet there is a major issue with this methodology in that size is affected by both genetic and epigenetic factors (Vigne et al., 2005) such as temperature, climate, diet, sexual dimorphism and individual variation. Climatic and environmental conditions, specifically 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). Comparative morphology can still be informative on the wild or domestic status of animals in the past if the issues associated with size are rectified e.g. climatic variation can be overcome by comparing samples from similar habitats and with adequate temporal sequences (to eliminate the affect of climate change over time). Such corrections are subject to the availability of well dated large samples and relevant climatic data, and this often excludes inter-regional comparisons (Rowley-Conwy et al., 2012). Alternatively, methodologies that study shape instead of size, like geometric morphometrics (GM) can provide an approach that is less affected by these biases (Vigne et al., 2005). 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 (Clutton-Brock, 1988). In his two part volume dedicated to the evolution of domestic species and the differences between them and their wild progenitors Darwin was the first to note that virtually all domesticated animals had undergone similar phenotypic and physiological changes (Darwin, 1868). These changes 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). It also includes 'paedomorphic' changes to the crania, expressed as snout shortening and increased concavity of the face, braincase reduction, tooth crowding and tooth length reduction, which in turn is linked to body size reduction in many species, including pigs and dogs (Cucchi et al., 2011).

The causal mechanisms of morphological change during domestication are, poorly understood. Some of these 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, Price, 1999, Vigne, 2011). Experimental data suggest that morphological changes may be trigged 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, Belyaev, 1979), where selection was based on a single criterion – reduced aggression towards human handlers (Trut, 1999). This experiment produced an entire suite of phenotypic changes found in domestic animals within as few as 8 to 10 generations (Trut, 1999). Rapid development of the domestic phenotype has been explained by a hypothesis 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 (*Canus 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 may be distinguished by their morphology.

To quantify the differences between wild and domestic cranial morphologies we applied a three dimensional Geometric Morphometrics (GMM) approach to pig crania. Pigs were chosen for this study as they have been an important resource throughout human history and are one of the first major livestock domesticates (Vigne, 2011). The evolution of pig morphology and behaviour in response to domestication, and the co-adaptation of pigs and humans, has been intensively studied over the last decades (Clutton-Brock, 1988, Price, 1984, Rosenberg and Redding, 1998, Scandura et al., 2011, Vigne, 2011, Zeder, 2006, 2012, Zeuner, 1963). They were and remain a major global food source and of central importance to the development of human societies across the world. We focus on crania as they have a noted response to domestication (Darwin, 1868) and can be used as a proxy for the post-cranial skeleton (Cardini et al., 2007). In order to determine whether, and how accurately, cranial morphology can be used to distinguish between wild-domestic pigs we apply GMM and traditional multivariate statistics to a single, well defined wild population and several different domestic breeds. To replicate the affects of the taphonomic processes bones may be subjected to in the archaeological record, e.g. breaking or abrasion (Lyman, 1994), we analyse specific regions of the skull, again quantifying differences in morphology and testing their accuracy.

The study of animal 'improvement' (selective breeding to promote desired traits) and the origin of breeds is an important one, as there is a suggestion that this practice occurred before the agricultural revolution of the 18th century (Davis et al., 2012) and the origin of many domestic breeds is unknown. Like the study of domestication, evidence for improvement is based on size increases over time, interpreted as deliberate breeding for larger animals (Davis, 2008), but with the same problems as using size to determine wild-domestic status. To determine whether it is possible to discriminate between domestic breeds on the basis of cranial morphology, we apply GMM to a variety of domestic pig breeds.

Materials

Our sample comprised 52 domestic and 142 wild adult (>18 months) *S. 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 pigs are housed in the Natural History Museum in Berlin and originate from the Białowieski national park in East Poland, and the vicinity of Nysa, South-West Poland. We chose a wild population from a limited region to reduce the confounding effects of geographic and climatic induced morphological variation that exists in *Sus*. The domestic breeds were Berkshire, Cornwall, Tamworth, Veredeltes Landschwein, Hannover-Braunschweig Landschwein and Deutsches Edelschwein, as well as a small sample of first generation Tamworth-Wild pig hybrids (domestic sows and wild boars). See supporting table (S1) for further details.

Methods

Forty-four unilateral three-dimensional coordinates were digitised from the right side of the cranium, using a Microscribe® GLS (EMicroscribe Inc), by the first author, and analysed using Geometric morphometric methods (GMM (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). GPA removes size but allows reintroduction into the analysis when relevant as Centroid Size (CS). CS is a geometric scale defined as the square root of the sum of squared distances between all landmarks and their centroid. Differences in size between groups were assessed with one-way ANOVA and explored with multivariate regression on pooled within group variation of both wild and domestic samples.

Principal Component Analysis (PCA) was used for initial data exploration and dimensionality reduction of morphological relationships between different groups. The morphological differences between group means were described and 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 (wild vs. domestic and between domestic breeds) was assessed using Multivariate Analysis of Variance (MANOVA). To assess the significance of differences between group shapes, discriminant functions with leave-one-out cross-validation were applied to the principle component scores. This was conducted on a reduced set of principal components to avoid over fitting the data (Kovarovic et al., 2011). Analysis was

conducted in MorphoJ (Klingenberg, 2008) and in the R statistical environment (version 2.13.0 R Development Core Team).

The dataset was broken down into smaller subsets of landmarks (see supplementary table S2), chosen to represent specific regions of the skull: the parietal, the zygomatic, the angle of the nasal, the orbit, the tooth row and the basicranium to determine areas of maximum discrimination which can then be applied to fragmentary archaeological material. The 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 using PCA, MANOVA and discriminant functions with leave-one-out cross-validation.

Measurement Error

Any possible effects of inter-observer error were tested with repeated digitisations following O'Higgins and Jones (1998) and found to be insignificant. The dataset was tested for sexual dimorphism, but no significant variation in shape or size between sexes in either wild or domestic pigs were found, so both sexes were used in the analysis.

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 introgression of Asian pig breeds into European pig breeds must be considered. To minimise this effect, we used older established breeds that have been subject to less improvement (intensive breeding). Theoretically error could also 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 wild European animals, including pigs, suggesting that there is little contamination from modern domesticates in modern wild populations (Scandura et al., 2011).

Results

Size differences between Wild vs. Domestic

ANOVA on cranial size differences between wild and domestic individuals is not statistically significant (p=0.0891, df=5, F=1.95). Multivariate regression of shape against log centroid size reveals only a weak positive relationship (r^2=0.677, 7.9% of total shape variation explained) between size and shape. No size differences were found between wild and domestic individuals on the basis of any of the cranial subsets.

Shape differences between Wild vs. Domestic

Principal components analysis of the complete skull reveals clear morphological differences between wild and domestic pigs, which are completely separated on PC1 (58.75% of total variance) with no overlap (figure 1). Wild pigs score positively on PC1 while domestic pigs score negatively. The sample of Tamworth x Wild crosses overlaps with the wild pigs, although they score slightly more negatively than many of the wild pigs. The morphological changes explained by PC1, and subsequently those that separate domestic from wild pigs include a relative straightening of the snout and elongation of the parietal. A one-way MANOVA on shape differences between wild and domestic individuals confirms that there are significant differences between them (p=<0.0001 df=625 F=6124.91). In a pair-wise discriminant function with leave-one-out cross-validation (on the first 30 principal components comprising of 95% of total variance), 92% of domestic pigs and 98% of wild pigs were correctly assigned. Distances and discriminant functions were subsequently calculated between wild and domestic individuals on the basis of the landmark sub-sets representing selected regions of the skull (Table 1)

Relative morphological differences in the cranial sub-sets also show differences between wild and domestic pigs, including a deepening of the angle of the nasal region in domestic pigs - wild pigs having a relatively long straight, narrow snout in contrast to domestic pigs' relatively short, deeply angled and wide snout. The angle of the parietal is more acute in wild pigs (figure 2c) while the angle in domestic pigs is far shallower. When combined with the differences in the nasal, the overall morphology of the parietal is more upright in domestic pigs than wild pigs (figure 2b). The zygomatic is relatively more robust in domestic pigs (figure 2d), compared

to the slender zygomatic of wild pigs. Features on the underside of the cranium (e.g. the tympanic bulla) are densely packed in domestic pigs (Figure 2a); while in wild pigs they are more widely spaced. The PCA plots accompanying the visualisations (figure 2) show that there is a degree of overlap between wild and domestic morphologies in the initial PCs of these regions. However table 1 shows that despite this, there are significant statistical differences between the wild and domestic morphologies in these regions when the overall pattern of variance is analysed.

Area	Procrustes distance	Mahalanobis´ distance	*p*-value	% Correctly Assigned Domestic	% Correctly Assigned Wild
Whole cranium	0.31822795	18.7093	<.0001	**91.7**	97.9
Parietal	0.17911991	4.0086	<.0001	**88.9**	97.9
Nasal	0.08217111	4.0121	<.0001	**86.1**	97.9
Orbit	0.06971527	2.3496	<.0001	77.8	93.0
Zygomatic	0.12391856	2.9801	<.0001	**88.9**	94.4
Tooth Row	0.0512221	2.1269	<.0001	72.2	88.0
Basi-cranium	0.13082737	4.0702	<.0001	**94.4**	95.1

Table 1: Procrustes distances and discriminant functions (Mahalanobis´ distances) between wild and domestic samples, *p*-values generated through permutation tests with 1000 permutations, percentages correctly assigned result from discriminant functions with leave-one out cross validation. Bolded values highlight results with high correctly assigned percentages.

The results in table 1 and figure 2 demonstrate that both whole and selected regions of the crania can be used to discriminate between wild and domestic pig morphologies. The strength of discrimination varies, with the basi-cranium, parietal, zygomatic and angle of the nasal giving best results. The orbit and tooth row, whilst correctly assigning most of the wild individuals, misclassify many domestic individuals, and are not reliable indicators of domestic status.

Shape differences between domestic pig breeds

There are significant differences between domestic breeds in both shape (MANOVA df=404 F=1095.43 $p<0.0001$) and size (ANOVA df=4 F=7.77 $p=0.0002$). In a discriminant function analysis with leave-one-out cross validation the majority of

pigs were correctly assigned to breed (table 2). These results suggest that although the cranial morphology of domesticated pigs may appear similar, it is specific enough to allow statistical discrimination between them.

	Berkshire	Cornwall	Edelschwein	Tamworth-Cross	Tamworth	Veredeltes Landschwein	Wild
Berkshire	**80.0**	20.0	-	-	-	-	-
Cornwall	-	**87.5**	-	-	-	12.5	-
Edelschwein	-	12.5	**75.0**	-	-	12.5	-
Tamworth-Cross	-	-	-	**90.0**	-	-	10.0
Tamworth	-	-	-	-	**80.0**	-	20.0
Veredeltes Landschwein	-	7.7	7.7	-	-	**84.6**	-
Wild	-	-	-	3.0	1.0	-	**96**

Table 2: Crossvalidation percentage scores of leave-one-out discriminant functions 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.

Discussion

Wild and domestic pig crania have distinctly different, quantifiable morphologies. Wild pig crania are more slender, with straighter snouts, whilst domestic pigs have deeply concave snouts and are relatively more robust. These morphological differences have very high supporting discriminant function values, demonstrating that wild and domestic pigs can be separated with a considerable degree of confidence on the basis of cranial morphology. These results are in contrast with the more traditional biometric techniques used in zooarchaeology, which can confidently establish the presence of wild and domestic populations in the archaeological record (Albarella, 2002, Payne and Bull, 1988) but have difficulty distinguishing between populations or assigning wild-domestic status to individuals within those populations. Application of GMM can give well supported and statistically quantifiable results. Additionally we have shown that GMM can differentiate between different pig breeds, which could have significant impact in the study of the origins of domestic animal breeds, and the development of breed improvement.

Partial Crania

Few complete skulls are recovered from archaeological sites, especially in species bred or hunted for human consumption. Breaking the crania into separate components allows us to simulate (to some degree at least) the effects of ante-, peri- and post-mortem taphonomic processes. The parietal, nasal, zygomatic and basicranium provide particularly good discrimination between wild and domestic pigs. In wild pigs the parietal is swept backwards at an acute angle, whereas in domestics the angle is wider as can be seen in the visualisations in figure 2. 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 (such as the pterygoid bone and the tympanic bulla) are crowded together in domestic pigs compared to wild boar. That these areas of the skull exhibit a strong domestic signal compared to others (e.g. the orbit, tooth row), suggests that stresses focused upon specific areas of the crania are important in forming specific domestic morphotypes. These results also suggest that discrimination between wild and domestic morphologies could be possible in fragmented archaeological assemblages.

Explaining the changes seen in 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 progenitors (Drake and Klingenberg, 2010). Domestication also results 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, and 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 pigs may be caused by biomechanical strain. Increased muscle use results in increased robusticity in their 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 muscles, 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 processing, it would help explain 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, depressor labii superioris) for manipulating the rostrum (Groves, 1981, Sack, 1982, Sisson and Grossman, 1910). Increased rooting would 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 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 is an additional factor to be considered when explaining changing morphology during domestication.

Cross-bred Wild-Domestic Pigs

One aspect of this study that requires further study is the inclusion of first generation wild (father) x domestic (mother) cross breeds. These animals are from the early stages of the Halle museum breeding experiments 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. Their morphological similarity to the wild form suggests that the influence of the domestic signal has been reduced, causing a reversion to a morphotype more similar to that of a wild pig within a single generation. Whether this would be the case if the parentage were reversed is unknown.

Rapid reversal of domestic morphotypes has also 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. Studies of feral animals have suggested that some differences, such as brain size reduction and coat colouration, remain in feral animal morphology (Kruska and Röhrs, 1974, O'Regan and Kitchener, 2005, Zeder, 2012). It is inconclusive whether the causal factor in the

retention of domestic phenotype is environmental pressure or the continuation of inherited traits, but our results would suggest that mixture of domestic morphotype with wild removes much of the domestic signature within a generation.

Conclusion

Cranial morphology can be used to discriminate between wild and domestic pigs. This is true for both whole and partial crania, as the paretial, zygomatic, angle of the nasal and the basicranium gave excellent discriminant values. The ability to determine between different morphologies, either in cranial or post cranial material has significant implications for zooarchaeology. Greater resolution allows clearer quantification of the proportion of wild and domestic animals on a site, elucidating evolving subsistence strategies and could help determine the origins of the transition from hunter-gathering to farming (Rowley-Conwy et al., 2012).

The sensitivity of GMM allows for the distinction between domestic breeds. This has important consequences for the study of the origins and development of such breeds, where currently the methodology for studying improvement is based on size increases (Davis et al., 2012), which has obvious difficulties overcoming size issues associated with sexual dimorphism. Breed improvement, for traction or increased meat bearing should be reflected in the morphology, not just size, and could be examined using the methods employed here without being confused with the effects of sexual dimorphism

Studies have already started applying GMM to zooarchaeological questions and material. Shape differences have been shown to exist between wild and domestic pig teeth in the early archaeological record (Cucchi et al., 2011), and GMM has been applied to both Palaeolithic horse metapodials to investigate phylogeography (Bignon et al., 2005) and cervid anatomy associated with locomotion for palaeo-climatic reconstruction of the Plio-Pleistocene (Curran, 2012). There is great scope for future applications on cranial and post-cranial material, to elucidate both the process and history of domestication.

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Figure 1: PCA of wild and domestic pigs

Figure 2: PCA of subsections of the suid crania, 2a: basicranium, 2b: nasal region, 2c: parietal, 2d: zygomatic.

Figure 1

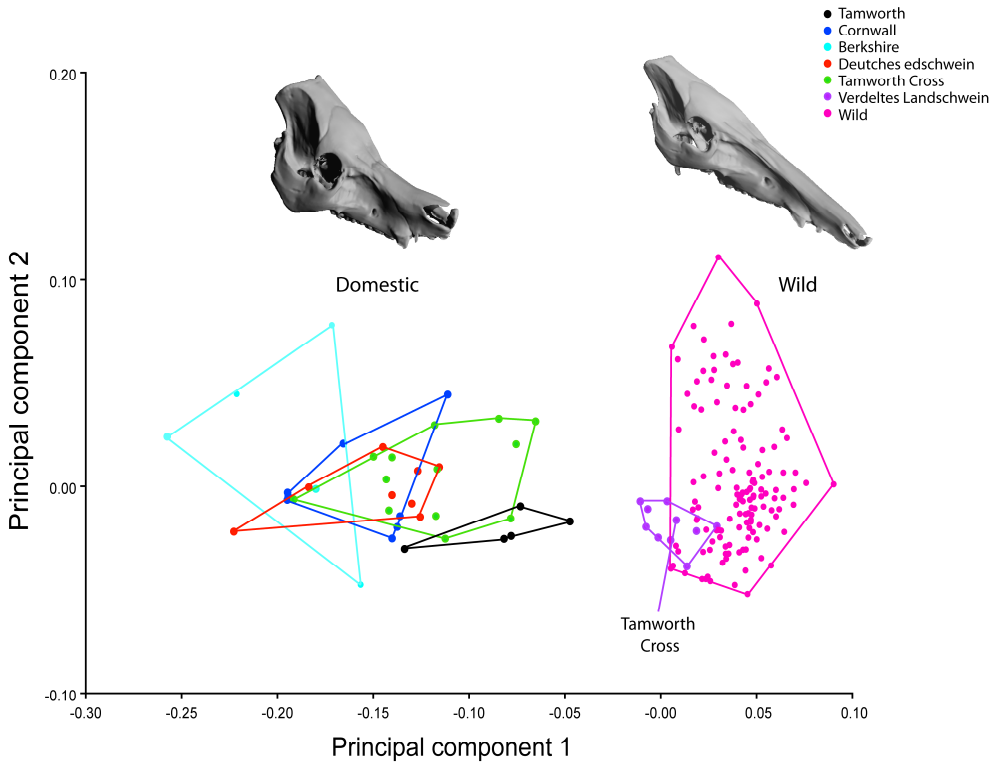

Figure 1: PCA of Wild and domestic pigs.
PC1=58.746% of total variance, PC2=9.961%

573 **Figure 2**

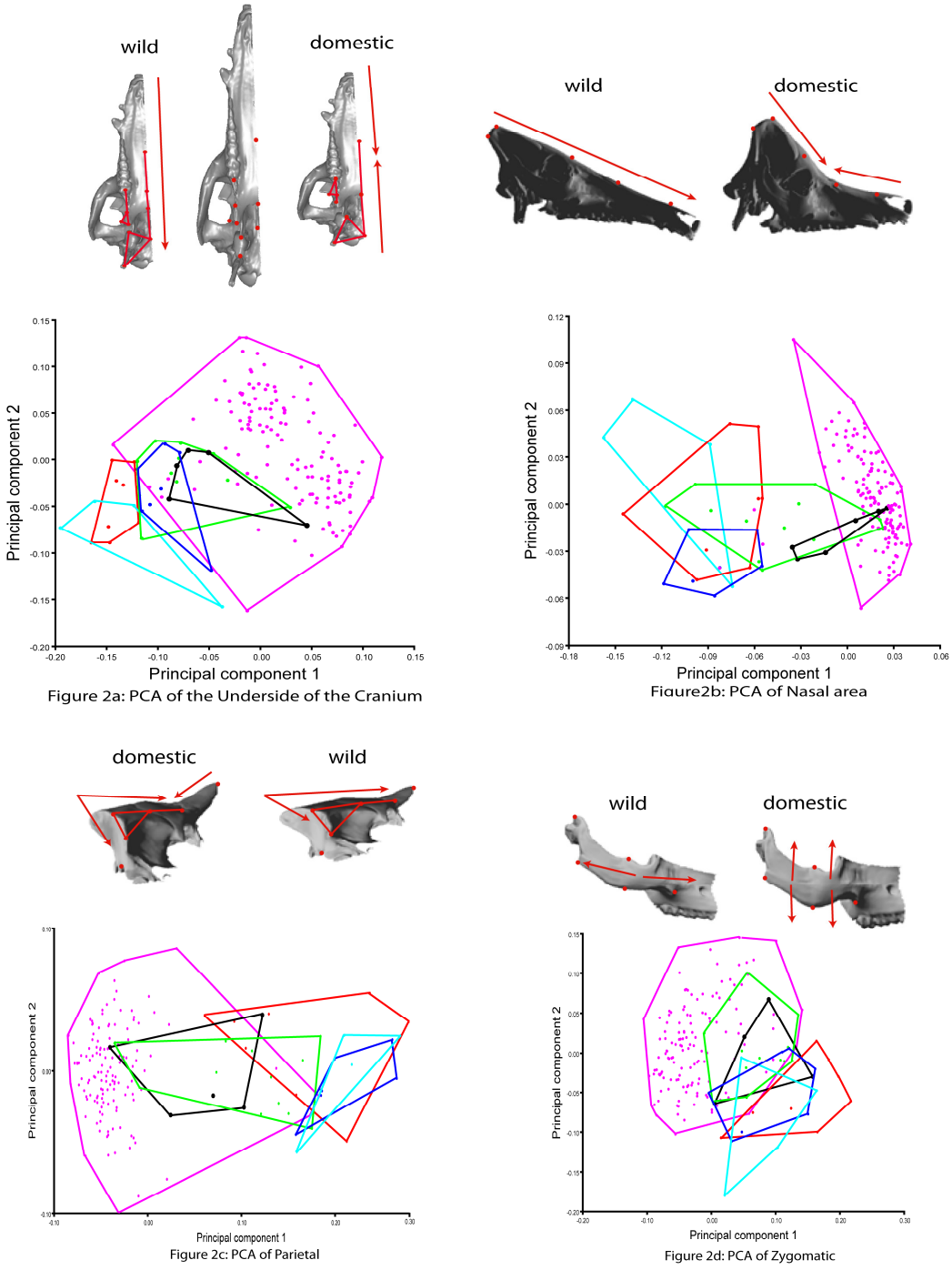

Figure 2a: PCA of the Underside of the Cranium

Figure2b: PCA of Nasal area

Figure 2c: PCA of Parietal

Figure 2d: PCA of Zygomatic

Figure 2: PCAs of sub-sections of the cranium: showing seperation of wild and domestic pigs

574

Chapter 6

Manuscript 4

Domestication and Heterochrony in *Sus scrofa*

Title: Domestication and Heterochrony in *Sus scrofa*

Joseph OWEN[a,b], Kieran MCNULTY[c], Keith DOBNEY[d], Greger LARSON[e], and Una STRAND VIDARSDOTTIR[b].

[a]Department of Archaeology, Durham University, South Road, Durham DH1 3LE, United Kingdom j.t.d.owen@dur.ac.uk;

[b]Department of Anthropology, Durham University, South Road, Durham DH1 3LE, United Kingdom una.vidarsdottir@durham.ac.uk

[c]Department of Anthropology, University of Minnesota, 395 Humphrey Center, 301 19th Ave S, Minneapolis, MN 55455, USA kmcnulty@umn.edu

[d]Department of Archaeology, University of Aberdeen, St.Mary's Building, Elphinstone Road, AB24 3UF, United Kingdom keith.dobney@abdn.ac.uk

[e]Durham Evolution and Ancient DNA Lab, Department of Archaeology, Durham University, South Road, Durham DH1 3LE, United Kingdom greger.larson@durham.ac.uk

Abstract

Domestication creates a variety of unique animal morphologies and behaviours. Traditionally these have been explained through the frame work of heterochrony: changes in the rate and timing of development. The domestic phenotype is often described as paedomorphic, resembling the juvenile ancestral state. Recent advances in techniques like Geometric Morphometrics (GM) have falsified hypotheses of paedomorphism in dogs (Drake, 2011), and examined cranial heterochrony in hominids and monkeys. Here we examine the theory of heterochrony being responsible for the development of domestic phenotype in pigs (*Sus scrofa*). We apply GM methods to 3 longitudinal ontogenetic series (one wild, two domestic), calculating the angles between ontogenetic trajectories and comparing morphological distances between the series at different ages. We also test wild and domestic pigs for evidence of paedomorphism. We conclude that heterochrony is not sufficient to explain the domestic morphology of pigs, nor is there evidence of paedomorphism in 5 of the 6 domestic breeds tested. Thus the traditional explanation of heterochrony as the causal mechanism for the domestic phenotypic is incorrect, and a new explanation must be sought.

Introduction

Domestication can cause radical morphological change in animals. Examples include reduction of cranial capacity, alterations to cranial size and shape, changes in body mass, changes in pelage colour and density, and changes to dentition and behavioural modifications (Bokonyi, 1974, Price, 1999, Zeder, 2012). These changes can occur rapidly and are seen in a wide variety of animals where the only commonality is some form of 'domestication'. There is some evidence for these changes being interlinked. In an experiment of domesticating foxes in Russia (Belyaev, 1979) the sole selection factor applied to a population of captive foxes was reduced aggression towards the human handlers (Belyaev, 1979, Trut, 1999). Within 8-10 generations this caused significant changes in morphology, including increases in the proportion of the fox population exhibiting floppy ears; piebald coat colouring, shortened, curled tails, submissive posturing, tail wagging and increased vocality towards humans. These changes in morphology and behaviour were thought to be linked to changes in the adrenal cortex and other hormone regulatory systems (Trut, 1999, Trut et al., 2009).

The changes associated with the domestic phenotype are traditionally explained as being paedomorphic, i.e. retaining the juvenile morphology or behaviour into adulthood (Moray, 1992, 1994, Price, 1999, Zeder, 2012). Paedomorphism is caused by heterochrony, the evolutionary process that generates diversity via changes in the rate or timing of ontogenetic pathways (Alberch et al., 1979). Gould (1977) described three components of ontogeny - age, size and shape. The evolutionary disassociation of these three components during ontogeny can produce a descendent morphology that either resembles the ancestral morphology at a younger stage of development (paedomorphosis) or at a continued stage of development (peramorphosis) (Alberch et al., 1979). Paedomorphism can arise from either the mechanisms of neoteny, slowing the growth rate of shape relative to age; progenesis, reducing the period of growth in shape, resulting in early sexual maturity; and post displacement, where shape growth occurs later (Godfrey and Sutherland, 1995). It is neoteny that is often invoked to explain the divergent morphology of domestic animals. However, closer examination of the cranial characteristics of dogs (Drake, 2011) has shown that they do not share the morphological characteristics of adult or

juvenile wolves, and that the vast range of phylogenetically novel dog skull shapes does not coincide with the expectations of the heterochronic model. This leaves the model of morphological change in domestic animals uncertain. In this study we analyse and compare ontogenetic pathways of wild and domestic pigs as well as assessing the hypothesis of paedomorphism, aiming to test whether the heterochrony really can explain the morphological changes caused by domestication.

Geometric Morphometrics is an ideal method for examining ontogeny as it allows a detailed analysis of shape independent of size, a provides a platform for a multivariate statistical analysis whereby the interactions of age, size and shape can be determined. Drake´s study of dog morphology used GMM techniques to successfully refute paedomorphism as a cause of morphological variation in domestic canids (Drake, 2011). It has been used successfully to analyse ontogeny in other species, where it has revealed that closely related species and individual populations within a species can develop along very different ontogenetic trajectories. For example Viðarsdóttir and Cobb (2004) demonstrated that for four species of apes: *Homo sapiens, Gorilla gorilla, Pan troglodytes* and *Pan paniscus*, closely related genera, or members of the same genus, do not share a common early post-natal ontogeny. Ontogenetic divergence can also be seen intra-specifically, in *H. sapiens* differences present at birth are accentuated and modified during growth to produce distinct facial morphologies in geographically distinct human populations (Viðarsdóttir et al., 2002). GMM has also been used to test hypotheses of heterochrony. Mitteroecker et al. (2004) used GMM to show that the differences in facial form between *H.sapiens, P. troglodytes* and *G. Gorilla* are most likely genetically controlled, and that suggest pure heterochrony can not explain the subsequent further divergence in cranial form. Heterochrony is also rejected as the causal mechanism for inter-specific differences in chimpanzee skulls (*P. paniscus* and *P. troglodytes*), a hypothesis that was often invoked to explain allometric scaling in hominid evolution (Mitteroecker et al., 2005). It has also been falsified as the cause of intra-specific sexual dimorphism in *Alouatta palliata* (Howler Monkeys) (Blanco and Godfrey, 2006).

It is unlikely that heterochrony affects the skull globally, as it has been shown that the cranium is developmentally modular (Mitteroecker and Bookstein, 2007, 2008), and independent evolution of different regions of the skull does not necessarily result

in a global growth pattern or global heterochrony. Instead, regional development can exist as localised allometric scaling (David, 1990) or 'dissociated' heterochrony (McKinney and McNamara 1991). It is difficult to determine whether different regions are undergoing independent heterochrony (Mitteroecker et al., 2005), so we attempt a broad approach examining two modules of the crania, the facial region and the neurocranium.

The pig (*Sus scrofa* L.1758) is a crucial food and economic resource in both its wild and domestic form. Pigs have a long standing affiliation with humans, hunted for their meat before the Pleistocene (Albarella et al., 2007) and first domesticated in South-Eastern Anatolia around 10,500BP (Zeder, 2008). From there domesticated pigs spread throughout Europe and North Africa (Larson et al., 2007), with additional separate domestication events in both Europe (Larson et al., 2005b) and China (Cucchi et al., 2011). It is now one of the most widespread terrestrial mammals on the planet, found on all the inhabited continents either through natural or human aided dispersal (Groves, 1981, Grubb, 2005). Pigs have a demonstrable morphological response to domestication, including cranial modification (Bokonyi, 1974), body mass reduction (Ervynck et al., 2001) and changes to coat colour (Fang et al., 2009), making them an ideal subject to test for heterochrony. Pigs are also well suited for a test of paedomorphism, as the domestic pigs direct ancestral population survives today in the form of the European wild boar (Larson et al., 2005a, 2007).

Materials

Three longitudinal ontogenetic series were examined in this study, a single wild series composed of 32 individuals and two domestic series, composed of 17 Berkshire pigs and 25 Deutsches Edeschwein pigs. The wild pigs were from Poland, mainly the Białowieski National Park, but also some from South-West Poland near Nysa, all collected in the Natural History Museum in Berlin. The domestic pigs were digitised at the Julius Kühn Museum of Domestication in Halle, East Germany, where they were also raised. Ontogenetic series of individual breeds or wild animals were taken from the same geographic area to reduce the effects of environmental factors. Complete ontogenetic sequences are rare, hence the use of an incomplete ontogenetic sequence in the Berkshire pigs (containing only two very young individuals) and the preliminary nature of this investigation.

The pigs were divided into three age stages based on dental characteristics: age stage 1 represents neonatal to two months; stage 2 three to fifteen months; and age stage 3 sixteen months and older. The wild pigs were aged according to tooth eruption following the protocol of Higham (1967). The exact birth and death dates were available the majority of the domestic individuals, the remainder were aged following the same protocol as the wild pigs. All pigs, wild and domestic, were split into the age stages using the Higham protocol for consistency (which assigned the domestic pigs of known age correctly).

The ontogenetic series was further split into two subsets, the face and neurocranium, to test the hypothesis of regional heterochrony. See table S1 for landmark details.

To test for paedomorphism the wild ontogenetic series was compared to a variety of adult domestic pigs, including Deutsches Edelschwein (9 individuals), Hannover-Braunschweig-Landschwein (3), Tamworth (5), Veredeltes Edelschwein (13), Cornwall (8) and Berkshire pigs (5).

Methods

Thirty-eight unilateral three-dimensional coordinates (Supporting Table S1) were digitised from the right side of the cranium, using a Microscribe® GLS (EMicroscribe Inc), by the first author. Specimens were standardised using Generalised Procrustes Analysis (GPA) (Bookstein, 1991, Mitteroecker and Gunz, 2009, Rohlf, 2003) and morphological relationships explored using Principal Component Analyses (PCA). Significance of differences in shape between groups was assessed using Multivariate Analysis of Variance (MANOVA). Mahalanobis´ and Procrustes distances between group means (tested with 10,000 permutations) were compared to examine the similarity/dissimilarity of shape between samples (Drake, 2011). Digitising and methodological error was assessed following O'Higgins and Jones (1998) and found to be negligible.

To investigate heterochrony taking into account size, shape and age, a multivariate analysis of shape using Geometric Morphometrics (GM) can be used to plot the ontogenetic trajectories of ancestral and descendant population through principal

components analysis. If the trajectories differ without overlap heterochrony can be rejected, if they overlap, it can be accepted. In a multivariate shape analysis overlap in the initial PCs is no guarantee of overlapping trajectories in wider shape space. To account for this a within group multivariate regression of shape on log size with permutation tests was computed for each sample within a multidimensional shape space with the origins centred. The angle between the ontogenetic trajectories of wild and domestic samples was determined to prove or disprove heterochrony (Mitteroecker et al., 2005).

To test for paedomorphism in pigs, the adult descendant morphology (here represented by domestic pigs) is compared to different ages of the ancestral morphology (wild pigs). To support a hypothesis of paedomorphism, the descendent morphology should be closer in shape to the young or juvenile ancestral morphology than to the adult ancestral morphology. If the adult descendant populations are further from the juvenile ancestral populations the hypothesis of paedomorphism will be rejected. To test the hypothesis the Mahalanobis´ and Procrustes distances between a variety of adult domestic pig breeds and the wild ontogenetic series were computed and tested with 10,000 permutations.

To test for regional ontogeny the sub-sets of data for the neurocranium and the facial region of the cranium (see supporting table S2) were subjected to the same tests as the whole cranium. Distances were calculated and compared between wild and domestic datasets, and the ontogenetic trajectories and the angles between them computed. All analyses were carried out in Morphologika (O'Higgins and Jones, 2006), MorphoJ (Klingenberg, 2008) and SAS.

Results

Differences between complete wild and domestic pig crania

Differences in shape between the wild and domestic groups, including all age stages were tested with MANOVA and found to be significantly different (p=<0.0001, df=214, F=6441.26), demonstrating that all three groups are morphologically distinct from one another. The morphological distances between groups (table 1) confirm the MANOVA result: the groups are all distinct from one another. Table 1 also shows that the domestic pig groups are closer, and thus more similar to each other in shape,

than either is to the wild pig group. These cranial shape differences between wild and domestic pigs are summarised through PCA (Figure 1). The first PC separates the domestic and wild morphologies (48.3% of total variance). The second PC (29.8% of total variance) shows ontogenetic trajectories, where the youngest and smallest pigs score lowest and the older pigs score highest. As the pigs age the ontogenetic trajectories between wild and domestic pigs diverge along PC1, so older pigs are at the extremes of PC1 and the younger pigs cluster in the middle.

Distance Between	Mahalanobis distance	*p*-value	Procrustes Distance	*p*-value
Edelschwein-Berkshire	9.5839	<0.0001	0.044	0.17
Edelschwein-Wild	13.3303	<0.0001	0.1559	<0.0001
Berkshire-Wild	14.5291	<0.0001	0.1808	<0.0001

Table 1: Distances between wild and domestic groups, for the complete crania for all ages.

When the groups were broken down into the age classes there were still significant differences between them at all ages, but the differences between the wild and domestic pigs increase with age. Table 2 (below) shows the distances between the age groups. At all age stages the distance between the domestic groups is less than the distance between wild and domestic pigs. The distances are smaller at age stage 1 than age stage 2 or 3.

Distance Between	Mahalanobis distance	*p*-value	Procrustes Distance	*p*-value
Age Stage 1 (0-2 months) group size = 17				
Edelschwein-Berkshire	7.0183	0.018	0.1604	0.015
Edelschwein-Wild	8.5019	<0.0001	0.1612	<0.0001
Berkshire-Wild	12.3636	0.005	0.2362	0.026
Age Stage 2 (3-15 months) group size = 31				
Edelschwein-Berkshire	10.4971	<0.0001	0.0987	<0.0001
Edelschwein-Wild	18.7865	<0.0001	0.3415	<0.0001
Berkshire-Wild	18.8497	<0.0001	0.3914	<0.0001
Age Stage 3 (15+ months) group size = 24				
Edelschwein-Berkshire	6.8572	<0.0001	0.1316	<0.0001
Edelschwein-Wild	15.5797	<0.0001	0.4148	<0.0001

Berkshire-Wild	18.4329	<0.0001	0.4537	<0.0001

Table 2: Morphological distances between complete pig crania at different ages.

Differences between ontogenetic trajectories

Angle of Trajectories Between	Angle Degree(°)	*p*-value
Edelschwein-Berkshire	29.747	n/a
Edelschwein-Wild	44.032	0.062
Berkshire-Wild	54.63	n/a

Table 3: Angle between ontogenetic trajectories

Table 3 (above) shows pair wise angles between the ontogenetic trajectories of the wild and domestic groups. The angle between the domestic breeds is smaller than the angle between the domestic and wild pigs; thus the domestic pigs are on a similar but not identical ontogenetic trajectory to each other, one that is different to the wild pigs. Permutation tests were not possible with the Berkshire group as there were not enough individuals in age stage 1, and the permutation test between the Deutsches Edelschwein and wild pigs returned a non-significant result, which is also linked to small sample sizes and the resulting low statistical power of the test.

Tests for paedomorphism

Distance Between	Mahalanobis distance	*p*-value	Procrustes distance	*p*-value
Wild Stages vs. Deutsches Edeschwein Adult (#9)				
Stage 1	7.9302	<.0001	0.2098	<.0001
Stage 2	9.1212	<.0001	0.2057	<.0001
Stage 3	8.2867	<.0001	0.2065	<.0001
Wild Stages vs. Berkshire Adult (#5)				
Stage 1	4.2620	<.0001	0.1957	<.0001
Stage 2	7.7199	<.0001	0.2031	<.0001
Stage 3	8.5302	<.0001	0.2109	<.0001
Wild Stages vs. Hannover-Braunschweig-Landschwein Adult (#3)				
Stage 1	6.2993	0.0100	0.2016	0.0060
Stage 2	10.2571	0.0020	0.1769	0.0010
Stage 3	6.2472	<.0001	0.1719	0.0010
Wild Stages vs. Tamworth Adult (#5)				
Stage 1	6.8805	0.0100	0.1803	<.0001
Stage 2	6.7945	<.0001	0.1045	<.0001
Stage 3	3.6291	<.0001	0.0907	<.0001
Wild Stages vs. Veredeltes Edelschwein Adult (#13)				
Stage 1	9.7828	<.0001	0.1759	<.0001
Stage 2	6.3832	<.0001	0.1396	<.0001
Stage 3	3.8714	<.0001	0.1400	<.0001
Wild Stages vs. Cornwall Adult (#8)				

Stage 1	7.7208	<.0001	0.2163	<.0001
Stage 2	12.8338	<.0001	0.2025	<.0001
Stage 3	10.1080	<.0001	0.1991	<.0001

Table 4: Tests for paedomorphism, morphological distances between the three ages stages of the wild group and different adult domestic pigs

For the hypothesis of paedomorphism to be true the adult descendent population (domestic pigs) must resemble the juvenile morphology of the ancestral population (wild pigs), i.e. it must be closer in morphological distances to wild stage 1 than to wild stage 3. The tests for paedomorphism (table 4) return negative results for Deutsches Edeschwein, Hannover-Braunschweig-Landschwein, Tamworth and Veredeltes Edelschwein. These adult pigs are either at similar distances or greater distances from wild age stage 1 than from wild age stage 3. The result for the Cornwall pigs gives an ambiguous result, the Mahalanobis distance suggests that adult Cornwall pigs are paedomorphic, but the procrustes distance does not. This may be due to Mahalanobis distances being a product of discriminant function, and thus not scaling directly as a true biological distance, unlike the procrustes distances which reflect the shape differences between samples. The result for the Berkshire pigs returns a positive result, suggesting that Berkshire pigs are possibly paedomorphic.

Partial crania

Distance Between	Mahalanobis distance	*p*-value	Procrustes distance	*p*-value
Partial Crania				
Neurocranium				
Edelschwein-Berkshire	17.935	<0.0001	0.0875	<0.0001
Edelschwein-Wild	37.8219	<0.0001	0.2299	<0.0001
Berkshire-Wild	38.9994	<0.0001	0.2646	<0.0001
Facial				
Edelschwein-Berkshire	9.1617	<0.0001	0.0967	<0.0001
Edelschwein-Wild	18.9819	<0.0001	0.3047	<0.0001
Berkshire-Wild	20.337	<0.0001	0.3414	<0.0001

Table 5: Distances in shape space between wild and domestic groups; within the whole crania and partial crania (neurocranium and face); also the distances between age stages between groups.

In the analysis of the partial cranium, both the neurocranium and the face reflect the results of the whole crania. The distances between the two domestic groups are much smaller than the distances between the wild and domestic groups. The neurocranial distances between the groups are larger than those for the face or the whole cranium,

perhaps suggesting that the neurocranium is more morphologically distinct between wild and domestic groups than is the face.

Ontogenetic angles of partial crania

Neurocranium Angle of Trajectories Between	Angle Degree(°)	*p*-value
Edelschwein-Berkshire	24.843	n/a
Edelschwein-Wild	27.584	n/a
Berkshire-Wild	34.615	n/a
Facial Angle of Trajectories Between	**Angle Degree(°)**	**p-value**
Edelschwein-Berkshire	25.343	n/a
Edelschwein-Wild	28.806	n/a
Berkshire-Wild	33.990	n/a

Table 6: Angles between ontogenetic trajectories for the partial crania.

Comparison of the ontogenetic trajectories for different regions of the cranium reveals that the angles between the domestic and wild pigs are larger than the angles between the two domestic groups, mimicking the result for the complete crania. The angles involved are smaller than the angles of the complete crania, most likely due to the reduced dimensionality of the dataset (as a result of the reduced number of landmarks).

Discussion

The cranial morphologies of wild and domestic pigs are distinct, at birth, in adulthood and at all stages in between. Their ontogenetic trajectories diverge, the distances between wild and domestic pigs increasing as the pigs age. This is demonstrated clearly in Figure 1, on PC1 the young wild and domestic pigs are close together, but the adult wild and domestic populations are far apart. This pattern is supported by the Mahalanobis and Procrustes distances between the domestic breeds and the wild pigs at all age stages (Table 3). While young (age group 1) the distances between the wild group and the two domestic groups are small, although young Deutsches Edelschwein are closer to wild piglet shape than are young Berkshire pigs. The older age groups (2 and 3) show the distances between the domestic pigs are small and the distance between wild-domestic pigs is large, the shapes are distinctly different. We are able to infer from these results that post-natal ontogeny is responsible for much of the adult cranial morphology in pigs, but that pre-natal growth has already established significant differences between wild and domestic cranial form at age stage 1.

306

307 A multivariate shape analysis of cranial ontogenetic trajectories produces three
308 different trajectories from three groups, with wild pigs further separated from the two
309 domestic trajectories. According to Mitteroecker et al. (2005) heterochrony is a
310 sufficient descriptor of morphological change only if the same morphological
311 processes are responsible for change, but differently timed. If the ontogenetic
312 trajectories in shape space differ the theory of heterochrony is falsified. Differences
313 in the angle of ontogenetic trajectories between wild and domestic pigs show that
314 heterochrony is not likely to be responsible for the observed morphological change.
315 Even though the sample size was very small, a *p*-value not far from significance
316 (0.062) was returned. Larger samples may rectify this problem.
317

318 The tests for paedomorphism show that the majority of the pig breeds are not
319 paedomorphic; the descendant populations (the domestic pigs) are not closer to the
320 young ancestral (wild) population than the adult ancestral population. The exception
321 is the Berkshire pig, which does satisfy these criteria for paedomorphism. Overall,
322 paedomorphism is not a sufficient descriptor of the changes seen in domestic pigs,
323 although these results suggest that pig breeds respond differently to domestication,
324 and the ontogenetic angles between the domestic breeds confirm this.
325

326 Both the neurocranium and face of the pig show significant differences in
327 morphology between wild and domestic pigs. As in the complete cranium there are
328 greater distances between the wild and domestic groups, than between the two
329 domestic groups. The ontogenetic trajectories are also distinct between all groups.
330 There is no evidence of modular heterochrony in our analysis as the regional data
331 mirrors the results for the whole crania. Note this does not completely rule out
332 modular heterochrony, as it could be taking place on a smaller scale than tested for.
333 However to determine this would require more detailed analysis (a greater number of
334 landmarks) on larger datasets, which are unavailable at this time.
335

336 **Conclusion**

337 Heterochrony is not the basis of the domestic phenotype, nor are most domestic pigs
338 paedomorphic. This paper thus joins a series of others rejecting heterochrony as the
339 causal mechanism for morphological change in a host of animals; including dogs

(Drake, 2011), chimpanzees (Mitteroecker et al., 2005) and howler monkeys (Blanco and Godfrey, 2006). However, in the literature of domestication heterochrony is still evoked as the underlying mechanism of morphological change (Zeder, 2012, Hare et al., 2012). Although paedomorphic behavioural characters in domestic animals have been identified (Coppinger et al., 1987, Moray, 1992, Moray, 1994, Trut et al., 2009), morphological characters classified as paedomorphic cannot be quantified in either pigs or dogs.

If heterochrony is not the causal mechanism for morphological change in domestic animals then what is? Clearly there is some pre- or post-natal mechanism or process that is enforcing changes to morphology, yet the traditional language of heterochrony appears inadequate to explain it. We must also keep in mind that the processes acting prenatally may not be the same as those acting postnatally. Further definition of the changes that occur during growth and development may help answer this question. Analysis of other domesticates, like horses, sheep or cattle may show commonalities in the development of domestication. There are experiments that manipulate the conditions of growth in domestic animals e.g. the fox farm experiment by Belyaev (Belyaev, 1979, Trut, 1999) or various experiments on mice or rats (Arbuckle, 2005). Multivariate analysis of the crania of the specimens in those experiments would allow specific links to be drawn between morphological development, hormone fluctuation and the genetic mechanisms behind them.

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Figure 1: PCA showing first two PCs of wild and domestic ontogenetic series. The two domestic series are on the left (negative score on PC1), and the wild series on the right (positive score on PC1). PC2 shows accruing size and age, and the increasing distance between the wild and domestic ontogenetic series. No discrimination was discernible on other PCs.

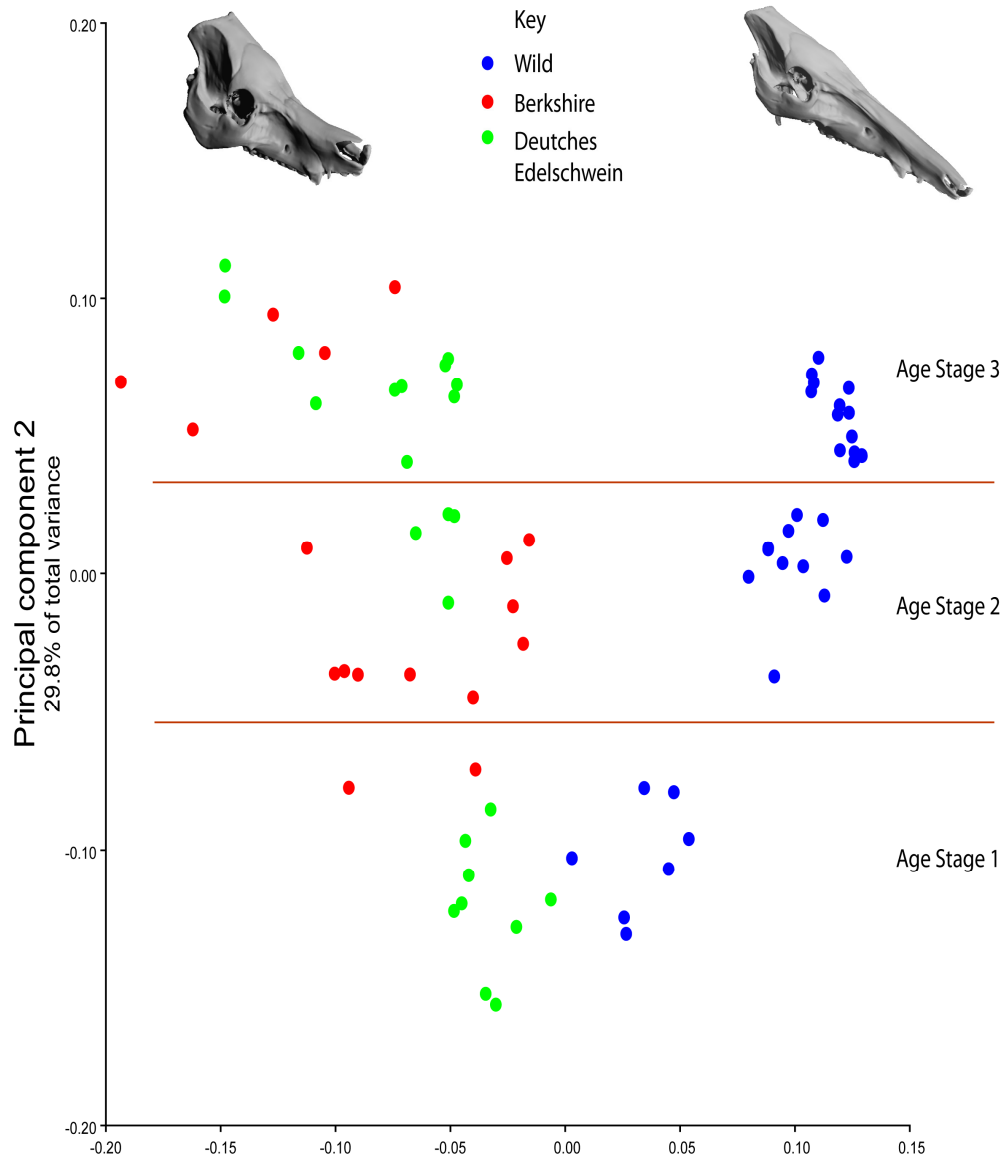


Figure 1a: PCA of allometric shape space
48.3% of total variance

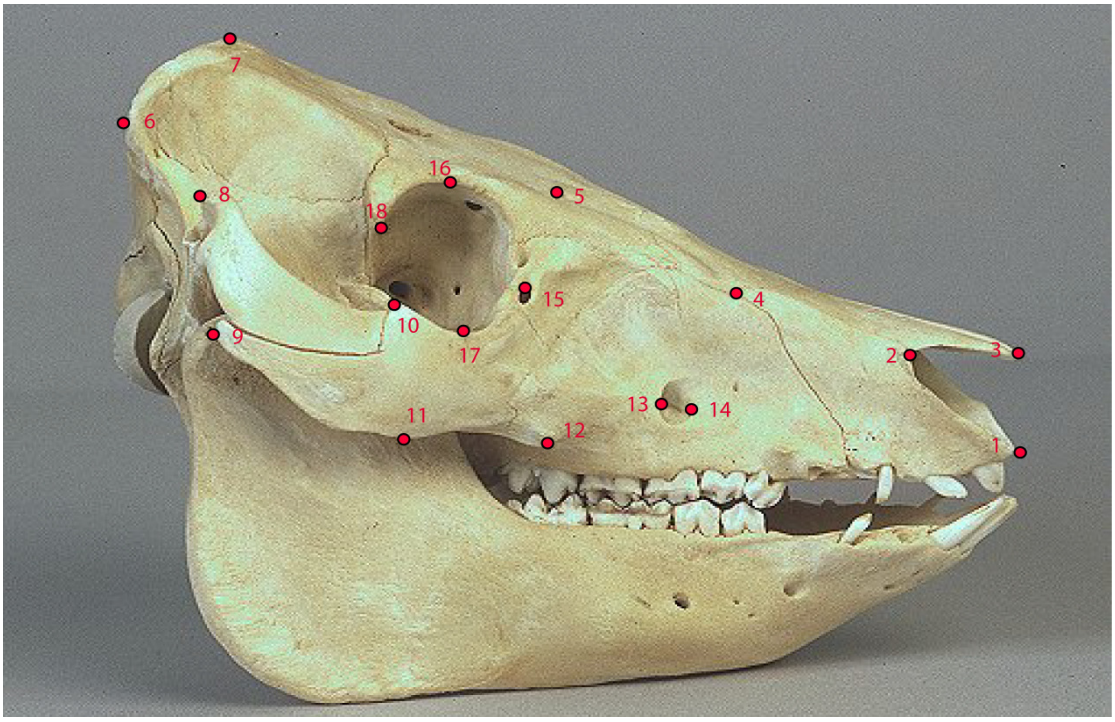
Table S1:Landmark List

Landmark	Description
1	Most anterior midline point on nasals.
2	Anterior join in nasal and pre maxilliar suture.
3	Anterior point of nasal.
4	Suture at the meeting point of the premaxillar, maxillar and nasal.
5	Most posterior point of superorbital foramen and groove.
6	Most laterial point of the Nuchal Crest.
7	Most anterior point of Nuchal Crest - on the midline of the paretial.
8	Most superior point of zygomatic process of temporal.
9	Most posterior point of zygomatic process of malar.
10	Superior point of the temporal process of malar.
11	Most inferior point of the malar (zygomatic arch).
12	Anterior most point of the process emerging of the malar (zygomatic arch).
13	Most posterior point of infraorbital foramen.
14	Most anterior point of infraorbital foramen.
15	Most superior point of the lower lacrimal formina.
16	Most superior point of the occipital.
17	Most inferior point of the occipital.
18	Base of supraorbital process.
19	Anterior point of incisive foramen/palatine fissure.
20	Posteriormost point of incisive foramen/palatine fissure.
21	Most anterior point of canine alveolus.
22	Most posterior point of canaine alveolus.
23	Anterior point of the alveolar margin of the tooth row.
24-27	Contact points between M3/M2, projected labially (buccally) onto alveolar margin.
28	Most posterior point of the alveolar margin of the tooth row.

29-32	Contact points between M3/M2, projected lingually onto alveolar margin.
33	Most anterior point of the pterygoid process of the palatine.
34	Most lateral point of the pterygoid process of the palatine.
35	Most posterior point of the pterygoid process of the palatine.
36	Suture of the nasal and palatine bones (on the midline).
37	Tip of posterior nasal spine.
38	Meeting point between the basisphenoid and basioccipital along midline, posterior of the vomer.
39	Anterior most point of the bulla tympanica.
40	Most anterior point of the paramastoid process.
41	Most anterior point on the margin of the Hypoglossal canal.
42	Lowest point on the orobasal border of foramen magnum.
43	Most posterior tip of occipital condyle.
44	Most superior point on the border of foramen magnum.

Table S2: Subsets of landmarks (Paper 3/Chapter 5)

Landmarks	Region
Parietal	4,5,6,7,44
Zygomatic	8,9,10,11,12
Angle of the Nasal	2,3,4,5,6,44
Orbit	15,16,17,18
Toothrow	21-32
Basicranium	33-41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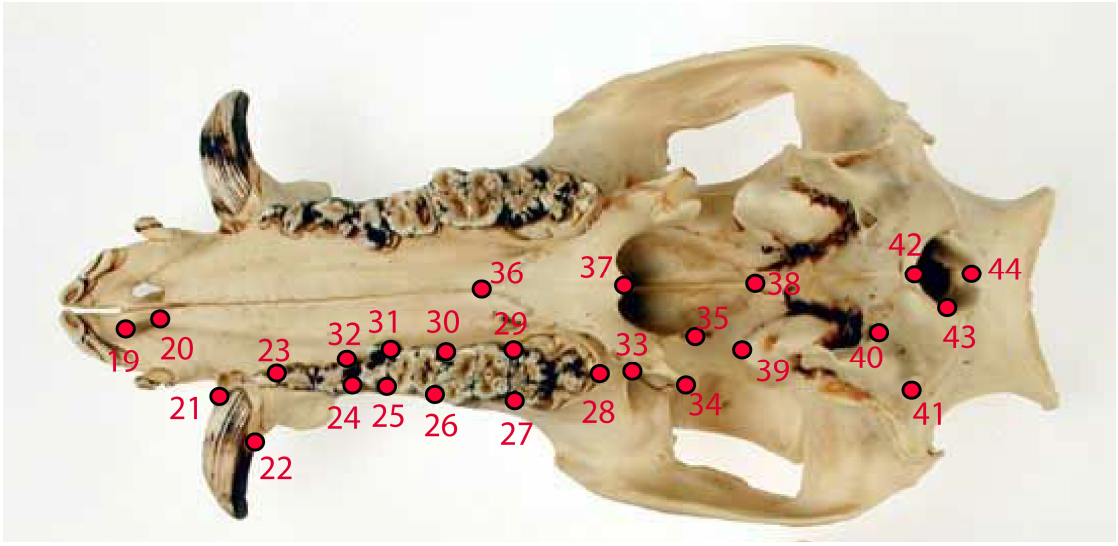
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Supporting Table S2

	S.s. Tunis	S.s. Berlin	S.s. Caucasus	S.s.Fukien	S.s.Szechuan	S.s.Hainan	S.s.Shanxi	S.s.Gansu	S.s. E.Poland
S.s. Tunis	**60.0**								
S.s. Berlin		**46.9**	3.1	3.1					9.4
S.s. Caucasus			**60.0**		5.0				5.0
S.s.Fukien				**61.5**	15.4	7.7			
S.s.Szechuan			1.0	30.0	**30.0**				
S.s.Hainan				66.6	33.3	**0.0**			
S.s.Shanxi							**57.1**	14.3	14.3
S.s.Gansu					25.0		25.0	**25.0**	
S.s. E.Poland		10.7	3.6						**67.9**
S.s.Geneva		6.1							6.1
S.s. Iraq/Iran			11.1	11.1					
S.s N.E.Iran			14.3						
S.s S.Iran		20.0							
S.s. Turkey	37.5		12.5						
S.s. S.W.Germany		7.7							
S.s. S.W.Poland		12.5	6.3						31.3
S.s.Burma					15.4				
S.s India			5.6	11.1			5.6		
S.s Japan									
S.s Malaysia					14.3	14.3			
S.s Papua				11.1					
S.s Sardinia									
S.s N.Sumatra									
S.s. Ligga Is									
S.s. Nias IS									
S.s W.Russia		16.7	33.3						

Supporting Table S2

S.s.Geneva	S.s. Iraq/Iran	S.s N.E.Iran	S.s S.Iran	S.s. Turkey	S.s. S.W.Germany	S.s. S.W.Poland	S.s.Burma	S.s India	S.s Japan	S.s Malaysia
10.0				30.0						
6.3					6.3	9.4				
				15.0	5.0			10.0		
							7.7	7.7		
							30.0			
								14.3		
							25.0			
3.6						14.3				
72.7				6.1	3.0					
	55.6	11.1	11.1							
		42.9	28.6			14.3				
		60.0	**20.0**							
				37.5						
23.1				7.7	**53.8**	7.7				
6.3						**37.5**				
							53.8	7.7		15.4
	5.6					5.6	5.6	**55.6**		
									100.0	
							14.3			**57.1**
							4.3	4.3		
16.7				16.7						

Supporting Table S2

S.s Papua	S.s Sardinia	S.s N.Sumatra	S.s. Ligga Is	S.s. Nias IS	S.s W.Russia
		3.1	3.1		9.4
					6.1
					12.5
		6.3			
		7.7			
			5.6		
89.9					
	100.0				
		91.3			
		57.1	**42.9**		
			40.0	**60.0**	
					16.7

7 Conclusion

This thesis comprised of four main research questions, conducted through the methodology of geometric morphometrics to answer questions about pig evolution (manuscript 1), to study in greater depth suid biogeographic variation (manuscript 2), to quantify differences between wild and domestic *Sus scrofa* (manuscript 3), and to investigate the effects of heterochrony on domestic pigs (manuscript 4). The results are summarised here, along with the implications of the results and some possible avenues of future research.

7.1 Evolutionary studies in suids (manuscript 1)

The relationship between the African suid Potamochoerus and the Eurasian suid *Sus* was investigated by combining shape analysis of modern material with evolutionary depth of genetic analysis. This answered a long standing question about the relationship between these two genera. Their morphological similarity had been noted for some time (Groves, 1981), but this appeared to be contradicted by the monophyly of African Suids as confirmed through genetic analysis (Gongora et al., 2011). The mechanism that could have brought this about was not known, only postulated. The results of manuscript 1 showed that the genetic analysis revealing African and Eurasian suids to be monophyletic was not incongruous with morphology, as suid morphology is explained by suid cranial shape reflecting signatures derived from its evolutionary and behavioural ancestry. Thus the genetic and morphological variation within suids reveals an important component of the evolutionary history of the family Suidae, a complete understanding of which can only be achieved through an analysis of both.

The approaches employed in this study, especially the combination of morphology and genetics, could be used to resolve a range of similar issues in other taxonomic groups, such as the Family Rhinocerotidae (Willerslev et al., 2009) and the tribe Papionini (Gilbert, 2011).

7.2 Biogeographic variation in suids (manuscript 2)

Sus scrofa is a species that shows strong biogeographic structuring, both in its morphology and genetics reflecting its large range throughout Eurasia and North Africa. A GMM approach returned a detailed resolution of the biogeography of *Sus*,

confirming that this approach has great scope for use in biogeographic studies as has also been shown in African monkeys (Cardini et al., 2007, Cardini and Elton, 2009). This is important implications where subspecies have been ascribed largely on the basis of cranial characteristics (Groves, 1981, 2007, Genov, 1999), which often rely on order of magnitude measurements. Our results have shown that size is more affected than shape by climate, which could impact taxonomic studies. A combined genetic and morphometric approach may prove to be the most informative approach in the future.

This result is also significant with regard to studies of determination of status as wild or domestic, these too are mainly based on size differences (Payne and Bull, 1988, Mayer et al., 1998). These investigations are based on the assumption that wild and domestic individuals are morphologically different from each other and that this difference is significant, be it in cranial characteristics, tooth size or overall body size. However, these characteristics are strongly affected by climate, diet, habitat and geography, making the individuals a product of their surroundings. Studies investigating domestic status of suids must therefore take into account possible dietary changes or environmental shifts. This will mainly affect regional or wide temporal studies which should include baseline comparisons with wild animals and other domestics to check for possible climatic shifts.

7.3 Discrimination between wild and domestic suid morphology (manuscript 3)

It is possible to discriminate between wild and domestic pigs on the basis of cranial morphology. This is true for both whole and partial crania such as the parietal, zygomatic, angle of the nasal and the basicranium. The ability to determine between different morphologies, either in cranial or post cranial material has significant implications for zooarchaeology. Greater resolution allows clearer quantification of the proportion of wild and domestic animals on a site, elucidating evolving subsistence strategies and could help determine the origins of the transition from hunter-gathering to farming (Rowley-Conwy et al., 2012).

The sensitivity of GMM allows for the distinction between domestic breeds. Currently the study of the history of breeds is focused around the industrial revolution, but there is tentative evidence in the archaeological record of distinct

breeds before this period (Davis, 2008, Davis et al., 2012). This has important consequences for the study of the origins and development of such breeds, where currently the methodology for studying improvement is based on size increases (Davis et al., 2012), which has obvious difficulties overcoming size issues associated with sexual dimorphism. Breed improvement, for traction or increased meat bearing should be reflected in the morphology, not just size, and could be examined using the methods employed here without being confused with the effects of sexual dimorphism.

The results of this paper demonstrate some of the possible applications for GMM in archaeology. Studies have already started applying GMM to zooarchaeological questions and material, for example shape differences have been shown to exist between wild and domestic pig teeth in the early archaeological record, and GMM can discriminate between human populations on the basis of mandibular morphology (Buck and Vidarsdottir, 2004). GMM can be applied to post-cranial material as well, e.g. it has been applied to both Palaeolithic horse metapodials to investigate phylogeography (Bignon et al., 2005) and cervid anatomy associated with locomotion for palaeo-climatic reconstruction of the Plio-Pleistocene (Curran, 2012). There is great scope for future applications on cranial and post-cranial material, not just to elucidate both the process and history of domestication, but any archaeological question that requires discrimination between populations, or wishes to examine morphological change or evolution.

7.4 Domestication and Heterochrony in *Sus scrofa* (manuscript 4)

In the archaeological literature of domestication, heterochrony is still evoked as the causal mechanism of morphological change, with domestic animals typed as paedomorphic wild animals (Zeder, 2012, Hare et al., 2012). Although some paedomorphic behavioural characters in domestic animals have been identified (Coppinger et al., 1987, Moray, 1992, Moray, 1994, Trut et al., 2009), morphological characters classified as paedomorphic cannot be quantified in either domestic pigs or dogs. Thus heterochrony is not the cause of the domestic phenotype, nor are most domestic pigs paedomorphic.

Clearly there is some pre- or post-natal mechanism or process that is enforcing changes to morphology, yet the traditional language of heterochrony appears inadequate to explain it. We must also keep in mind that the processes acting prenatally may not be the same as those acting postnatally.

If heterochrony is not the causal mechanism for morphological change in domestic animals then there is currently no explanation for why the domestic phenotype exists in many varied and different species. Further definition of the changes that occur during growth and development may help answer this question. Analysis of other domesticates, like horses, sheep or cattle may show commonalities in the development of domestication. There are experiments that manipulate the conditions of growth in domestic animals e.g. the fox farm experiment by Belyaev (Belyaev, 1979, Trut, 1999) or various experiments on mice or rats (Arbuckle, 2005). Multivariate analysis of the crania of the specimens in those experiments would allow specific links to be drawn between morphological development, hormone fluctuation and the genetic mechanisms behind them.

7.5 Strengths, weaknesses and recommendations for future work.

A weakness in this study is the lack of complete geographic coverage for the biogeographic study (Manuscript 2). Adequate samples were not available for the Iberian peninsular, south east Europe, central and eastern Russia, central Asia and especially North Africa. The paucity of North African material is a more widespread problem with suid studies as there are not many samples in museum collections (Groves, 1981), their relationship with Near Eastern and European pigs is not fully understood (Groves, 1981, Larson et al., 2005). Future work would ideally fill in these gaps, and attempt to resolve the relationships of pigs in the western Mediterranean Basin, central Asia and North Africa. Future studies of taxonomy could use a combined GMM and genetics approach, which would resolve the morphology and genetics to produce a confident, comprehensive taxonomy for pigs.

A lack of data is also hindering the study of domestic suid ontogeny; with only two and half complete ontogenetic series the results are tentative, although even with a limited amount of data we nearly returned a significant result. With more data this study would be considerably strengthened. This study also presents one of the major

avenues for future research. Studies of domestication are of increasing importance as they have become recognised as studies of evolution (Zeder, 2006, Zeder et al., 2006a). GMM is appreciably more powerful and flexible than traditional biometrical approaches, which combined with genetics and hormone studies could produce major breakthroughs in this field.

GMM as a tool is only just starting to find applications within the field of archaeology. As this thesis demonstrates GMM is an excellent at discriminating between populations and also tracing and explaining evolutionary patterns. It can be directly integrated with the other major innovative field of current archaeology, genetics (Zeder et al., 2006b) in a way that traditional methods have not (Davis et al., 2012), and perhaps may struggle to. Overall this thesis has used GMM as a tool in biological and archaeological contexts, demonstrating its ability to answer varied and complex questions. Hopefully applications of GMM in these contexts will continue, as I firmly believe that GMM has the ability to provide more detail to standing archaeological questions, and help explain the evolution of human society.

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