

Macro- and micromorphological features of lifestyle differences in pigs and wild boar

Ingrid MAINLAND
Holger SCHUTKOWSKI
Amy F. THOMSON

Archaeological Sciences,
School of Life Sciences,
University of Bradford,
Bradford BD7 1DP (United Kingdom)
i.l.mainland@bradford.ac.uk
h.schutkowski@bradford.ac.uk

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ABSTRACT

It is known that since the beginnings of domestication human communities have, in one way or another, restricted the activity of their livestock in order to gain better control of the animal management process. The exact nature of this human-animal relationship, however, is difficult to assess from faunal remains in the archaeological record through conventional methods. Taking suids as an example, we propose a novel approach to detect differences in activity patterns of animal domesticates using features of cross-sectional geometry (CSG) and histomorphometry. The present study analysed mid-shaft tibia samples from free-ranging wild boar (n = 40), domestic pigs raised indoors having limited mobility (n = 24) and pigs raised outdoors, free to roam in a paddock (n = 15). Geometric features were found to differ between wild boar and both groups of domestic pigs with regard to the amount of cortical bone (higher in wild boar) as well as in the shape of the bone cross section (more triangular in wild boar). The density of secondary osteons was higher in wild boar than in both groups of pigs. The results were controlled for possible effects of age and weight of the animals and, even though some variables co-vary with these growth-dependent measures, the overall trend of a clear association between activity levels, CSG and micro-morphology can be validated. Thus, the study demonstrates the potential for detecting husbandry systems through the analysis of activity levels reflected in the combined assessment of gross and histo-compositional morphology of a load-bearing long bone.

KEY WORDS

Cross-sectional geometry,
histomorphometry,
pigs,
wild boar,
domestication,
animal husbandry,
activity level.

RÉSUMÉ

Dispositifs macro- et micromorphologique des différences de style de vie chez les porcs et les sangliers.

Depuis l'origine de la domestication, on sait que les communautés humaines ont limité, d'une manière ou d'une autre, l'activité des animaux domestiqués afin d'améliorer la maîtrise de la gestion de ceux-ci. Cependant, la nature exacte de ce rapport homme-animal est difficile à évaluer à partir des restes fauniques (os d'animaux) dans les assemblages archéologiques par des méthodes conventionnelles. Prenant des suidés comme exemple, nous proposons une approche nouvelle pour détecter des différences dans des modèles d'activités liés à l'animal domestique en utilisant les dispositifs de la géométrie de la section transversale (CSG) et l'histo-morphométrie. La présente étude a analysé des échantillons mi-axe de tibias provenant de sangliers en liberté (n = 40), de porcs domestiques gardés à l'intérieur avec mobilité limitée (n = 24) et parqués au pré (n = 15). Des dispositifs géométriques ont été mis en évidence pour différencier les sangliers et les deux groupes de porcs domestiques, en ce qui concerne la quantité d'os cortical (plus importante pour les sangliers) et la forme de la coupe d'os (plus triangulaire pour les sangliers). La densité des ostéons secondaires était plus haute pour le sanglier que pour les deux groupes de porcs. Les résultats ont été examinés en vue d'effets possibles de l'âge et du poids des animaux et, bien que quelques variables changent avec ces mesures croissance-dépendantes, la tendance globale d'une association claire entre les modèles d'activité, CSG et micromorphologie peut être validée. Ainsi, l'étude démontre la possibilité de mettre en évidence des systèmes d'élevage par l'analyse de modèles d'activité reflétés dans l'évaluation combinée de la morphologie brute et histo-compositionnelle d'un os long porteur.

MOTS CLÉS

Géométrie de la section transversale, histo-morphométrie, porc, sanglier, domestication, élevage, modèle d'activité.

RESUMEN

Rasgos macro y micromorfológicos de las diferencias en el estilo de vida del cerdo y el jabalí.

Desde los comienzos de la domesticación es conocido que las comunidades humanas de una manera u otra han limitado la actividad de su ganado en función de tener un mejor control del proceso de manejo animal. La naturaleza exacta de esta relación entre humanos y animales es, sin embargo, difícil de determinar a partir de restos faunísticos con los métodos convencionales. Tomando a los suidos como ejemplo, proponemos un enfoque novedoso para detectar diferencias en los patrones de actividad de los animales domesticados usando rasgos de la geometría de corte transversal (GCT) y la histomorfometría. El presente estudio analizó muestras de diáfisis de tibia de jabalíes silvestres (n = 40) y de cerdos domésticos criados al interior con movilidad limitada (n = 24) y al exterior, errantes en un prado (n = 15). Se encontró que los rasgos geométricos fueron diferentes entre el jabalí y ambos grupos de cerdos domésticos, tanto con respecto a la cantidad de hueso cortical (más alto en jabalí) y la forma de la sección transversal del hueso (más triangular en jabalí). La densidad de los ostiones secundarios fue más alta en el jabalí que en ambos grupos de cerdos. Los resultados fueron controlados para evaluar posibles efectos de la edad y peso de los animales y, aunque algunas variables covarían con estas medidas dependientes del

PALABRAS CLAVE

Geometría de sección transversal,
 histomorfometría,
 cerdos,
 jabalí,
 domesticación,
 cría,
 nivel de actividad.

crecimiento, puede validarse la tendencia general de una clara asociación entre los niveles de actividad, GCT y micromorfología. De esta manera, el estudio demuestra el potencial para detectar regímenes de cría a través del análisis de los niveles de actividad reflejados en la determinación combinada de la morfología total e histocomposicional de huesos largos sometidos a carga.

INTRODUCTION

Humans control the activity levels of their domestic livestock by restricting mobility/foraging through, at the one extreme, stalling, penning or hobbling, and at the other, supervised herding, transhumant systems and range-managed animals. Identification of such variation in the lifestyle of an animal is potentially of great interest for archaeology, allowing insight into much debated human-animal relationships such as the nature of human-animal contact during the early stages of domestication (*e.g.* Harris 1996; Zeder 2001), the prevalence of stalled animals in the past (*e.g.* Ward & Mainland 1999; Wilkie *et al.*, in press), herd mobility (*e.g.* Halstead 1996) and the intensification of animal husbandry in later prehistory (*e.g.* Wilkie *et al.*, in press). This variation is, however, very difficult to identify using conventional archaeozoological evidence.

Bone microstructure is known to sensitively react to varying biomechanical regimes likely to reflect different ways of keeping animals but has received little attention by archaeozoologists. In this paper we present data drawn from ongoing research which aims to explore the potential of histomorphometric studies for archaeozoology through a large scale controlled modern study of the effects of activity of bone micro- and macrostructure in wild boar (*Sus scrofa*) and domestic pig (*Sus domesticus*).

BONE MICROSTRUCTURE AND ARCHAEOZOOLOGY

The suggestion that bone microstructure can be used to elucidate animal domestication and other aspects of animal husbandry within the archaeological past is not new but was first mooted in the

late 1960s/1970s (Drew *et al.* 1971; Gilbert 1989). These early attempts at methodological development, however, were unsuccessful and subsequently criticised, because analysis primarily focused on the orientation of hydroxyapatite crystallites as indicated by X-ray diffraction, a technique which was subsequently shown to be inappropriate (Gilbert 1989). This critique seems to have largely halted research into the potential of histomorphometric techniques for addressing animal lifestyle histories within archaeozoology despite its wide adoption in both anthropological (Larsen 1997) and palaeontological contexts (*e.g.* Laurine *et al.* 2004). Later research, however, in particular Zeder's (1978) identification of lifestyle-related variation in trabecular morphology, and more importantly the recent work on bone microstructure within the life sciences and biological anthropology (*e.g.* Ruff 2000) does provide support for Drew *et al.*'s (1971), central premise that an animal's lifestyle will be reflected in its skeletal microstructure.

BIOMECHANICAL STRESS AND BONE RESPONSE

Bone is a living structure and responds to habitual strain and metabolic factors by an adjustment of its histological composition. There are only two principal response routes to prevailing and changing load patterns and activity regimes: bone formation and bone resorption, carried out by osteoblasts and osteoclasts, respectively. In combination, these two processes accomplish the dynamics of bone modelling and remodelling, *i.e.* the organisation and reorganisation in the histocompositional make-up of bone geometry and microstructure following Wolff's law (*i.e.* that bone adapts to the stresses of biomechanical

loading). Bone modelling typically occurs in the growing skeleton. Formation of osteoid, with subsequent mineralisation, and resorption occur independently, yet co-ordinated, and result in an alteration of bone shape and size. Remodelling takes place throughout life and involves periosteal and trabecular as well as cortical and cancellous bone. Resorption and formation occur in a coupled sequence at the same bone site with little change in bone shape or size (Frost 1987).

Exercise has a measurable effect on bone tissue properties. Mechanical loading in conjunction with skeletal morphology elicit specific patterns of biomechanical stress (Marcus 2002). In general, an increase in exercise-related strain will result in enhanced secondary osteon remodelling and osteoblastic activity (*e.g.* O'Connor *et al.* 1982). The density of secondary osteons is affected by exercise levels in miniature pigs kept in laboratory conditions (Lieberman 1997). More recent research also suggests that secondary osteons are more frequent, smaller and more circular in highly strained areas of the cross section compared to less strained areas (Skedros *et al.* 2004). It follows that structural adaptation of skeletal macro and micro morphology to a given load regime is dependent on the intensity of the biomechanical stress imposed (Raab *et al.* 1991). The process of adaptive adjustment is maintained until sufficient modelling and/or remodelling has occurred and strain levels are registered as normal. This creates the typical curvilinear pattern of bone response to load (Marcus 2002). It can therefore be expected that certain exercise regimes or load characteristics, for example those caused by habitual mobility patterns, will create distinctive bone morphology both in terms of geometric and microstructural features.

The underlying processes governing the relationship between mechanical loading and skeletal adaptation are not fully understood (*e.g.* Lee *et al.* 2002), but recent studies suggest (*e.g.* Metz *et al.* 2003) that osteocytes play a vital role in regulating osteon morphology (Marotti 1996; Martin 2000). The general lack and inconsistency of evidence pertinent to adaptational features in bone microstructure and applicable or relevant to archaeolo-

gical questions calls for a systematic approach to the effects of known keeping regimes on bone structural elements. Taking suids as a model this preliminary study analyses geometrical and micromorphological features in bones of wild boar and domestic pigs raised with different husbandry practices. We aim to test the hypotheses that there are systematic differences between species and animals that were allowed different habitual activity patterns with regard to the following features: (i) cross-sectional geometry; (ii) total area of remodelled bone; and (iii) density of Haversian systems.

MATERIALS AND METHODS

We analysed bone from free-ranging wild boar ($n = 40$), domestic pigs raised indoors ($n = 24$) and outdoors, roaming in a paddock ($n = 15$), representing all samples available at the time of analysis (Autumn 2006). They were derived from animals of known provenance and life history data (Table 1, see Appendix). Wild boar was sampled from the forest in the vicinity of Esch-sur-Alzette, Luxembourg during the spring of 2005 and all specimens derive from wild-shot animals culled by hunters. Both males ($n = 20$) and females ($n = 20$) are represented and age-at-death ranges from three months to > 25 months (adult) of age. The domestic pigs were collected from pig farms and butchers in Yorkshire during 2006 and were derived from intensive piggery units keeping animals with no outdoor access and limited exercise, and from units that keep pigs in enclosed outdoor paddocks. Males and females of various breeds were sampled, including Large White and Gloucester Old Spot. The narrower age range (usually 5-7 months) covered by the domestic sample reflects culling practices for fast-maturing modern breeds. All suid samples used in this study were collected and prepared by the authors and are archived in the Division of Archaeological, Geographical and Environmental Sciences, University of Bradford.

Tibia sections of c.1.5 cm length were taken at midshaft (50-60% section), freed from the mar-

row, rinsed under running tepid tap water and stripped of any adhering soft tissue, if necessary aided by cooking the samples at 60°C. Ultrasound treatment was used to free samples from saw dust infill. The samples were defatted in diethyl ether for a total of eight hours using a soxhlet apparatus and left to dry. Thin sections of c. 50µm thickness were cut using a saw microtome (Leica 1600, Leitz) and mounted on slides using customary mounting medium (Histomount™, Lamb).

Microscopic inspection was carried out at 100x magnification for osteon analysis using light microscopy (Olympus BX-51). Geometrical features were obtained from scanned cross-sectional samples (Figs 1A, 1B). All images were digitally captured and examined using advanced image analysis software (analySIS™, Olympus, version 3.1, 2002).

Quantification of histo-compositional characteristics included cortical area of bone sections and total cross-sectional area to obtain shape diffe-

rences through geometrical properties; as well as number (osteons per mm²) and fractional area of secondary osteonal bone (% of total area) to account for the detection of different strain regimes. Secondary osteons were distinguished from primary osteons by the presence of a cement line. Osteon density was calculated by counting the total number of secondary osteons present in 10 randomly selected 1mm² grids. The data were tested for between-group differences using Mann-Whitney statistics, correlations were tested with Spearman's Rho.

RESULTS

CROSS-SECTIONAL GEOMETRY

Overall, clear differences in cross-sectional morphology are apparent between the wild boar and both groups of domestic pigs (Table 2, Figs 1, 2A-2F). Wild boar exhibit a significantly higher ratio of cortical bone to

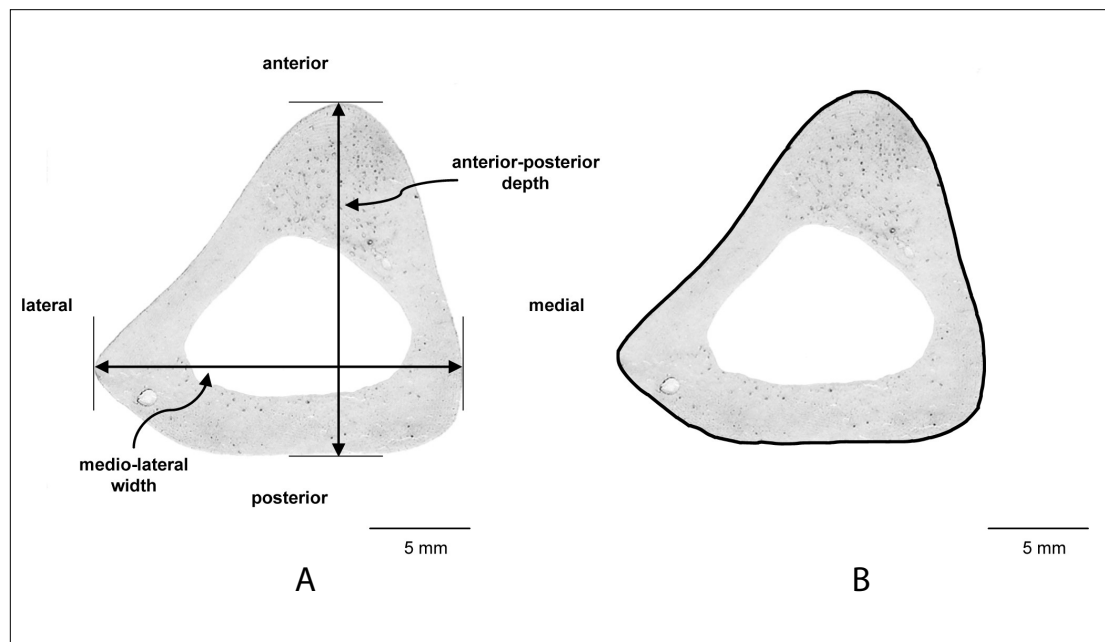


FIG. 1. – Measurements taken from the mid-shaft region of the tibia in wild boar, indoor- and outdoor-reared pigs.

TABLE 2. – Statistics for geometric shape and mean osteon density in indoor- and outdoor-reared domestic pigs and wild-boar

Variable	Group	N	Mean	Median	Std. Deviation	Std. Error Mean
medio-lateral breadth (mm)	indoor domestic	24	24.35	24.13	1.65	.34
	outdoor domestic	15	22.81	22.48	1.76	.46
	wild boar	40	18.43	18.79	3.38	.53
anterio-posterior depth (mm)	indoor domestic	24	17.04	16.88	.93	.19
	outdoor domestic	15	17.62	17.46	.80	.21
	wild boar	40	16.66	16.47	3.55	.56
medio-lateral breadth (mm)/ anterio-posterior depth (mm)	indoor domestic	24	1.43	1.42	.11	.02
	outdoor domestic	15	1.29	1.29	.07	.019
	wild boar	40	1.19	1.10	.12	.02
total area of bone (mm ²)	indoor domestic	24	307.09	303.14	28.70	5.86
	outdoor domestic	15	294.00	284.44	36.98	9.55
	wild boar	40	233.80	238.65	76.85	12.15
area of cortical bone (mm ²)	indoor domestic	24	215.90	220.03	28.56	5.83
	outdoor domestic	15	207.51	203.81	24.57	6.34
	wild boar	40	173.85	183.55	55.98	8.85
ratio of cortical bone (%)	indoor domestic	24	70.32	72.57	6.78	1.38
	outdoor domestic	15	70.74	70.26	4.37	1.13
	wild boar	40	74.64	75.03	4.05	.64
mean osteon density	indoor domestic	24	3.79	3.72	1.54	.31
	outdoor domestic	15	7.18	7.32	1.75	.45
	wild boar	40	20.73	19.51	9.16	1.45

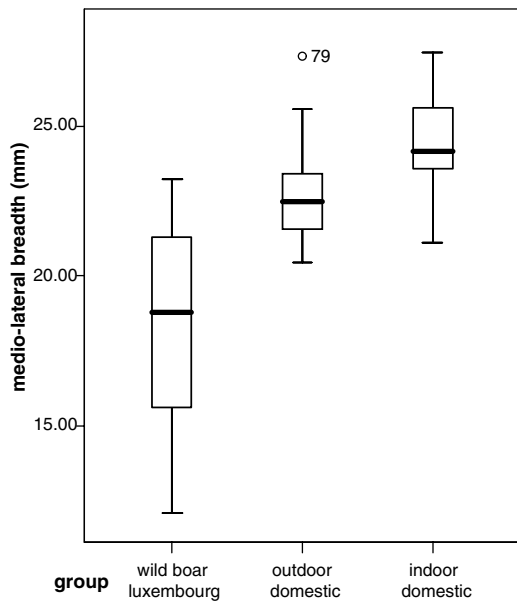


FIG. 2A. – Medio-lateral breadth (mm) in wild boar, indoor- and outdoor-reared pigs (the box indicates the interquartile range, the solid line the median; sample n° 79 is an outlier).

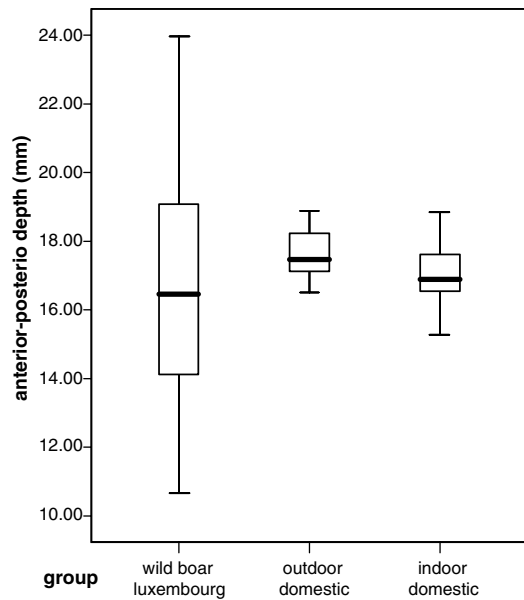


FIG. 2B. – Antero-posterior depth (mm) in wild boar, indoor- and outdoor-reared pigs (the box indicates the interquartile range, the solid line the median).

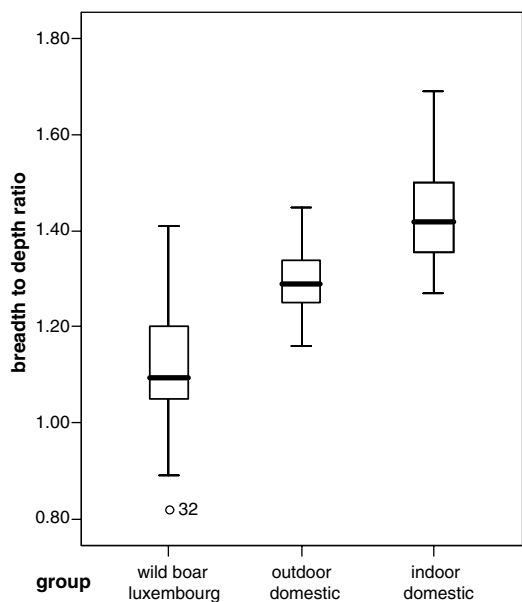


FIG. 2C. – Medio-lateral breadth (mm) to anterior-posterior depth (mm) in wild boar, indoor- and outdoor-reared pigs (the box indicates the interquartile range, the solid line the median; sample n° 32 is an outlier).

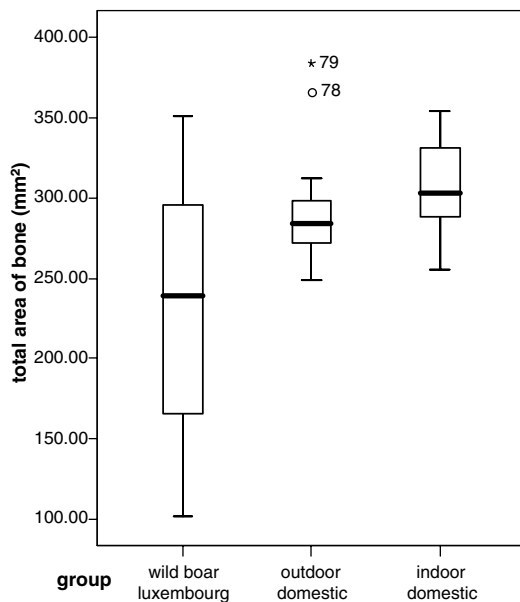


FIG. 2D. – Total area of bone (mm²) in wild boar, indoor- and outdoor-reared pigs (the box indicates the interquartile range, the solid line the median; samples n^{os} 78 and 79 are outliers).

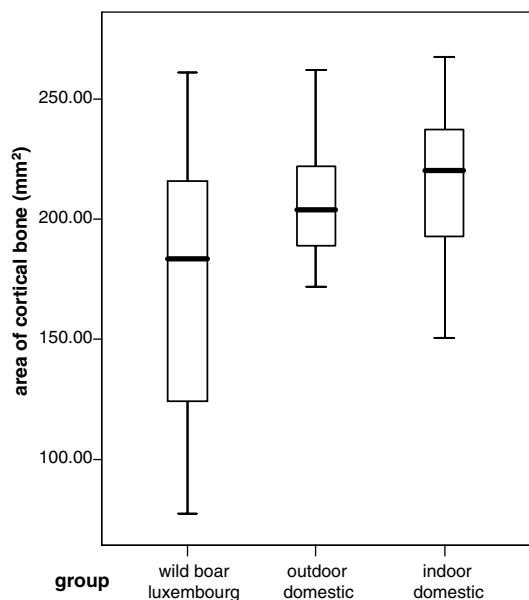


FIG. 2E. – Total area of cortical bone (mm²) in wild boar, indoor- and outdoor-reared pigs (the box indicates the interquartile range, the solid line the median).

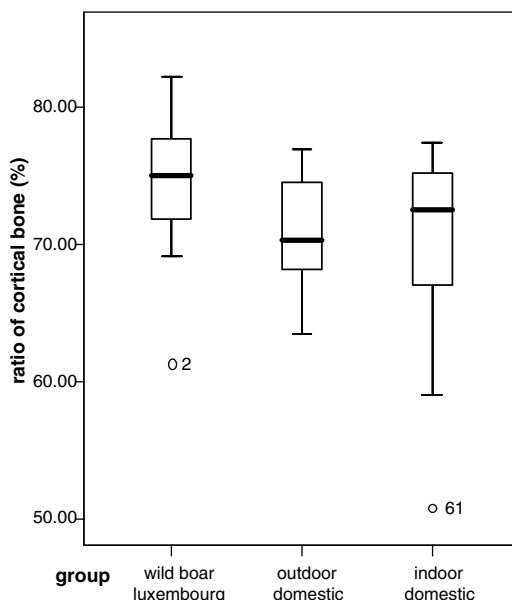


FIG. 2F. – The ratio of cortical bone (%) in wild boar, indoor- and outdoor-reared pigs (the box indicates the interquartile range, the solid line the median; samples n^{os} 2 and 61 are outliers).

total bone area at the mid-shaft region of the tibia than indoor- and outdoor-reared domestic pigs and display diaphyses in which the breadth to depth ratio (*i.e.* medial-lateral distance/ anterior-posterior distance) is significantly lower. This indicates a mid-shaft morphology which is, on average, narrower medio-laterally and more triangular in wild boar and broader and more ovoid in the domestic pigs (Table 2, Fig. 3). Diaphysis shape in the outdoor-reared pigs occupies an intermediate position between the wild boar and the stalled pigs (Fig. 2C) and is significantly different from both (Table 2). Cortical thickness in the outdoor-reared pigs again falls between wild boar and indoor-reared pigs (Fig. 2E), though here significant differences are only evident for the wild boar and are not apparent between the two domestic groups (Table 3, $p > 0.05$).

SECONDARY OSTeon DENSITY

There are significant differences in secondary osteon density between the wild boar, the indoor-, and the outdoor-reared pigs (Tables 2 and 3, Fig. 4). The data exhibit a trend comparable to cross-sectional geometry with values for the outdoor-pigs falling between the wild boar and the indoor pigs. Secondary osteon density is considerably more variable in wild boar than in either of the domestic groups (Table 2, Fig. 4). This is likely to be an effect caused by the wide age range of the population sampled as

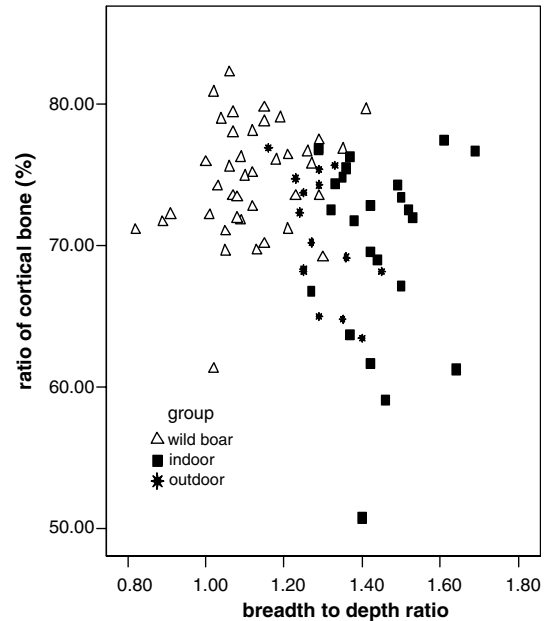


FIG. 3. – Key differences in CSG between wild boar, indoor- and outdoor-reared pigs.

it comprised both immature and adult animals which would display differing stages of microstructural adaptation to the habitual activity patterns of wild boar. Therefore, possible effects of age on the analysed variables were explored in order to understand which variables genuinely vary independent of life history parameters.

TABLE 3. – Identifying differences in geometric shape and mean osteon density in indoor- and outdoor-reared domestic pigs and wild-boar: results of the Mann-Whitney U-test; significant results in bold face.

Variable	Wild boar vs. outdoor-reared pigs p-value	Wild boar vs. indoor-reared pigs p-value	Indoor- vs. outdoor-reared pigs p-value
medio-lateral breadth (mm)	0.000	0.000	0.004
anterio-posterior depth (mm)	0.115	0.382	0.071
medio-lateral breadth (mm)/ anterio-posterior depth (mm)	0.000	0.000	0.000
total area of bone (mm ²)	0.013	0.000	0.071
area of cortical bone (mm ²)	0.056	0.003	0.270
ratio of cortical bone (%)	0.006	0.014	0.809
mean osteon density	0.000	0.000	0.000

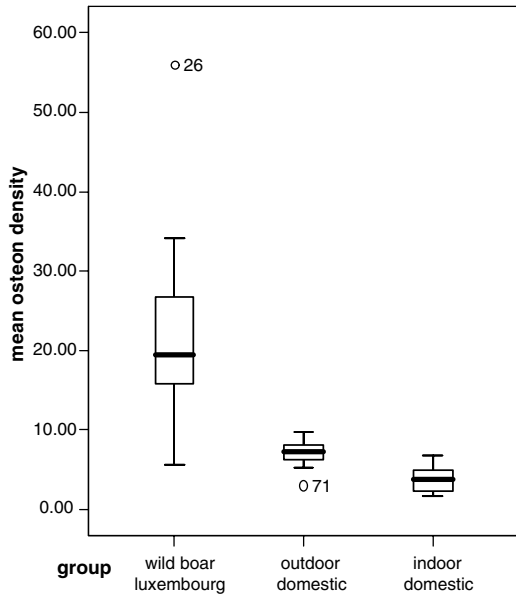


FIG. 4. – Mean osteon density in wild boar, indoor- and outdoor-reared pigs (the box indicates the interquartile range, the solid line the median; sample nos 26 and 71 are outliers). Osteon density was calculated by counting the total number of secondary osteons present in 10 randomly selected 1mm² grids.

AGE EFFECTS

Due to common culling practice there was insufficient variation in age for the indoor- and outdoor-reared pigs to enable the consideration of this variable on both cross-sectional geometry and osteon density. All but two pig tibiae were derived from animals aged between five and seven months at death (indoor-reared: < six months: n = 1, five to six months: n = 23, six to seven months: n = 1; outdoor-reared: < six months: n = 1, five to six months: n = 7, six to seven months: n = 6). Hence this analysis was restricted to wild boar, however on a slightly smaller sample (n = 36), because in this group no age data were available for four individuals (122, 6991, 8695, 9043).

Spearman's Rho indicates a significant correlation between age and five bone variables in wild boar: medio-lateral breadth, anterior-posterior depth, total area of bone, area of cortical bones, and osteon density (Table 4). The breadth to depth ratio and the percent area of osteon bone are not correlated with age.

TABLE 4. – Statistics for geometric shape and mean osteon density in indoor- and outdoor-reared domestic pigs and wild-boar weighing between 50 and 100kg

Variable	Group	N	Mean	Median	Std. Deviation	Std. Error Mean
medio-lateral breadth (mm)	wild boar	16	20.6819	21.28	2.01488	.50372
	outdoor domestic	7	22.2300	22.48	1.11373	.42095
	indoor domestic	7	23.3486	23.78	.98493	.37227
anterio-posterior depth (mm)	wild boar	16	18.7425	17.72	3.19280	.79820
	outdoor domestic	7	17.4429	17.46	.56115	.21210
	indoor domestic	7	16.7071	16.6	.77863	.29429
medio-lateral breadth (mm)/ anterio-posterior depth (mm)	wild boar	16	1.1225	1.10	.14271	.03568
	outdoor domestic	7	1.2743	1.27	.03155	.01192
	indoor domestic	7	1.3986	1.37	.07010	.02650
total area of bone (mm ²)	wild boar	16	286.7975	292.50	52.04236	13.01059
	outdoor domestic	7	285.2500	284.44	21.11360	7.98019
	indoor domestic	7	288.3443	296.24	18.27972	6.90909
area of cortical bone (mm ²)	wild boar	16	213.6256	209.58	34.15638	8.53909
	outdoor domestic	7	201.6100	193.87	20.72700	7.83407
	indoor domestic	7	204.6214	206.98	26.66884	10.07987
ratio of cortical bone (%)	wild boar	16	74.8932	74.20	3.90071	.97518
	outdoor domestic	7	70.6210	70.26	3.76042	1.42130
	indoor domestic	7	71.0952	74.29	9.04901	3.42021
mean osteon density	wild boar	16	25.1200	24.54	10.64858	2.66214
	outdoor domestic	7	7.4229	7.32	1.15767	.43756
	indoor domestic	7	2.8100	3.00	1.01635	.38414

The potential impact of age on osteon density is considered less important for the indoor- and outdoor-reared pigs, where all animals were culled under a year old, and most are likely to be aged between seven and twelve months. It is, however, more critical for the wild boar, where the youngest animal is under six months of age and the oldest greater than 25 months. To assess whether the wider age range in the wild boar might have influenced differences in osteon density between wild boar and the two domestic pig groups, a further between-group comparison was undertaken, which considered only individuals less than twelve months old. This reduced the sample sizes to 36 wild boar, three indoor-reared, and thirteen outdoor-reared pigs. Domestic pigs were hence treated as one group. Wild boar under twelve months of age again demonstrate a significantly higher density of secondary osteons than do domestic pigs of a comparable age (Fig. 5). This, combined with the

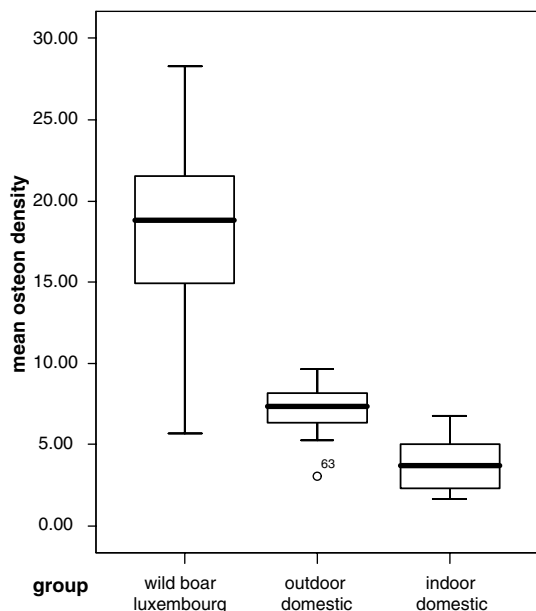


FIG. 5. – Mean osteon density in wild boar, indoor- and outdoor-reared pigs aged under 12 months (the box indicates the interquartile range, the solid line the median; sample n° 63 is an outlier). Osteon density was calculated by counting the total number of secondary osteons present in 10 randomly selected 1mm² grids.

previously identified significant difference between indoor- and outdoor reared pigs suggests that while age will influence osteon density, it is not the only factor involved.

WEIGHT EFFECTS

Besides age, weight was also controlled for. Data were available for 36 wild boar, 18 indoor-, and seven outdoor-reared pigs (see Table 1). The sample size of the latter was considered too small for correlation analysis and hence this test was restricted to wild boar and indoor-reared pigs. For the wild boar, Spearman's Rho indicates a significant correlation between body weight and all but two variables (depth to breadth ratio and ratio of cortical bone/total bone area) (Table 4). Body weight was less clearly related to cross-sectional geometry in indoor-reared pigs, with three variables (medio-lateral breadth, total area of bone, area of cortical bone) exhibiting a significant correlation. Osteon density shows a negative correlation with body weight in wild boar, and a positive correlation in domestic pigs.

Since body weight is correlated both with cross-sectional geometry and osteon density, a further series of between-group comparisons was carried out. To assess how these correlations might affect the interpretation of activity-related modification of the tibia, a restricted sub-sample, comprising individuals with body weights of 50 to 100 kg was chosen, representing the range of greatest overlap between the three groups. Sample sizes are small for each group but indicate similar trends to those documented in the full data set (Tables 5 and 6) suggesting that while body weight will affect many of the variables considered there is a considerable influence of activity levels as well.

DISCUSSION

Consideration of the relationship between age and each of the variables indicates, perhaps unsurprisingly, that age is likely to have an effect on bone cross-sectional geometry. In wild boar, as an animal gets older its tibia shaft gets broader,

TABLE 5. – Identifying differences in geometric shape and mean osteon density in indoor- and outdoor-reared domestic pigs and wild-boar weighing between 50 and 100kg: results of the Mann-Whitney U-test; significant results in bold face.

Variable	Wild boar vs. outdoor-reared pigs	Wild boar vs. indoor-reared pigs	Indoor- vs. outdoor-reared pigs
	p-value	p-value	p-value
medio-lateral breadth (mm)	0.089	0.001	0.073
anterio-posterior depth (mm)	0.720	0.798	0.073
medio-lateral breadth (mm)/ anterio-posterior depth (mm)	0.010	0.000	0.001
total area of bone (mm ²)	0.671	0.769	0.902
area of cortical bone (mm ²)	0.413	0.535	0.602
ratio of cortical bone (%)	0.047	0.624	0.259
mean osteon density	0.000	0.000	0.001

Table 6. – Correlation between age, weight, geometric shape and mean osteon density in outdoor-reared domestic pigs and wild-boar: results of the Spearman's Rho test; significant results in bold face.

Variable	Wild boar: age	Wild boar: weight	Indoor- pigs: weight
	r; p-value	r; p-value	r; p-value
medio-lateral breadth (mm)	r = 0.69; p = 0.000	r = 0.80 p = 0.000	r = 0.59; p = 0.01
anterio-posterior depth (mm)	r = 0.65; p = 0.000	r = -0.06; p = 0.000	r = 0.36; p = 0.14
medio-lateral breadth (mm)/ anterio-posterior depth (mm)	r = 0.02; p = 0.89	r = 0.09; p = 0.601	r = 0.30; p = 0.23
total area of bone (mm ²)	r = 0.68; p = 0.000	r = 0.79; p = 0.000	r = 0.75; p = 0.000
area of cortical bone (mm ²)	r = 0.68; p = 0.000	r = 0.80; p = 0.000	r = 0.70; p = 0.003
ratio of cortical bone (%)	r = -0.5; p = 0.79	r = -0.06; p = 0.723	r = 0.07; p = 0.772
mean osteon density	r = 0.50; p = 0.002	r = 0.42; p = 0.01	r = 0.61; p = 0.007

deeper and bigger overall. The ratio of bone depth to breadth is not, however, affected by age nor is the proportion of cortical bone. Secondary osteon density is also correlated with age, with a greater frequency of osteons noted in older animals. A strong correlation between body weight and cross-sectional geometry was identified in the wild boar and to a lesser extent in the indoor-reared pigs. In both groups, mid-shaft dimensions are greater in heavier individuals. Body weight does not affect the proportion of cortical

bone exhibited in either wild boar or domestic pigs. Breadth to depth ratio, however, is linked with body weight in wild boar but not in indoor-reared pigs. Mean osteon density was significantly correlated with age for both wild boar and indoor-reared pigs.

Three variables exhibit clear differences between pigs with varying levels of activity, medio-lateral breadth, the depth to breadth ratio and secondary osteon density. Of these, the depth to breadth ratio appears to be unaffected by the complicating

effects of body weight or age, suggesting that it is potentially useful for exploring suid mobility. Overall cross-sectional geometry in the mid-shaft of a load-bearing bone is thus shaped from the outset and reflects different exercise levels and concomitant load patterns that are related to rearing practices. The strong correlation observed between body weight and age for medio-lateral breadth suggests that this variable is not suitable for detecting activity levels. It does, however, provide an indication that the body weight of archaeological suids may potentially be reconstructed from simple diameter dimensions, though further research on animals with a more diverse spread of body weights and ages is required to substantiate this observation.

The ratio of cortical bone, *i.e.* the relative amount of cortical bone per total area of bone, appears also to be unaffected by age or weight. For this variable, however, significant differences were only apparent between wild boar and each of the two domestic groups; no clear separation was evident between the indoor- and outdoor-reared pigs. This may reflect genetic differences between wild boar and domestic pigs with little or no involvement of biomechanical factors. However, the small number of domesticated pigs, both indoor- and outdoor-reared, available at present prevents a clear statement to this effect. Moreover, cortical thickness is known to reflect activity levels in other species, including primates and felids (Ruff *et al.* 1984, O'Regan 2006). It is anticipated that ongoing research which aims to increase sample size and to include free-ranging domestic pigs and paddock-kept wild boar will help clarify the relationship between relative cortical bone thickness and activity levels in suids.

Mean osteon density, *i.e.* the amount of remodelled bone, exhibits a meaningful trend: there are significantly less osteons in the tibia cross sections of indoor-reared pigs, *i.e.* those animals reared under the most restricted activity regime. Outdoor-reared pigs occupy an intermediate position between indoor-reared pigs and wild boar, the latter having the highest density of osteons. These results are in accordance with

experimental research on pigs which demonstrated that individuals subjected to increased levels of exercise on a treadmill exhibited a higher density of secondary osteons (Lieberman 1997). While a correlation does exist between osteon density, age and weight in all three groups, the actual distribution of values reveals that indoor-reared pigs have absolute low osteon density for their weight, and outdoor-reared pigs have slightly higher but still overall low figures as well. If weight played a decisive role in determining osteon density, then heavy indoor-reared pigs would be expected to display a high density of osteons as well. This, however, is not the case (Fig. 6). On the contrary; only wild boar follow the expected pattern of increased remodelling and an attainment of higher weights with age, and all three groups show significant differences between them.

Osteon size is known to vary with body size, species and perhaps breed (Dittman 2003; Lasota-Moskalewska & Moskalewska 1980). In suids,

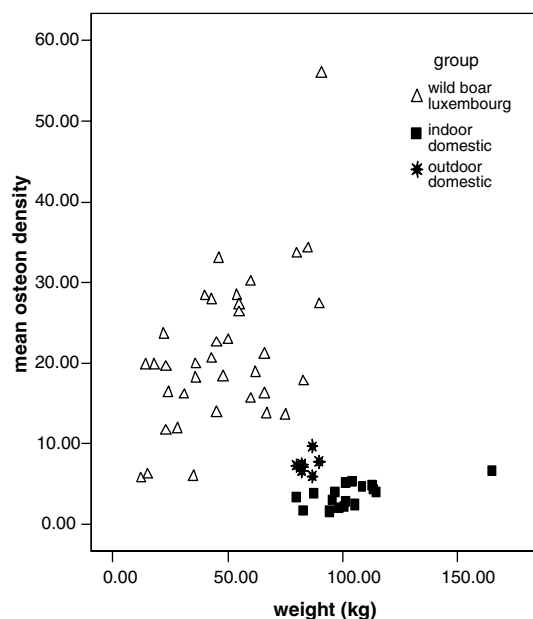


Fig. 6. – Correlation between body weight and osteon density in wild boar, indoor- and outdoor-reared pigs. Osteon density was calculated by counting the total number of secondary osteons present in 10 randomly selected 1mm² grids.

however, the only published study which has considered variability in osteon size between wild boar and domestic pig could find no differences between the two (Lasota-Moskalewska & Moskalewska 1980). Moreover, while genetic variability in osteon size might explain some of the variation in osteon density between the wild boar and the domestic pigs studied here, it cannot account for the differences between the indoor- and outdoor-reared pigs which as indicated above, also runs contrary to the expected pattern for body size (*i.e.* higher density/smaller osteons in heavier animals). This strongly suggests that while there is a component of remodelling that is related to ontogenetic development and most likely also to species differences (*cp.* Lasota-Moskalewska & Moskalewska 1980, Dittmann 2003), activity patterns and load regimes measurably exert the largest influence on the level of remodelling. Nevertheless, it is recognised that documenting variability in osteon size between the activity groups studied is a critical factor in ascertaining the potential of histometric techniques for archaeozoology. While data on osteon dimensions have not been presented here, this analysis is part of the larger study on micromorphological features in suids currently in progress and will be reported elsewhere (Schutkowski *et al.* in prep).

These results imply, therefore, that it is possible to detect evidence for differences in husbandry practices and subsequent variance in biomechanical load regimes in animals reared under known and controlled conditions. Ongoing analyses aim to expand on the range of histocompositional features studied with regard to activity-related changes in bone morphology. These include diameter and perimeter of secondary osteons, Haversian canal dimensions, as well as fractional area and dimensions of osteocytes to obtain quantifiable data on bone remodelling and formation known to reflect habitual load histories. Quantification of back-scattered electron microscopic images will include fractional area of secondary osteons of different grey values, *i.e.* different stages of mineralisation representing different intensities of remodelling activity.

CONCLUSIONS AND OUTLOOK

The results of this study are encouraging. In particular, the breadth to depth ratio of the tibia at mid-shaft demonstrates a strong correlation with activity level and more significantly does not appear to be affected by complicating factors such as age and body weight. As such it is likely to be a useful variable for exploring activity levels in suids. Two further variables also show promising trends. The ratio of cortical bone, which is also unaffected by age or weight, was significantly greater in the more active wild boar than the paddocked/penned domestic groups, a pattern anticipated from the response of cortical bone to activity levels in other species (Ruff *et al.* 1984; O'Regan 2006). However, because of a lack of any clear difference in the area of cortical bone evident between the indoor- and outdoor-reared domestic pigs, a more definitive statement on the potential of this variable for elucidating animal lifestyle must await the analysis of larger samples and more diverse populations currently in progress. Likewise, although osteon density does indicate a response to biomechanical factors, the extent to which this variable is rendered useable because of the complicating effect of factors such as body size, species and age remains to be unravelled with future research.

These results suggest that the archaeological application of histomorphometric techniques will potentially enable new and innovative insights into various aspects of pig husbandry. These include the process and timing of pig domestication, the intensification of pig husbandry and the shift to stall-fed populations during later prehistory. The transition from hunting to herding animals represents a major landmark in human history and as such has generated considerable archaeological interest over the past hundred years (Harris 1996, Zeder 2001). Despite the long history of research, however, there remain major gaps in our understanding of the actual process of animal domestication (Zeder 2001). While most researchers agree that initial domestication is likely to have involved some form of control over animal populations, such as a

restriction of breeding, the control of diet and the manipulation of home ranges and activity patterns (Zohary *et al.* 1998, Price 1999, Ervynck *et al.* 2001, Zeder 2001), whether this process involved close segregation of specific captive animals from the outset or developed more gradually from symbiotic/commensal relationship between humans and animals, and even if it varied between the different species is still unclear (Harris 1996, Hongo & Meadow 1998, Redding & Rosenberg 1998, Zohary *et al.* 1998, Ervynck *et al.* 2001, Zeder 2001). This reflects limitations inherent in extant archaeozoological methodologies (Zeder 2001).

While the control of an animal's mobility is widely cited as an important feature of early animal management practices, current archaeozoological methods cannot provide the evidence to empirically demonstrate this in sufficient detail. Price (1999) and Zohary *et al.* (1998), *e.g.*, have argued that domestication will be associated with a reduction in overall activity levels through penning and corralling, but also because of a reduced need for extensive foraging when humans are providing supplementary fodder. Hongo and Meadow (1998) envisage more extensive systems for early suid management, perhaps akin to free-ranging wild boar, but they too suggest that at least some individuals may have been kept penned for short periods of time in order to habituate them to humans. The results presented in this article suggest that the plastic response of bone to lifestyle and activity levels, *i.e.* to differences in biomechanical stress during the lifetime of an animal, is uniquely placed to provide insight into such aspects of the domestication process across the entire spectrum of pre- proto- and fully domestic sites. Cross-sectional geometry and histomorphometry will enable distinction between free-ranging and, perhaps, minimally controlled populations, and those which have a much greater restriction in their movement, reflecting animals over which human control is more heavily exercised. The application of histomorphometric approaches to early domestication assemblages may thus provide much needed insight into the kinds of management strategy which led even-

tually to the creation of the domestic genotype, and as such will contribute significantly to current debate over the nature, timing and provenance of pig domestication.

This research also has significance for later archaeological periods. Very little is currently known about the organisation and articulation within the landscape of pig husbandry in pre/history (Wilkie *et al.*, in press) or its impact on the environment (Amorosi *et al.* 1997). In Europe, extensive outdoor systems of pig husbandry, traditionally associated with woodland, are well documented in the recent past and historically (Trow-Smith 1957, Grigson 1982, Ward & Mainland 1999), but, although widely assumed to have been important during earlier periods, there is little direct evidence for such practices in prehistoric contexts (Grigson 1982). Similarly, stall-fed pigs are known in the historical record for the Roman and Medieval periods (Trow-Smith 1957) but archaeological evidence is once again sparse (Grigson 1982). Finally, while this project has as its focus the pig, it is anticipated that the biomechanical and histomorphometrical approach will ultimately be applicable to other domesticated livestock, cattle, sheep, goats, llama, horses, etc., thus significantly widening its likely potential for elucidating the process of domestication, animal management strategies and herd mobility in the past.

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REFERENCES

- AMOROSI T., BUCKLAND P., DUGMORE A., INGIMUNDARSON J. H. & MCGOVERN T. 1997. — Raiding the landscape: human impact in the Scandinavian North Atlantic. *Human Ecology* 25: 491-518.
- BENECKE N. 1994. — *Der Mensch und seine Haustiere*. Theiss, Stuttgart.

- DITTMANN K. 2003. — Histomorphometrische Untersuchung der Knochenmikrostruktur von Primaten und Haustieren mit dem Ziel der Speziesidentifikation unter Berücksichtigung von Domestikationseffekten. *Anthropologischer Anzeiger* 61: 175-188.
- DREW I. M., PERKINS D. & DALY P. 1971. — Prehistoric domestication of animals: effects on bone structure. *Science* 171: 280-282.
- ERVYNCK A., DOBNEY K., HONGO H. & MEADOW R. H. 2001. — Born free? New evidence for the status of *Sus scrofa* at Neolithic çayönü Tepesi (Southeastern Anatolia, Turkey). *Paléorient* 27(2): 47-73.
- FROST H. M. 1987. — Bone "mass" and the "mechanostat": A proposal. *Anatomical Record* 219: 1-9.
- GILBERT A.S. 1989. — Microscopic bone structure in wild and domestic animals: a reappraisal, in CRABTREE P. J., CAMPANA D. & RYAN K. (eds), *Early Animal Domestication and its Cultural Context*. MASCA Research Papers in Science and Archaeology 6 Suppl. University of Pennsylvania, Philadelphia: 47-86
- GRIGSON C. 1982. — Porridge and pannage: pig husbandry in Neolithic England, in BELL M. & LIMBREY S. (eds), *Archaeological Aspects of Woodland Ecology*. British Archaeological Reports 146. Archaeopress, Oxford: 297-315.
- HALSTEAD P. 1996. — Pastoralism or household herding? Problems of scale and specialisation in early Greek animal husbandry. *World Archaeology* 8: 20-42.
- HONGO H. & MEADOW R. H. 1998. — Pig exploitation at Neolithic çayönü Tepesi (southeastern Anatolia), in NELSON S. M. (ed.), *Ancestors for the Pigs: Pigs in Prehistory*. MASCA Research Papers in Science and Archaeology 15. University of Pennsylvania, Philadelphia: 77-98.
- HARRIS D. R. 1996. — *The Origins and Spread of Agriculture and Pastoralism in Eurasia*. UCL Press, London.
- LARSEN C. S. 1997. — *Bioarchaeology. Interpreting behavior from the human skeleton*. Cambridge University Press, Cambridge.
- LASOTA-MOSKALEWSKA A. & MOSKALEWKA S. 1980. — Microscopic comparison of bones from medieval domestic and wild pgs. *Ossa* 7: 173.178.
- LAURINE M., GIRONDOT M. & LOTH M.-M. 2004. — The evolution of long bone microstructure and lifestyle in lissamphibians. *Paleobiology* 30: 589-613.
- LIEBERMAN D. E. 1997. — Making behavioural and phylogenetic inferences from hominid fossils: Considering the developmental influence of mechanical forces. *Annual Review of Anthropology* 26: 185-210.
- LEE T. C., STAINES A. & TAYLOR D. 2002. — Bone adaptation to load: microdamage, as a stimulus for bone remodeling. *Journal of Anatomy* 201: 437-446.
- MARCUS R. 2002. — Mechanisms of exercise effects on bone, in BILEZIKIAN J. P., RAISZ L. G. & RODAN G. A. (eds), *Principles of Bone Biology*. Academic Press, London: 1477-1488.
- MAROTTI G. 1996. — The structure of bone tissues and the cellular control of their deposition. *Italian Journal of Anatomy and Embryology* 101: 25-79.
- MARTIN R. B. 2000. — Towards a unifying theory of bone remodelling. *Bone* 26: 1-6.
- O'CONNOR J. A., LANYON L. E. & MACFIE H. 1982. — The influence of strain rate on adaptive bone remodelling. *Journal of Biomechanics* 15: 767-781.
- O'REGAN H. 2006. — *Zooarchaeology and the archaeology of zoos*. Paper presented in the "Archaeozoo" session at the 10th ICAZ Conference, Mexico City, 23-28th of August 2006. S.éd.,s.l.
- PETERS J., HELMER D., VON DEN DRIESCH A. & SANA SEGUI M. 1999. — Early animal domestication in the Northern Levant. *Paléorient* 25: 27-47.
- PRICE E. O. 1999. — Behavioral development in animals undergoing domestication. *Applied Animal Behavior Science* 65: 245-271.
- RAAB D. M., CRENSHAW T. D., KIMMEL D. B. & SMITH E. L. 1991. — A histomorphometric study of cortical bone activity during increased weight-bearing exercise. *Journal of Bone and Mineral Research* 6: 741-749.
- REDDING R. W. & ROSENBERG M. 1998. — Ancestral pigs: a new (Guinea) model for pig domestication in the Middle East, in NELSON S. M. (ed.), *Ancestors for the Pigs: Pigs in Prehistory*. MASCA Research Papers in Science and Archaeology 15. University of Pennsylvania, Philadelphia: 65-76.
- RUFF C. 2000. — Biomechanical analyses of archaeological human skeletons, in SAUNDERS S. R. & KATZENBERG A. M. (eds), *Biological anthropology of the human skeleton*. Wiley, New York: 71-102.
- RUFF C., LARSEN C. S. & HAYES W. C. 1984. — Structural changes in the femur with the transition to agriculture on the Georgia coast. *American Journal of Physical Anthropology* 64: 125-136.
- SKEDROS J. G., HUNT K. J., & BLOEBaum R. D. 2004. — Relationships of loading history and structural material characteristics of bone: Development of the mule deer calcaneus. *Journal of Morphology* 259: 281-307.
- TROW-SMITH R. A. 1957. — *History of British Livestock Husbandry to 1700*. Routledge, London.
- WARD J. & MAINLAND I. L. 1999. — Microwear in modern free-ranging and stall-fed pigs: the potential of dental microwear analysis for exploring pig diet and management in the past. *Environmental Archaeology* 4: 25-32.
- WILKIE T., MAINLAND I., ALBARELLA U., DOBNEY K. & ROWLEY-CONWAY P., in press. — A dental microwear study of pig diet and management in Iron-Age/Romano-British, Anglo-Scandinavian and Medieval contexts in England, in ALBARELLA A.,

- DOBNEY K. & ROWLEY-CONWY P. (eds), *Pigs and Humans*. Oxford University Press, Oxford.
- ZEDER M. A. 1978. — Differentiation between the bones of caprines from different ecosystems in Iran by the analysis of osteological microstructure and chemical composition, in MEADOW R. H. & ZEDER M. A., *Approaches to Faunal Analyses in the Middle East*. Peabody Museum of Archaeology and Ethnology Bulletin 2. Harvard University, Harvard: 69-84.
- ZEDER M. A. 2001. — A metrical analysis of a collection of modern goats (*Capra hircus aegagrus* and *C. b. hircus*) from Iran and Iraq: implications for the study of animal domestication. *Journal of Archaeological Science* 28: 61-79.
- ZOHARY D., Tchernov E. & KOLSKA HORWITZ L. 1998. — The role of unconscious selection in the domestication of sheep and goats. *Journal of Zoology* 245: 129-135.

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APPENDIX

TABLE 1. – Activity groups analysed.

OUTDOOR-RAISED DOMESTIC PIGS

Identifier	Sex	Age [months]	Weight [kg]*	Breed
001	Female	< 6	80	Unknown
006	Female	5-7	115	Large White, Landrace, Duroc
007	Female	5-7	90	Large White, Landrace, Duroc
008	Female	5-7	Unknown	Large White, Landrace, Duroc
009	Female	5-7	Unknown	
011	Female	5-7	95	Large White, Landrace, Duroc
012	Female	5-7	105	Large White, Landrace, Duroc
013	Female	5-7	100	Large White, Landrace, Duroc
014	Female	5-7	100	Large White, Landrace, Duroc
018	Female	5-7	165	Large White, Landrace, Duroc
019	Female	5-7	95	Large White, Landrace, Duroc
020	Female	5-7	110	Unknown
022	Female	5-7	Unknown	Large White, Landrace, Duroc
027	Female	5-7	115	Large White, Landrace, Duroc
028	Female	5-7	100	Large White, Landrace, Duroc
033	Female	5-7	105	Large White, Landrace, Duroc
034	Female	5-7	115	Large White, Landrace, Duroc
040	Female	5-7	85	Large White, Landrace, Duroc
041a	Female	5-7	100	Large White, Landrace, Duroc
041b	Female	5-7	100	Large White, Landrace, Duroc
023	Male	5-7	Unknown	Large White, Landrace, Duroc
004	Unknown	5-7	Unknown	Large White, Landrace, Duroc
005	Unknown	5-7	100	Large White, Landrace, Duroc
029	Unknown	5-7	Unknown	Unknown
042	Unknown	7	Unknown	Saddleback/Gloucester Old Spot
043	Unknown	5-7	Unknown	Saddleback/Gloucester Old Spot

* Weights are given to the nearest 5kg.

INDOOR-RAISED DOMESTIC PIGS

Identifier	Sex	Age [months]	Weight [kg]*	Breed
016	Female	6	80	Gloucester Old Spot
021	Female	6	90	Gloucester Old Spot
024	Female	5-7	80	Gloucester Old Spot
025	Female	5-7	80	Gloucester Old Spot
030	Female	6-7	85	Gloucester Old Spot
010	Male	6	85	Saddleback/Gloucester Old Spot
015	Male	6	90	Saddleback/Gloucester Old Spot
031	Male	6-7	85	Saddleback/Gloucester Old Spot
032	Male	6-7	85	Saddleback/Gloucester Old Spot
002	Unknown	<6	100	Unknown
003	Unknown	5-7	100	Unknown
037	Unknown	7	90	Saddleback/Gloucester Old Spot
038	Unknown	7	90	Saddleback/Gloucester Old Spot
039	Unknown	7	90	Saddleback/Gloucester Old Spot

* Weights are given to the nearest 5kg.

WILD BOAR

Identifier	Sex	Age [months]	Weight [kg]*
2231	Female	5.5	20
2386	Female	16	60
2750	Female	8	50
3231	Female	7	30
3932	Female	11	35
5271	Female	4	10
6106	Female	8	20
6109	Female	14	55
6240	Female	20	75
6494	Female	7	35
7265	Female	9	50
7504	Female	>25	90
7603	Female	4	25
7604	Female	3.5	15
7605	Female	23	65
7607	Female	>25	90
7971	Female	23	80
8495	Female	15	55
8641	Female	10	40
10276	Female	11	45
122	Male	3	Unknown
2858	Male	11	60
2859	Male	14	65
5083	Male	14	45
5381	Male	9	45
5395	Male	18	85
6248	Male	8	25
6251	Male	9	30
6991	Male	Unknown	Unknown
7032	Male	20	83
7764	Male	4	25
8126	Male	8	35
8142	Male	13	60
8658	Male	3	15
8695	Male	Unknown	Unknown
8793	Male	12	55
8809	Male	10	45
9043	Male	Unknown	Unknown
10032	Male	9	43
11885	Male	10	65

* Weights are given to the nearest 5kg.