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**Title:** Long-Term Morphological Changes and Evolving Human-Pig Relations in the Northern Fertile Crescent from 11,000-2000 cal. BC

**Abstract:** The pig (*Sus scrofa*) was one of the earliest animals in the ancient Middle East to undergo domestication. Scholars have long been interested in the pig's unique history, especially in the northern Fertile Crescent (NFC), the region in which the first steps towards pig domestication took place in the 9<sup>th</sup>-8<sup>th</sup> millennia cal. BC. Yet, few zooarchaeologists have studied the morphological changes in pigs and other animals over the long term, especially in the periods after the initial appearance of domesticates. We combine Geometric Morphometrics (GMM) and more traditional biometrics to demonstrate how suid morphology evolved over a long timespan: 11,000-2000 cal. BC. Our GMM and biometrical data from Jarmo and Domuztepe, Neolithic sites occupied after the first domestic pigs emerged in the region, show that wild boar continued to play important roles in human-suid relations. More generally, our data show a gradual reduction in size and the attainment of a "morphological plateau" in the 4<sup>th</sup> millennium cal. BC. We suggest that these changes reflect 1) the evolution of pig husbandry practices over time in response to deforestation, intensive agriculture, and urbanism; and 2) a reduction in the frequency of hybridizations between wild boar and domestic pigs.

**Keywords:** Pigs, *Sus*, Biometrics, Geometric Morphometrics, Near East, Domestication

## Introduction

The pig (*Sus scrofa*) is a dynamic and flexible animal that has changed remarkably since its domestication. These changes include brain size reductions almost unparalleled in other animals (Kruska 2005), coat color variation (Fang et al. 2009), and a high tolerance for human management (Hemmer 1990). Pigs also underwent significant skeletal transformations during domestication. With an eye primarily turned towards understanding the timing and contexts of domestication, zooarchaeologists have long studied morphological changes in pigs (Angröss 1960; Ervynck et al. 2001; Flannery 1961; Kusatman 1991; Rowley-Conwy et al. 2012; Rüttimeyer 1862). Little attention, however, has been paid to pig morphology in the millennia after domestication, the period in the Middle East that saw the rise of complex societies, urbanization, and the increasing impact of humans on the natural environment. Such a gap is surprising given pigs' tortuous history in the region and the accepted idea that domestication is a long-term process (e.g., Clutton-Brock 1992; Meadow 1989).

In this paper, we investigate the long-term evolution of human-suid relations in the northern Fertile Crescent (NFC) of the Middle East, a region roughly defined by the northern parts of the Tigris and Euphrates rivers, their tributaries, and adjacent areas. The NFC was the earliest core region of domestication, with pigs and other animals undergoing domestication in the 9<sup>th</sup>-8<sup>th</sup> millennia cal. BC (Zeder 2011). Several millennia later, this region also saw some of the earliest complex societies and cities in the Middle East. To track the effects of these large-scale changes on pigs, we analyze traditional biometric and geometric morphometric (GMM) data from the Epipaleolithic through the development of cities in the Chalcolithic and Early Bronze Age (ca. 11,000-2000 cal. BC).

## Metrical Approaches to Pig Domestication

Suid morphology has primarily been studied in order to determine the timing and cultural contexts of domestication (for reviews, see Albarella et al. 2006; Girdland-Fink and Larson 2011; Rowley-Conwy et al. 2012), beginning with the pioneering work of Ludwig Rüttimeyer (1862), who was the first to note the importance of dental metrics. Pig teeth are ideal for zooarchaeological studies for two reasons. First, they are often recovered intact as a consequence of their robustness and protection within pigs' massive jaws and skull. Second, measurements of molariform teeth vary less than measurements of the postcranial skeleton by age and sex – factors that could otherwise obscure the differences between wild and domestic animals. Although dental breadths and lengths do exhibit minor degrees of sexual dimorphism, the effect sizes are very low (Mayer et al. 1998).

Traditionally, third molar (M3) lengths have been used to distinguish wild from domestic *Sus scrofa* (e.g., Flannery 1983; Higham 1968; Stampfli 1983). While these measurements remain important, later studies found that molar breadths (WA and WP) were somewhat more reliable (Kusatman 1991; Mayer et al. 1998; Payne and Bull 1988; Rowley-Conwy et al. 2012). Other useful metrics for discerning wild boar from domestic pigs, identified by Umberto Albarella and Sebastian Payne (Albarella and Payne 2005) in their work on fauna from the British Neolithic site of Durrington Walls, include two postcranial measurements: the length of the astragalus (GL1) and the breadth of the distal tibia (Bd or BdP).

Recently, the use of geometric morphometrics (GMM) has revolutionized the analysis of dental morphology in pigs. At its core, GMM is no different from traditional metrical approaches. Indeed, the techniques were developed in order to add mathematical rigor to biological

studies of morphology (Bookstein 1996; Zelditch et al. 2004). GMM has been applied extensively to pigs across Eurasia, often in combination with other techniques, to distinguish *Sus scrofa* populations (i.e., wild, domestic, feral, and hybrid) and to track pig domestication and dispersal (e.g., Balasse et al. 2016; Cucchi et al. 2016; Cucchi et al. 2009; Evin et al. 2013; Evin et al. 2014; Evin et al. 2015; Larson et al. 2007a; Ottoni et al. 2012; Owen et al. 2014; Vigne et al. 2009). The analysis of shape using GMM is even more reliable at distinguishing wild from domestic pigs than the size criteria alone suggested by traditional biometrics (Evin et al. 2013).

Metrical approaches are not without complications. The relative plasticity of pigs' dental morphology combined with the frequency in both the past and present of episodes of feralization or hybridization, especially under free-range or other "extensive" forms of husbandry, can cause considerable overlap between so-called wild and domestic forms (Jarman 1971; Rowley-Conwy et al. 2012). Nevertheless, metrical approaches – including traditional biometrics and GMM – remain the most analytically straightforward and least destructive means of tracking pig domestication.

### **Studies of Pig Domestication and Morphology in the Northern Fertile Crescent (NFC)**

The northern Fertile Crescent includes the semi-arid Syrian Jezireh to the south, the Mediterranean to the west, and the foothills of the Taurus and Zagros Mountains to the north and east (**Figure 1**). Today, the region experiences a temperate climate, with rainfall levels between 200 and 1000 mm per year on average (Buringh 1960; Wilkinson 2003). Since the beginning of the Holocene, the region has supported steppic grasslands, xeromorphic scrub, riparian vegetation (willow, tamarisk, and poplar), and woodlands dominated by oak, pistachio, and almond trees (Deckers and Riehl 2007; Miller 1997; Riehl and Deckers 2012). The woodland and riparian ecosystems, in addition to the anthropogenic environments carved out by permanent human settlements, are ideal for populations of wild boar and domestic pigs.

The NFC was the setting for the earliest process of pig domestication and that of other animals (Zeder 2011). Pig domestication has been studied since the second half of the 20<sup>th</sup> century, when Kent Flannery, as a Masters student at the University of Chicago joined Robert Braidwood's expedition to the Neolithic site of Jarmo in Iraq. Working with Charles Reed (see e.g., Reed 1959), Flannery (1961; 1983) studied the lengths of third molars and showed that domestic pigs, with their characteristically shorter M3s, were present in the later phases of the site (see also Price and Arbuckle 2015; Stampfli 1983).

Hitomi Hongo and colleagues studied the process of pig domestication at another Braidwood site: Çayönü Tepesi. The data from Çayönü, representing a robust sample size and a long timespan, is currently the best evidence for pig domestication in the NFC. Hongo and colleagues found evidence for a slow process of pig size diminution over the 9<sup>th</sup>-7<sup>th</sup> millennia cal. BC (Ervynck et al. 2001; Hongo and Meadow 1998a; Hongo and Meadow 1998b). Based on the biometrical data, as well as those derived from other methods, Ervynck *et al.* (2001) argued that pig domestication was extremely gradual, involving a transition from hunting to a form of free-range husbandry that allowed continued introgression of wild boar (see also Redding and Rosenberg 1998).

The late Berrin Kusatman made a major contribution to the study of ancient suid biometrics in her dissertation (1991). Focusing on pig domestication in the Middle East as a whole, Kusatman collected pig metrics from an astounding number of archaeological sites to track size and shape change. Kusatman demonstrated that domestication involved a decrease in size in several skeletal measurements, but highlighted the utility of molar breadths for discerning between

domestic and wild populations. Moreover, by including data from the Paleolithic, Kusatman's research was the first to track long-term changes in pig biometrics in the Middle East.

Despite the history of research on pig morphology in the Middle East and other regions, scholars have focused little attention on the changes to pig morphology in the millennia *after* domestication in the Pre-Pottery Neolithic. This is a curious omission since many scholars stress that domestication is a fluid process without clear endpoints in which animals adapt morphologically to human management (Clutton-Brock 1992; Meadow 1989; Redding 2005; Vigne 2015; Zeder 2009). How animals changed in the periods after initial domestication is just as important, from an analytical standpoint, to the story of human-animal relations. Moreover, in the ancient Middle East, researchers have documented pigs' changing roles in later prehistory, such as the importance of pork (or lack thereof) in early cities and their hinterland economies in the Bronze Age (e.g. Falconer 1995; Rufolo 2015; Zeder 1996; Zeder 2003). How did pigs adapt to these new roles? How did pig morphology continue to evolve as human societies transitioned from a scattering of nascent agricultural villages to a full-fledged urban economy?

## Materials and Methods

### *Materials*

Our data (**Table 1**) consist of a total of 735 teeth, including upper and lower molars (M1-M3) as well as deciduous fourth premolars (dP4), from 11 archaeological sites spread across the NFC and spanning the Epipaleolithic through Early Bronze Age (ca. 11,000-2000 cal. BC). Postcranial metrics were also collected on eight assemblages, and are fully reported elsewhere (Price 2016). For this study, we included 61 postcranial bones, using measurements of tibia distal breadths (Bd) and astragalus greatest lengths (GLI). These measurements have been shown by Albarella and Payne (2005) to be ideal for comparing between assemblages.

All measurements were taken by MDP and, when available, we included published data from other studies (Doll 2010; Ilgezdi 2008; Kusatman 1991; Monahan 2000; Piatkowska-Malicka and Smogorzewska 2010) to fill gaps in our dataset. For reference populations, we used the metrical data from modern wild boar published by Payne and Bull (1988). The 18 individual animals in Payne and Bull's reference collection were shot near the town of Kizilcahamam, Turkey between 1974 and 1976. For comparative GMM data, 37 modern Turkish wild boar teeth from jaws located in the Museum für Naturkunde in Berlin were photographed by Evin. All of the raw data from this study can be accessed freely through Open Context (Price 2015).

The sites are shown in **Figure 1**. Sites were spread across the NFC and include a variety of natural environments. Çayönü Tepesi and Hallan Çemi Tepesi are located in the oak-dominated hilly region near the modern city of Diyarbakir, Turkey, where a series of small wadis feed into the Tigris river. To the southeast, Qalat Jarmo and Gird Banahilk are located in the foothills of the Taurus/Anti-Taurus mountains, an area defined by deep-cutting wadis, steep hills, and oak-pistachio parklands (van Zeist and Bottema 1991). Moving west, Tell Mozan, Tell Arbid, and Tell Leilan lie in the Khabur Basin, a flatland area abutting the Anti-Taurus foothills to the north and the dry Jezirah steppe to the south. Historically, the Khabur Basin served as a major breadbasket of the region, but it also supported abundant swamplands as well as riverine and gallery forests (Deckers and Riehl 2007). Riverine forests also persisted along the middle and southern part of the Khabur River (Tell Atij, Tell Raqa'i, Tell Umm Qseir, Tell Ziyadeh, Tell Mashnaqa), a major tributary of the Euphrates, as well as in the upper Euphrates (Hacinebi Tepe, Mezraa-Teleilat, and Gritille Höyük) (Deckers and Pessin 2010). Finally, on the western edge of our

study region, Domuztepe lies on a flat plain at the base of the Taurus Mountains. The area around the site is today dominated by cereal agriculture, but, in the past, there were abundant swamplands that were home to wild pigs (in Turkish, *domuz*), which lent their name to the site (Geary et al. 2011).

Site	Location of Collection	Teeth	Postcran.	Reference
Hallan Çemi*	Smithsonian Institution (USA)	65	0	This study
Çayönü Tepesi	Diyarbakir Museum (Turkey)	153	201	Kusatman 1991
Mezraa-Teleilat	Sanliurfa Museum (Turkey)	0	24	Ilgezdi 2008
Gritille Höyük	University of Chicago (USA)	14	7	Monahan 2000; Kusatman 1991
Jarmo*	Field Museum of Natural History (USA)	147	14	This study
Domuztepe*	Kahramanmaras Archaeology Museum (Turkey)	104	15	This study
Gird Banahilk*	Field Museum of Natural History	47	7	This study
Tell Umm Qseir*	Smithsonian Institution	42	0	This study
Tell Mashnaqa*	Smithsonian Institution	8	0	This study
Tell Ziyadeh*	Smithsonian Institution	21	0	This study
Hacinebi Tepe*	University of Chicago	106	0	This study
Tell Mozan	Not Specified in Publication (Syria?)	0	56	Doll 2010
Tell Arbid	Not Specified in Publication (Syria?)	0	5	Piatkowska-Malecka and Smogorzewska 2010
Tell Atij	Smithsonian Institution	37	3	This study
Tell al-Raqa`i	Smithsonian Institution	20	1	This study
Tell Leilan*	Harvard University (USA)	138	21	This study
Modern Turkish Wild Boar	Museum für Naturkunde (Germany)	37	0	This study
Modern Kizilcahamam (Turkey) Wild Boar	Sebastian Payne, personal collection	76	35	Payne and Bull 1988

Table 1. Sites analyzed in this study with mention of the location of the collection, and number of teeth and postcranial elements examined. Starred assemblages were examined by the authors for biometrics and geometric morphometrics. The modern wild boar from the Museum für Naturkunde were examined only for geometric morphometrics. All others included only published biometrical data.

### *Methods*

Three traditional measurements were taken on teeth: the greatest length along the mesial-distal axis (L), greatest breadth along the buccal-lingual axis of the anterior cusp (WA) and of the posterior cusp (WP) (Albarella and Payne 2005; Payne and Bull 1988). In order to compare between multiple types of teeth, these measurements were converted to log-size index values (LSI) using Payne and Bull's (1988: Appendix 2) proposed standard, which is based on the mean values of a sample of their modern Kizilcahamam (Turkey) wild boar (see also Meadow 1999). These standard values are set, by definition, at  $LSI = 0$ . LSI values enable a synoptic comparison of all dental breadth measurements over time.

For both LSI values and unconverted measurements, we conducted one-way ANOVAs to determine if there was significant change over time, pairwise Wilcoxon ranked-sum tests to determine differences between assemblages (see **Supplementary Information 1**), and mixture analysis (using expectation-maximization of assumed Gaussian distributions, see below) to estimate the proportion of wild boar and domestic pigs in the Jarmo and Domuztepe assemblages. The coefficient of variation (CV; the standard deviation divided by the mean) allowed us to compare the spreads of distributions with different means. As a rule-of-thumb, CVs larger than about .05 are often taken to indicate multiple populations (Payne and Bull 1988). However, this is not a hard-and-fast benchmark. To compare changes in variance statistically, we conducted Fligner-Killeen tests of homogeneity across assemblages. Finally, we estimated shoulder height using the astragalus length and the multiplication factor of 17.9 suggested by Teichert (1969).

GMM was performed on unbroken second and third molars (upper and lower) with unworn cusps following the methodologies set forth by Cucchi et al. (2011) and Evin et al. (2013). Photographs of the occlusal aspect of each tooth were taken with a DSLR camera (Nikon D3200) with an attached 60 mm macrolens in order to minimize the effects of parallax and lens distortion. Landmarks were plotted at replicable locations on the four types of teeth and semi-landmarks along their perimeters (see Evin et al. 2013): upper M2 (11 landmarks, 60 semi-landmarks), upper M3 (10 landmarks, 70 semi-landmarks), lower M2 (9 landmarks, 70 semi-landmarks), and upper M3 (11 landmarks, 80 semi-landmarks).

A General Procrustes Analysis (Rohlf and Slice 1990) was performed to compare shapes. Proportion of wild boar vs. domestic pigs in each assemblage followed the linear discriminant analysis technique developed by Evin et al. (2015), using the Hallan Çemi and a set of modern Turkish wild boar teeth to define our "wild" shape reference, and the later-period data (Banahilk, Ziyadeh, Mashnaqa, Hacinebi, Atij, Raqa'i, and Leilan) to define our "archaeological domestic" shape reference. The wild or domestic status of specimens from Jarmo and Domuztepe was then determined based on their proximity in shape to these two reference groups.

Gaussian mixture models were used to determine the proportions of wild boar and domestic pigs in the assemblages. In order to avoid false groupings, mixture analysis was only conducted on the largest samples of dental breadth measurements and, additionally, only on assemblages with wide distributions of measurements. Because the main component of variation of

dental breadth measurements is population (esp. wild vs. domestic), as opposed to age, sex, or health status (see Payne and Bull 1988), we assumed that the wide spreads in the metrical data were caused by mixtures of wild and domestic animals. Thus, we set the number of components at  $k = 2$  and ran expectation-maximization to determine the parameters of these two components.

Statistics were performed in R (R Core Team 2014) with the packages “ape” for neighbor-joining trees (Paradis et al. 2004); Rmorph (Baylac 2012); “Mixtools” for mixture analysis of traditional biometrics (Benaglia et al. 2009); and the R functions developed by Evin *et al.* (2013; 2015) to identify the status of the specimens and the proportion of wild and domestic animals based on their molar shape.

## Results

### *Modern vs. Ancient Wild Boar*

**Figure 2** and **Figure 3** show the traditional biometrical data collected on modern Kizilcahamam wild boar by Payne and Bull (1988) in comparison to the data from archaeological sites. The data enable an assessment of potential size difference between ancient and modern wild boar. Turning first to dental LSI data (**Figure 2**), the modern wild boar distribution is somewhat smaller than that of Hallan Çemi, but the difference is (just barely) not significant at the .05 level (Welch two-sample t-test:  $t = 1.983$ ,  $df = 88.63$ ,  $P = .051$ ). Moreover, the difference in means is not great: Hallan Çemi's mean LSI is  $-.002$ , while the Kizilcahamam mean LSI is  $-.010$ . The difference mainly stems from the presence in the Hallan Çemi assemblage of a few large specimens ( $LSI > .05$ ), which were also found at Çayönü. On the other hand, **Figure 5**, which compares the centroid sizes of M2s and M3s (derived from GMM), shows that there was no apparent difference in size between the Hallan Çemi wild boar and the modern sample of Turkish wild boar from the Museum für Naturkunde collection in Berlin (for Wilcoxon rank-sum test results, see **Supp. Info. 1**).

The postcranial data from the modern Kizilcahamam wild boar show an even greater difference from ancient wild boar. Although we did not collect postcranial data from Hallan Çemi (nor have any been published up to this point), **Figure 3** shows that the Kizilcahamam astragalus GLI and tibia Bd measurements are, on average, smaller than those from 9<sup>th</sup>-8<sup>th</sup> millennium Çayönü (astragalus GLI Welch two-sample t-test:  $t = 1.839$ ,  $df = 35.37$ ,  $P = .074$ ; tibia Bd Welch two-sample t-test:  $t = 6.663$ ,  $df = 27.28$ ,  $P < .001$ ), with Çayönü containing a mix of wild and early domestic pigs according to Ervynck et al. (2001). This difference is significant. The mean astragalus GLI of the Kizilcahamam wild boar was 47.4 mm, while the mean tibia Bd was 32.0 mm; at Çayönü the means were 49.1 mm and 36.0 mm, respectively. Incidentally, although an imperfect comparison because of its temporal and geographic distance, Kusatman's (1991) data from the Middle-Upper Paleolithic Lebanese coastal site of Ksar Akil had even larger mean astragalus GLI and tibia Bd measurements of 52.1 mm and 37.0 mm, respectively. These metrical data thus suggest that early Holocene wild boar were, on average, a bit larger than their present-day counterparts (see Discussion).

### *Size Change Over Time*

Traditional biometrical data show a pattern of significant decrease in size over time for all elements studied (Teeth LSI ANOVA:  $F(10, 684) = 161.7$ ,  $P < .001$ ; Astragalus GLI:  $F(10, 180) = 54.1$ ;  $P < .001$ ; Tibia BD:  $F(10, 136) = 46.66$ ;  $P < .001$ ).

In teeth, median LSI values (**Figure 2**, shown as black lines in the centers of the box-plots) drop from near 0 at Hallan Çemi to  $-.04$  at Jarmo to  $-.11$  at Hacinebi and later sites. This



pattern is not simply one of initial decrease in the Neolithic, but rather one of continued decrease over time. It highlights the importance of persistent morphological change in the millennia after the first domestic pigs appeared in northern Mesopotamia.

The trend of size decrease plateaus in the 4<sup>th</sup> millennium, a period corresponding to the Late Chalcolithic and the emergence of complex societies in the region. At this point, pigs seem to have stopped getting smaller. Wilcoxon ranked-sum tests showed no significant differences between sites dated to the 4<sup>th</sup> and 3<sup>rd</sup> millennia cal. BC (see **Supp. Info. 1**). Another, earlier, plateau might also exist at the 6<sup>th</sup> and 5<sup>th</sup> millennia since Wilcoxon ranked-sum tests revealed no significant differences between 6<sup>th</sup> and 5<sup>th</sup> millennium sites. However, skepticism is warranted given the very small samples sizes of the 5<sup>th</sup> millennium sites.

The presence of large specimens (outliers) after the first appearance of domestic pigs in the region (in the 9<sup>th</sup>-8<sup>th</sup> millennium) likely represent wild boar. If so, it would appear that wild boar occurred in increasingly smaller proportions. However, it is important to note that some of these specimens could represent large domestic animals. Indeed, one might expect a right-skewed distribution of size data given that large outliers are evident in the (presumably homogenous) assemblage of wild boar at Hallan Çemi. On the other side of the extreme, the smallest pigs, represented by six teeth (2 M<sub>1</sub>, 1 M<sub>2</sub>, and 3 M<sub>3</sub>), were found at Tell Atij, a 3<sup>rd</sup> millennium town located on the banks of the Khabur River. These specimens are much smaller than those found at contemporaneous sites.

The specific dental and postcranial measurements useful for comparing between assemblages established by Albarella and Payne (2005) are shown in **Figure 3** and **Figure 4**. All elements display the same general trends observed in the dental LSI data: reduction in dental size until the 4<sup>th</sup> millennium, with another potential plateau in the 6<sup>th</sup> millennium. **Figure 3** and **Figure 4** also show a reduction over time in the *smallest* specimens in each period, with the exception of the small sample of 5<sup>th</sup> millennium pigs. This phenomenon of the-smallest-getting-smaller corroborates (pace Eryvynck et al. 2001) the persistent decrease in the size of domestic pigs over time. Note, however, that even in the 8<sup>th</sup>-7<sup>th</sup> millennium, small-sized domestic pigs comparable to those in the 4<sup>th</sup> and 3<sup>rd</sup> millennia, were present in low proportions (see especially **Figure 4**).

Postcranial bones also allow an approximation of overall body size. Using the astragalus GLI data in **Table 2** and the conversion factor of 17.9 suggested by Teichert (1969), we can estimate the average withers (shoulder) heights of pigs and wild boar. At Çayönü, wild boar and early domestic pigs reached an average shoulder height of 87.9 cm, which is comparable to, but a bit larger, than modern Turkish wild boar from Kizilcahamam (84.8 cm). They are, incidentally, smaller than the wild boar from Paleolithic Ksar Akil (93.3 cm). The average 6<sup>th</sup> millennium domestic pigs, meanwhile, stood at 78.6 cm and those in the 3<sup>rd</sup> millennium reached only 59.8-66.4 cm – roughly 3/4 the height of the modern wild boar and probably close to 2/3 the size of ancient wild boar.

Despite a few outliers, each site or each period displays relatively minor variations in spread (**Figures 2-4**). Differences in spread can be explained, at least partially, by a mixing of populations (i.e., wild and domestic). In general, the Coefficients of Variation (**Table 2**) are consistent over time and tend to be around .05 for the dental breadths and in the .05-.10 range for the distal tibia and the astragalus GLI, which are expected to have somewhat more variation than teeth (Payne and Bull 1988; Price 2016).

This consistency over time indicates that exploited *Sus* populations tended to be rather homogenous. It is interesting to note, however, that in each dataset, the coefficients of variation

at sites occupied in the Neolithic (9<sup>th</sup>-6<sup>th</sup> millennia cal. BC) are *slightly* higher than in other periods. Indeed, Fligner-Killeen tests showed that the variances of the Pre-Neolithic, Neolithic, and Post-Neolithic measurements in **Table 2** were all significantly different at the .05 level (**Supp. Info. 2**). It is possible that the slightly higher variation in the Neolithic datasets reflects a higher complexity in the population composition reflecting expectations for a slow process of domestication and the continued interbreeding between wild and domestic pigs in the Neolithic. However, it is important to take into consideration that sample sizes tended to be larger in Neolithic assemblages, which could also explain the higher CV values.

Measurement	Site	N	Mean	SD	CV
M1 WA					
	11 <sup>th</sup> Millennium (Hallan Çemi)	10	11.7	.56	.05
	9 <sup>th</sup> -8 <sup>th</sup> Millennium (Çayönü) <sup>1</sup>	61	11.3	.60	.05
	Late 8 <sup>th</sup> -7 <sup>th</sup> Millennium (Gritille) <sup>1</sup>	10	11.0	.85	.08
	7 <sup>th</sup> Millennium (Jarmo)	24	10.7	.76	.07
	6 <sup>th</sup> Millennium (Domuztepe, Banahilk, Umm Qseir)	34	9.8	.60	.06
	5 <sup>th</sup> Millennium (Mashnaqa, Ziyadeh)	4	9.9	.26	.03
	4 <sup>th</sup> Millennium (Hacinebi)	16	9.0	.54	.04
	3 <sup>rd</sup> Millennium (Atij, Raqa'i, Leilan)	34	9.0	.55	.05
	Modern Wild Boar <sup>6</sup>	18	11.5	.39	.03
M2 WA					
	11 <sup>th</sup> Millennium (Hallan Çemi)	12	15.5	.64	.05
	9 <sup>th</sup> -8 <sup>th</sup> Millennium (Çayönü) <sup>1</sup>	40	15.5	1.0	.07
	Late 8 <sup>th</sup> -7 <sup>th</sup> Millennium (Jarmo)	10	14.2	.86	.06
	6 <sup>th</sup> Millennium (Domuztepe, Banahilk, Umm Qseir)	17	12.8	.67	.05
	5 <sup>th</sup> Millennium (Mashnaqa, Ziyadeh)	3	13.3	.62	.04
	4 <sup>th</sup> Millennium (Hacinebi)	18	11.7	.55	.05
	3 <sup>rd</sup> Millennium (Atij, Raqa'i, Leilan)	23	11.7	.74	.06
	Modern Wild Boar <sup>6</sup>	15	15.4	.53	.03
Astrag. GLI					

	9 <sup>th</sup> -8 <sup>th</sup> Millennium (Çayönü) <sup>1</sup>	127	49.1	3.7	.08
	Late 8 <sup>th</sup> -7 <sup>th</sup> Millennium (Mezraa-Teleilat) <sup>2</sup>	14	41.5	3.7	.09
	Late 8 <sup>th</sup> -7 <sup>th</sup> Millennium (Gritille) <sup>3</sup>	2	45.1	NA	NA
	Late 8 <sup>th</sup> -7 <sup>th</sup> Millennium (Jarmo)	12	44.7	4.0	.09
	6 <sup>th</sup> Millennium (Domuztepe, Banahilk, Umm Qseir)	18	43.9	3.8	.10
	3 <sup>rd</sup> Millennium (Atij, Raqa'i, Leilan)	6	37.1	2.9	.08
	3 <sup>rd</sup> Millennium (Moza) <sup>4</sup>	39	35.0	1.7	.05
	3 <sup>rd</sup> Millennium (Arbid) <sup>5</sup>	5	33.4	1.1	.03
	Modern Wild Boar <sup>6</sup>	17	47.4	2.7	.06
Tibia Bd					
	9 <sup>th</sup> -8 <sup>th</sup> Millennium (Çayönü) <sup>1</sup>	74	36.0	2.4	.07
	Late 8 <sup>th</sup> -7 <sup>th</sup> Millennium (Mezraa-Teleilat) <sup>2</sup>	10	31.3	2.2	.07
	Late 8 <sup>th</sup> -7 <sup>th</sup> Millennium (Gritille) <sup>3</sup>	5	32.3	2.0	.07
	Late 8 <sup>th</sup> -7 <sup>th</sup> Millennium (Jarmo)	2	31.8	NA	NA
	6 <sup>th</sup> Millennium (Domuztepe, Banahilk, Umm Qseir)	4	29.1	.64	.02
	3 <sup>rd</sup> Millennium (Atij, Raqa'i, Leilan)	18	26.0	1.7	.06
	3 <sup>rd</sup> Millennium (Moza) <sup>4</sup>	17	26.3	.65	.03
	3 <sup>rd</sup> Millennium (Arbid) <sup>5</sup>	0	NA	NA	NA
	Modern Wild Boar <sup>6</sup>	18	32.0	2.2	.07

Table 2. Sample size (N), mean, standard deviation (SD), and coefficient of variation (CV) data for Sus measurements. All measurements in millimeters. <sup>1</sup>Data from Kusatman (1991). <sup>2</sup>Data from Ilgezdi (2008). <sup>3</sup>Data from Monahan (2000). <sup>4</sup>Data from Doll (2010). <sup>5</sup>Data from Piatkowska-Malecka & Smogorzewska (2010). <sup>6</sup>Data from Payne and Bull (1988).

The evolution of centroid size (**Figure 5**) largely corroborates the pattern of a reduction in median size across tooth types. However, because of much smaller samples sizes than those of

traditional biometrics (because GMM requires complete, clean, and intact teeth), differences between successive sites tend not to be significant at the .05 level. However, they are significant when one compares assemblages separated by large periods of time (**Supp. Info. 1**).

*Sorting the Domestic from the Wild*

A major wrinkle in any attempt to track morphological changes in domestic animals is the persistence of their wild counterparts in the archaeological record. Morphologically wild animals can be incorporated into zooarchaeological assemblages through interbreeding (i.e., hybridization) or hunting. Because of their more pronounced size difference in later periods, traditional biometrics allow a relatively easy separation of wild from domestic *Sus*. The distinction is less clear in the Neolithic. Expectation-maximization mixture analysis of traditional metrical data and linear discriminant analysis of tooth shapes provide a way forward. We used these methods to specimens from the two largest Neolithic assemblages – Jarmo and Domuztepe – both of which contained wide distributions that overlapped with wild and domestic size categories (**Figure 2**).

Mixture analysis results are presented in **Table 3**. At Jarmo and Domuztepe, the means returned by the mixture analysis for the M1 WA and M2 WA are broadly comparable with the means from Hallan Çemi (M1 WA = 11.7 mm; M2 WA = 15.5 mm) on the one hand, and the 6<sup>th</sup>-5<sup>th</sup> millennium assemblages (excepting Domuztepe) on the other (M1 WA = 9.6 mm; M2 WA = 12.8 mm). This suggests that the mixture analysis did indeed capture wild and early domestic components. The mixing components indicate that wild boar made up approximately 38% or 52% of the specimens at Jarmo. Meanwhile, at Domuztepe, which was occupied a few centuries after the settlement at Jarmo was abandoned, the M1 WA, wild boar made up approximately 22% or 27% of the assemblage.

Linear discriminant analyses of molar shapes (**Table 4**) identified 35% of the teeth from Jarmo and 30% from Domuztepe as possessing wild boar shape. While all of the teeth from Jarmo that were used for shape analysis were isolated specimens, at Domuztepe, three specimens were represented by M2 and M3 teeth in the same jaw. Of these three pairs, one was identified as having domestic pig shapes for both teeth. The two other pairs consisted of an M2 identified as having a domestic shape and an M3 identified as having a wild shape.

	<b>M1 WA</b>	<b>M2 WA</b>
<b>Jarmo</b>		
Number of specimens	24	10
% Wild Boar	38%	52%
Mean “Wild” WA (mm)	11.9 ± .28	14.7 ± 1.01
Mean “Domestic” WA (mm)	10.8 ± .10	13.4 ± .05
Log-likelihood at estimate	-26.506	-8.559
<b>Domuztepe</b>		
Number of specimens	19	9

% Wild Boar	27%	22%
Mean “Wild” WA (mm)	11.0 ± .08	14.5 ± .15
Mean “Domestic” WA (mm)	9.6 ± .48	12.7 ± .30
Log-likelihood at estimate	-17.027	-7.375

Table 3. Results of expectation-maximization mixture analysis for M1 and M2 anterior breadths (WA) at Jarmo and Domuztepe.

	<b>Domestic</b>	<b>Wild</b>
<b>Jarmo</b>		
Lower M2	4	1
Lower M3	2	0
Upper M2	4	2
Upper M3	1	3
Total	11 (65%)	6 (35%)
<b>Domuztepe</b>		
Lower M2	2	0
Lower M3	7	1
Upper M2	6	2
Upper M3	4	5
Total	19 (70%)	8 (30%)

Table 4. Determination of wild/domestic status based on tooth shape, using the technique described by Evin et al. (2013; 2015).

## Discussion

As one would expect, domestic pig size decreased significantly over time. Domestic pigs first appeared in the 9<sup>th</sup> or 8<sup>th</sup> millennium cal. BC. Our data show that size decreased significantly not only in this first period of domestication, but in the millennia that followed. In fact, pig dental and postcranial size decreased by 20-30% between the 8<sup>th</sup> millennium and 4<sup>th</sup> millennia cal. BC. This process of continued size decrease over five millennia – a timeframe, one should remember, that represents several thousand generations of pigs – progressed at a slowing rate. It reached a plateau in the 4<sup>th</sup> millennium, the period in which complex societies developed in the NFC.

Turning first to the wild boar, our data suggest that wild boar might have been somewhat larger in the past than today. The difference in traditional dental metrics was minimal and just barely not significant at the .05 level (**Figure 2**), and it was not significant in terms of centroid size (**Figure 5**). Note, however, that the centroid size and traditional biometrics were derived from different populations: only GMM data were collected from the Museum für Naturkunde, while Payne and Bull (1988) only published traditional biometrics. Thus, it is difficult to compare these results. There may, however, be a significant degree of metrical variation within/between wild boar populations in the region today. If a slight reduction in dental size over the Holocene did occur in the NFC and its adjacent regions, that would be consistent with Davis' (1981) observation that third molars lengths from modern southern Levantine wild boar were smaller than those from Late Pleistocene contexts. It is, however, at odds with previous assessments that found no significant size change between ancient and modern wild boar in the NFC (Kusatman 1991; Price and Arbuckle 2015). Clearly, the magnitude of size change between modern and ancient wild boar requires further assessment.

Molecular data provide some insight into wild boar population dynamics. Modern wild boar from the southern Levant and Anatolia share a mitochondrial genetic signature with European wild and domestic pigs (Meiri et al. 2013). These observations likely result from admixture between autochthonous Middle Eastern wild boar and European domestic pigs, which appear to have been introduced to the Middle East in the mid-late 2<sup>nd</sup> Millennium cal. BC (Ottoni et al. 2013; Meiri et al. 2013, 2017). This introduction of non-local pigs likely influenced suid morphology and may explain, at least partially, the differences observed between the modern and ancient wild boar populations in the region.

The difference in our data between the modern and ancient wild boar is more apparent in the postcranial measurements (**Figure 3**), where the modern wild boar distribution falls below the upper fences of the 9<sup>th</sup>-8<sup>th</sup> millennium Çayönü specimens. Note, however, that the modern wild boar are larger than the lower fence of the 9<sup>th</sup>-8<sup>th</sup> millennium distribution, which represents the earliest domestic pigs. It is likely that this difference is, in part, an artifact of the high number in Payne and Bull's (1988) collection of juveniles and females, animals that have smaller body sizes. Indeed, the single older male from Payne and Bull's collection had an astragalus GLI of 50.8 mm and a tibia Bd of 36.4 mm. Still, these measurements are about 10% smaller than the largest ones from Çayönü, and again point to the conclusion that wild boar were larger in the late Pleistocene/early Holocene. We can speculate that modern wild boar might have been smaller as a result of a combination of factors including climate change, hunting pressure, and hybridization/feralization of domestic pigs (see Davis 1981). However, we again emphasize the need to test this size difference further.

The large size of *Sus scrofa* specimens at Hallan Çemi is also intriguing in light of the suggestion by Redding and colleagues (Peasnell et al. 1998; Redding and Rosenberg 1998) that the inhabitants of the site practiced a system of loose management of the wild boar. Their suggestion derives from the survivorship and sex ratio data, which indicate a kill-off of younger males. Our data clearly show that the Hallan Çemi suids were definitively wild in terms of their morphology. This could be taken to refute Redding's hypothesis. On the other hand, if wild boar really were under some form of loose management in the Epipaleolithic – an argument that finds support in the transportation of live wild boar to Cyprus in the 10<sup>th</sup> millennium cal. BC or earlier (Vigne 2015; Vigne et al. 2009) – then this would extend the timeline of suid morphological adaptation to human niches even further.

Domestication involves the morphological adaptation to a new niche, one co-constructed by humans and pigs. The first domestic niche, however, seems to have emerged gradually – and perhaps seamlessly – from those occupied by wild boar. Similar to Redding’s (Redding and Rosenberg 1998) hypothesis for wild boar management at Hallan Çemi, Ervynck et al (2001) argue that the first domestic pigs at Çayönü were managed in a free-range manner, with pigs allowed to wander into and out of human settlements and breed with wild boar ad libitum. Such extensive forms of husbandry, for which we have numerous modern-day examples in the Mediterranean and Papua New Guinea (e.g., Albarella et al. 2011; Hadjikoumis 2012; Halstead 2011; Sillitoe 2007), likely evolved out of intensive hunting practices – Zeder’s (2012) “prey pathway” (see also Marom and Bar-Oz 2013).

Extensive pig husbandry would have facilitated feralization and hybridization (although it must be noted that some modern-day swineherds actively prevent hybridization in order to maintain breed standards; see Albarella et al. 2007, 2011; Hadjikoumis 2012). In addition, wild boar hunting probably continued alongside these loose forms of husbandry. This combination of loose herding and hunting would result in a zooarchaeological assemblage defined by a significant proportion of morphologically wild boar, domestic pigs (frequently hybrids or hybrid offspring) close in size to wild boar, and metrical distributions with large spreads. All of these are found in the NFC in the 9<sup>th</sup>-6<sup>th</sup> millennia cal. BC.

The results from the mixture and linear discriminant analysis add weight to the hypothesis that extensive pig husbandry was commonplace (perhaps the dominant mode of pig production) until around the 6<sup>th</sup> millennium cal. BC. Our results suggest that around ¼ - ½ of the specimens from Jarmo and Domuztepe were wild. Moreover, analyses of shape and size did not always yield similar results; large specimens were found to have tooth shapes consistent with our domestic population, and vice versa. Additionally, two of the three M2/M3 pairs at Domuztepe yielded different shape identifications. The blending of wild and domestic characteristics possibly relates to the presence of hybrid or feral individuals, as Balasse et al. (2016) have suggested for Neolithic Romania based on a combined reconstruction of suid diet (stable isotopes) and morphometrics (GMM). Moreover, the high percentage of wild boar alongside domestic pigs in the Jarmo and Domuztepe assemblages and the grading of one population into the other are strongly reminiscent of the pig data from Çayönü, which Ervynck et al.’s (2001) interpreted as evidence of free-range husbandry.

Why allow pigs to breed with wild boar? Marshall et al. (2014) argue

intentional interbreeding of pigs with wild relatives confers no productive advantage. Gene flow is most likely to result from wild-capture as a herd-building strategy, or from chance breeding of domestic pigs with wild relatives (Marshall et al. 2014: 3).

In fact, there *is* an advantage to introducing wild stock: genetic diversity. Inbreeding is a frequent cause for concern among stock-keepers and, in pigs, a lack of genetic diversity tends to lead to reduced birth rates and other problems (Köck et al. 2009). One can imagine that, in isolated Neolithic villages, reliable supplies of new breeding animals were limited and that hybridization was the most reasonable option for preventing the deleterious effects of inbreeding. Whatever the reasons, the interbreeding of wild boar and domestic pigs would have introduced local genotypes into pig populations. This could explain why Ottoni et al. (2012) identified at least two distinct and regionalized mtDNA domestic pig haplotypes in the prehistoric NFC (Y1 and Arm1T). It

could also explain the introgression of European mtDNA into domestic pig populations in Europe (Evin et al. 2015; Larson et al. 2007b).

If extensive pig husbandry was the main way to raise pigs since the 8<sup>th</sup> millennium (or earlier), why do our later-period data not show much evidence for it? Indeed, it seems to have ceased being the dominant mode of pig production during or after the 6<sup>th</sup> millennium. The growth of inter-community economic networks created by complex societies may have limited the necessity of wild boar for genetic variability. Meanwhile, the expansion of human settlements provided ideal places to raise pigs, but they may have been less accessible to wild boar. The intensification of cereal production, too, may have encouraged the penning pigs in order to prevent damage to fields. At the same time, farmers may have tried to eliminate wild boar and feral pigs, as they cause considerable damage to crops (e.g., Herrero et al. 2006; Schley et al. 2008). The growth of cities in the 4<sup>th</sup> and, especially, 3<sup>rd</sup> millennium, meanwhile, probably accelerated all of these processes, further separating pigs from wild boar. Additionally, the environmental impact of urbanization was immense and caused a decline in the size of riverine and gallery forests across the NFC (Deckers and Pessin 2010), which are prime environments for wild and feral swine.

If these scenarios did indeed take place, then wild boar populations probably experienced a decline in the periods after the Neolithic as a result of deforestation and/or targeted hunting. Wild population depression, in conjunction with new management strategies that placed pigs in pens, would have led to a decline in the number of opportunities for introgression on a regional scale. The result would be a narrowing of the conduit between domestic pigs and local wild boar and increased genetic isolation. Such an explanation is consistent with Bartosiewicz and colleagues' (2013) interpretation of pig husbandry in Late Chalcolithic central Anatolia. Using data from Çamlıbel Tarlasi, they argued that woodland habitat destruction, as a result of increasingly intensive caprine grazing strategies, led to the elimination of pig husbandry systems that allowed interbreeding with wild boar.

The gradual elimination of husbandry systems that allowed or encouraged interbreeding with wild boar is consistent with the results established in this study and other publications. Our data support the argument that continued introgression, albeit on a decreasing scale, of wild boar genotypes and phenotypes into “domestic” stock was partly responsible for the slow pace of change in pig morphology. Indeed, the GMM data indicate high numbers of wild boar and, perhaps, hybrids in the 7<sup>th</sup> and 6<sup>th</sup> millennia cal. BC. But after that point, wild boar became less common. By the 3<sup>rd</sup> millennium, only a handful – out of hundreds of measured specimens – fall within the wild size range.

Other possibilities, by themselves or in combination with the loss of wild boar alleles, can explain the reduction in size. These explanations recall the long-standing debate over the causes of size reduction observable in most domestic animals (Higham 1968; Meadow 1984; Tchernov and Horwitz 1991). One explanation is that there was a decline in the health or nutrition status of domestic pigs throughout the 8<sup>th</sup> through 3<sup>rd</sup> millennia. It is possible that, as they were increasingly raised on lower-quality foods and confined with greater frequency to pens, pigs developed heritable small sizes (e.g., Meadow 1984). Indeed, epigenetic factors, including those related to nutrition, have been linked to heritable body size in other animals (for a comparison to human stature, see e.g., Wells and Stock 2011). It is also possible, in conjunction with Tchernov and Horwitz's (1991) thesis of domestic animal size reduction, that, over time, the environmental niches in which pigs were raised experienced a relaxation in selection pressures. This relaxation would have the side-effect of r- (as opposed to K-) selection: accelerating maturation, improving



fecundity, and increasing the tendency for small-sized parents to spawn small-sized offspring (Tchernov and Horwitz 1991).

Both the epigenetic and the r-selection hypotheses would be further impacted by changing husbandry conditions. That is, it is possible that new intensive forms of pig husbandry may have increased the selection pressure for smaller pigs even further, as Frémondeau et al. (2017) have recently argued at Hellenistic-Byzantine Sagalassos. In particular, the switch from free-ranging/herding to more intensive forms of pig husbandry, such as penning, may have selected for smaller-size pigs. These intensive forms of pig husbandry would also have limited (or eliminated) contact between domestic pigs and wild boar. Intensive husbandry, which may have begun on a regional scale in the 6<sup>th</sup> millennium (Price 2016), likely increased in prevalence, especially after the birth of complex societies in the 5<sup>th</sup>-3<sup>rd</sup> millennia and the increased human impact on the landscapes of the NFC. The tightening of the ecological niche for pig husbandry (within settlements) would have coincided with a decline in hybridization, the generation of new selection pressures, and, at least at times, reduced nutritional quality.

## Conclusion

The data presented in this paper offer an initial perspective on pig morphological change in the NFC during the prehistoric period using the available data. In doing so, this paper highlights the dynamic history of the pig in its earliest center of domestication. The data reveal long-term morphological changes to pigs that extended well beyond the period of initial domestication. Indeed, pig morphology continued to evolve over time, decreasing by about 20-30% along various metrics. We suggest these changes were due to a combination of two factors: 1) a decline in the frequency of hybridization with wild boar and 2) adaptation to new forms of pig husbandry.

Our datasets are small and contain chronological gaps; many more data are needed to complete the picture, especially from the 5<sup>th</sup> and 4<sup>th</sup> millennia cal. BC. More GMM data are likewise needed from all periods, especially the earlier ones, to explore the variation in pig morphologies during domestication. In that vein, our study highlights the importance of applying techniques typically reserved for studying the first steps of domestication more broadly. Pigs – and other animals – had long histories after domestication. Studying them exposes the pace and process of evolving human-animal relations.

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## Figure Captions

Figure 1. Map of the northern Fertile Crescent and adjacent regions. Sites used in this study are shown along with their main period of occupation.

Figure 2. Chronological evolution of upper and lower molar breadths (WA and WP). Ordinal

numbers at top of figure indicate millennium. Boxplots of Tooth LSI value for sites analyzed in this study. Çayönü data from Kusatman (1991) represents the earliest morphologically domestic pigs. Modern wild boar data from Payne and Bull (1988). Note that this modern sample is represented by 76 teeth belonging to 18 individuals.

Figure 3. Boxplots Astragalus GLI, Tibia Bd, M1 WA, and M2 WA. Gray line indicates the first appearance of domestic pigs in the northern Fertile Crescent. See Table 2 for more information, including sample sizes.

Figure 4. Scatterplot of upper and lower M3 lengths vs. breadths. Çayönü (9<sup>th</sup>-8<sup>th</sup> mill. cal. BC) data (from Kusatman 1991) are presented as means, standard deviations (extent of solid lines), and maximum range (dotted lines). See Table 2 for sites included in each Millennium group.

Figure 5. Centroid sizes arranged in chronological order.

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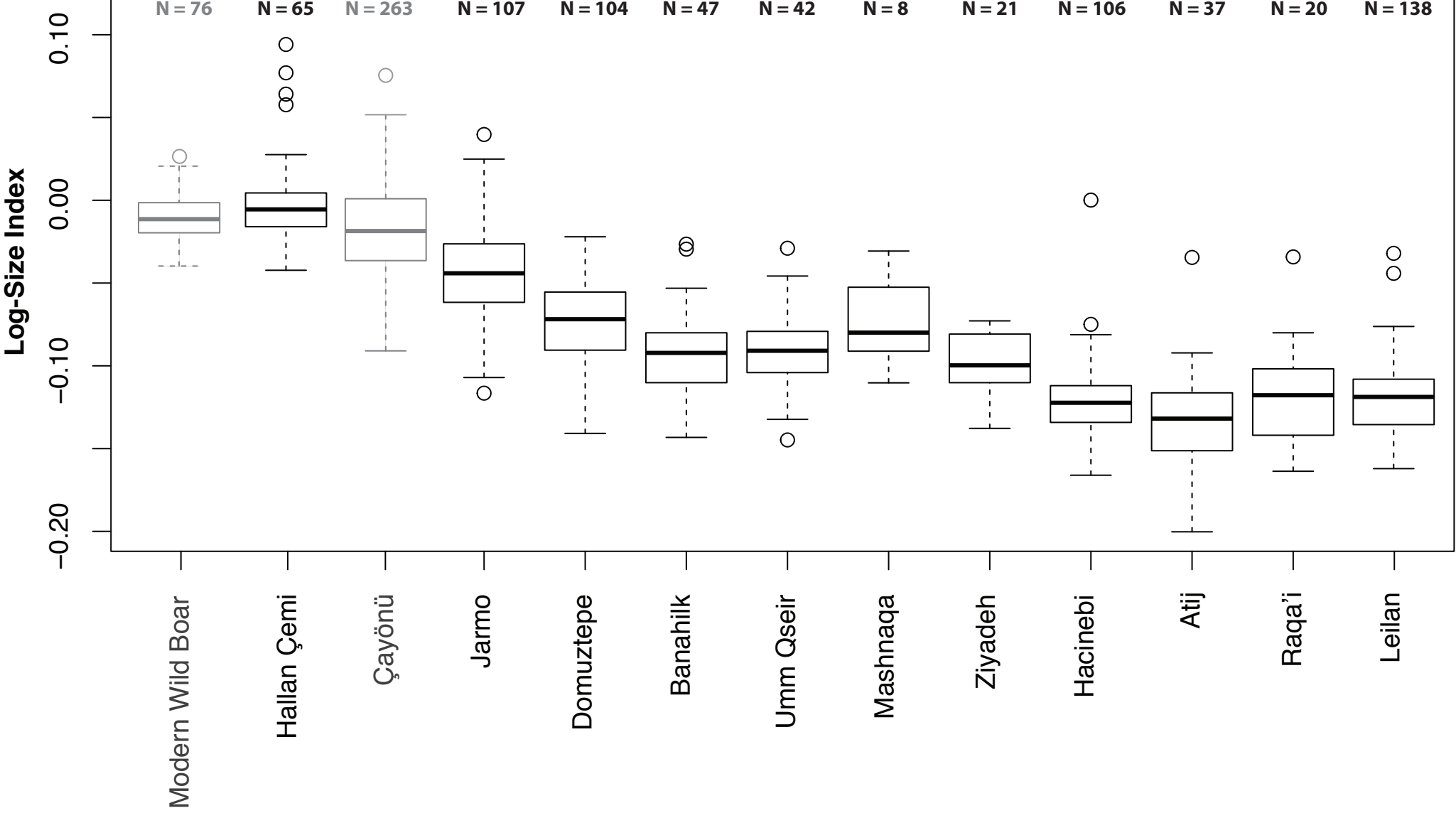


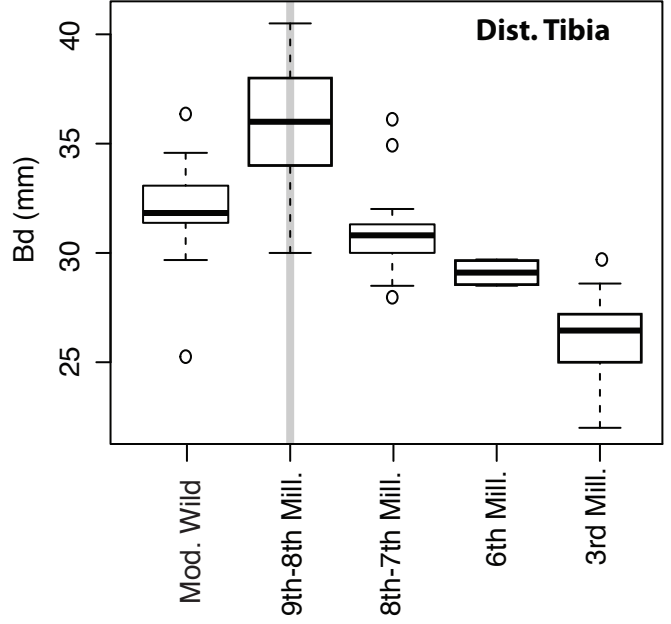
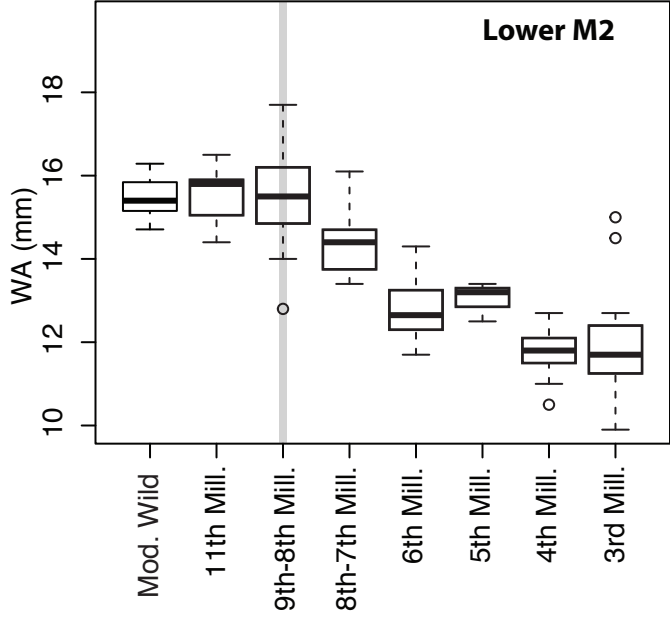
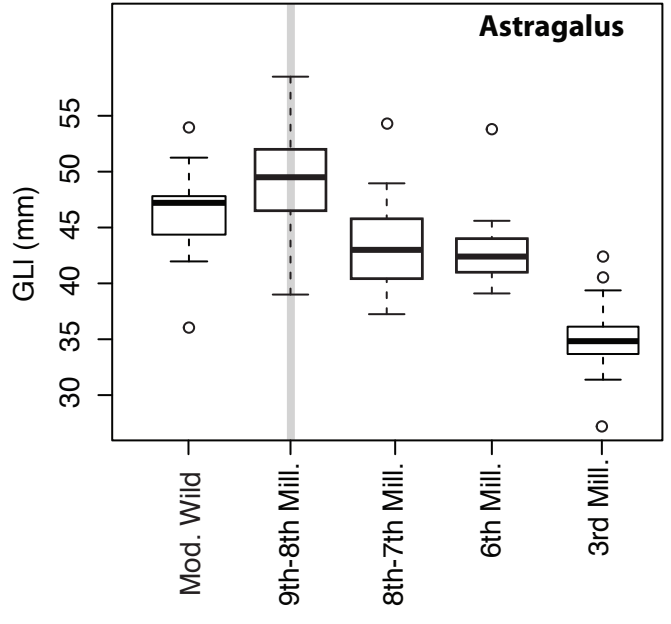
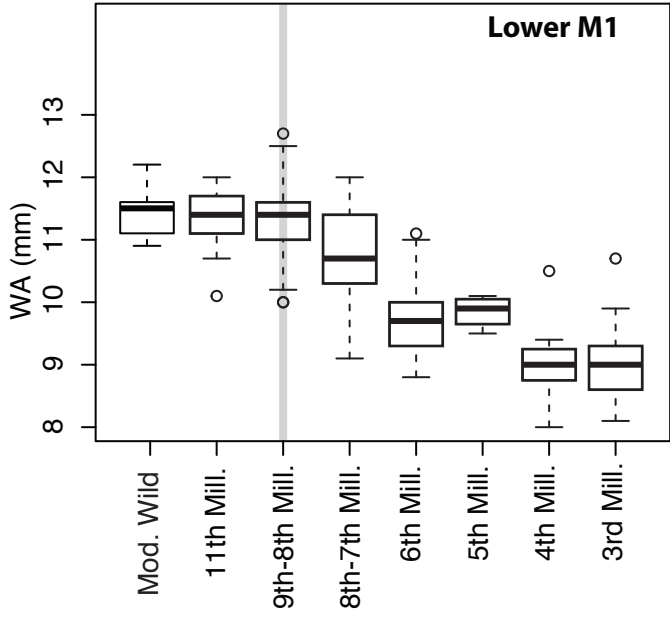
- Epipaleolithic (13,000-10,000 BC)
- + Early-Late Pre-Pottery Neolithic (PPN) (10,000-7500 BC)
- Late PPN - Pottery Neolithic (7500-5000 BC)
- ✕ Chalcolithic (5000-3000 BC)
- ★ Early Bronze Age (3000-2000 BC)

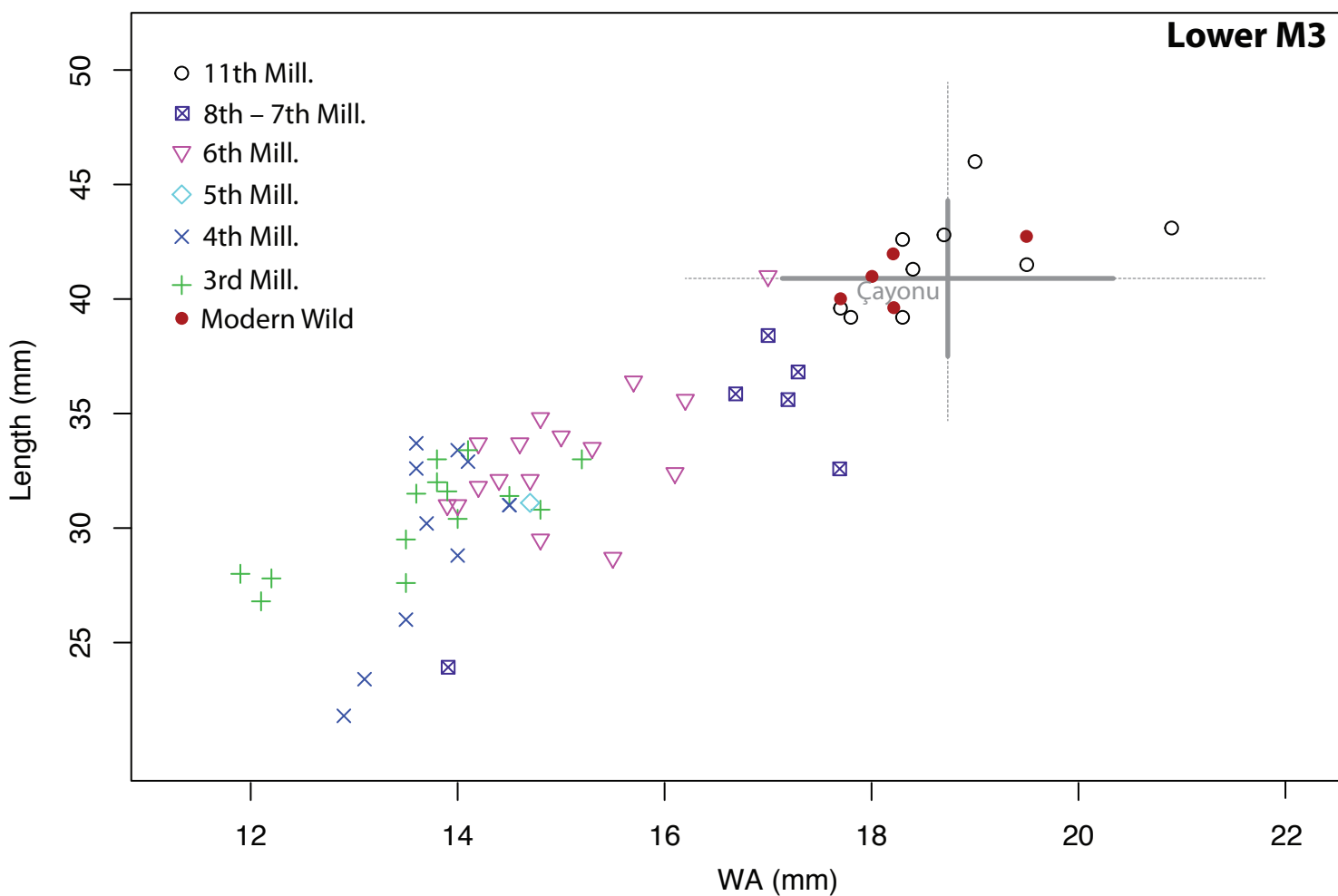
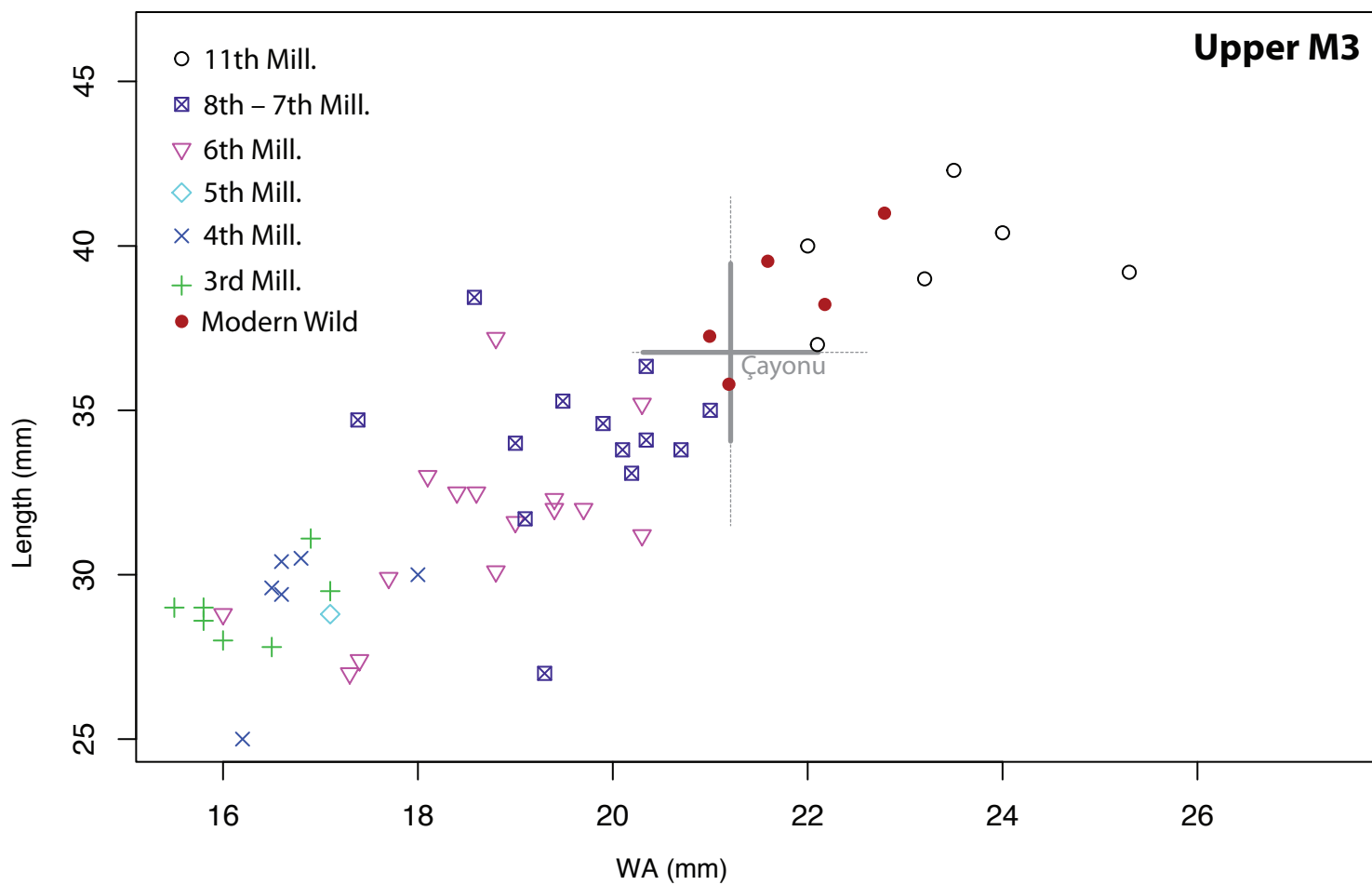


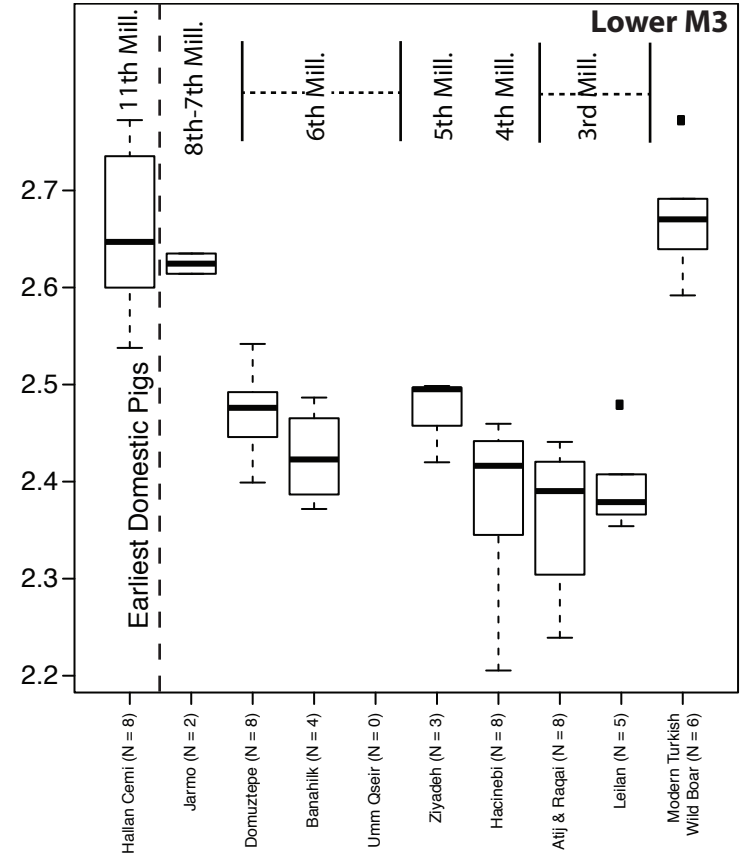
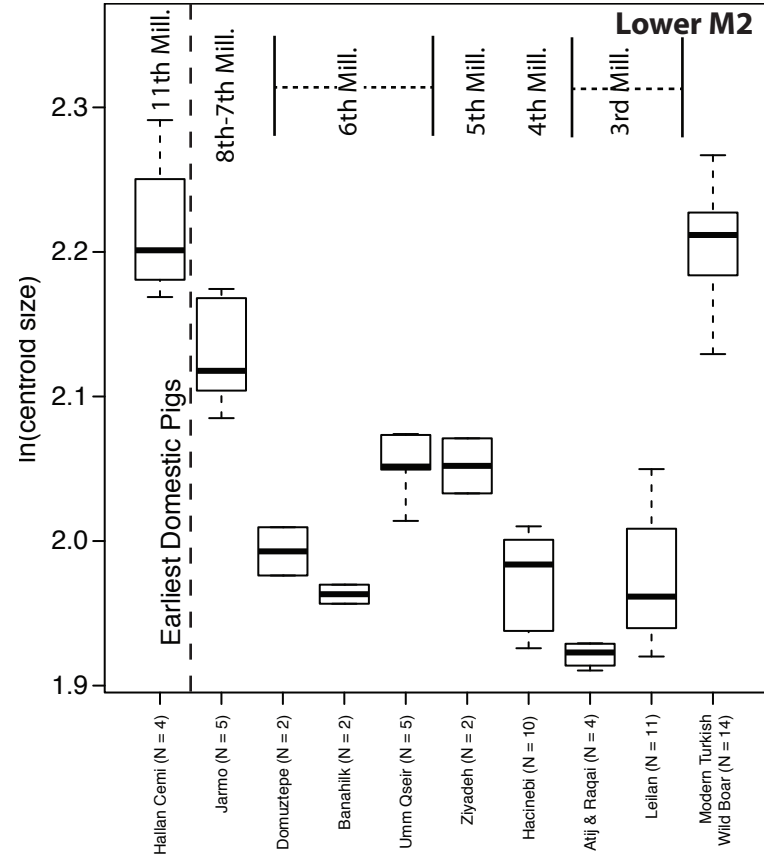
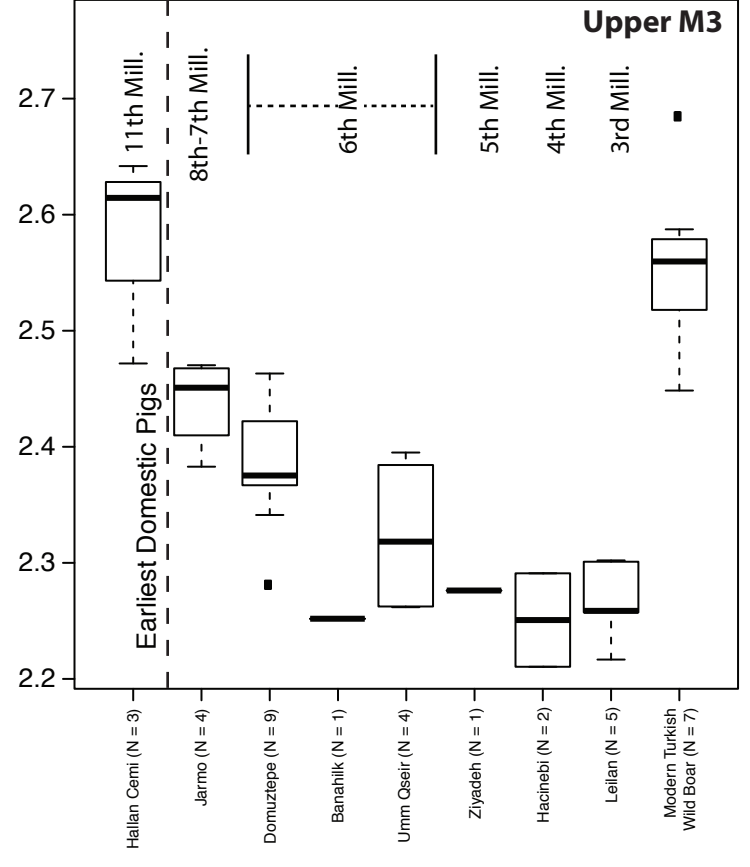
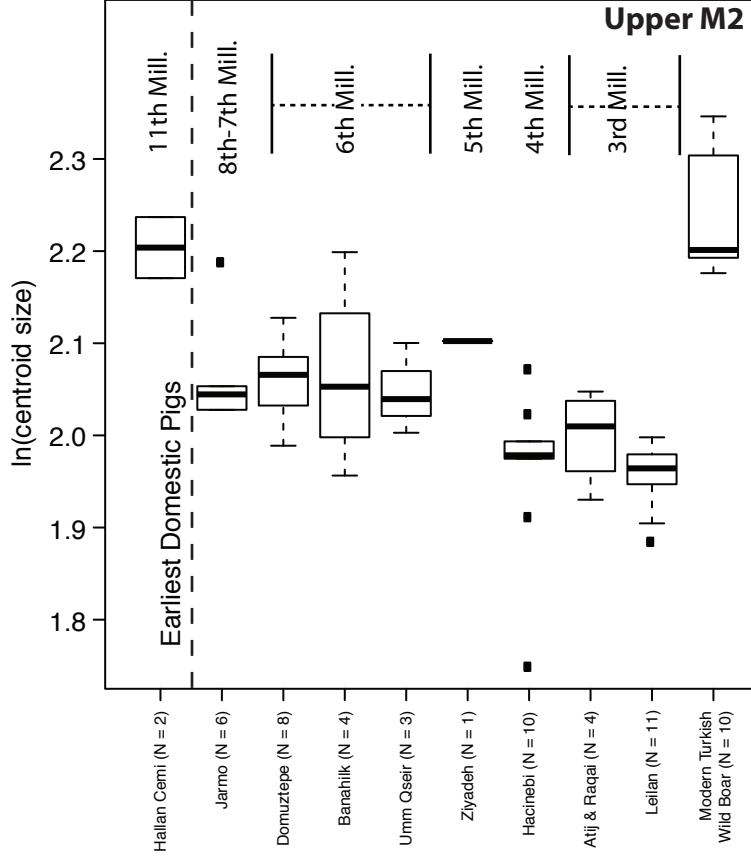
**Tooth LSI**

Modern N = 76    11th N = 65    9th-8th N = 263    8th-7th N = 107    6th N = 104    6th N = 47    5th N = 42    5th N = 8    4th N = 21    4th N = 106    3rd N = 37    3rd N = 20    3rd N = 138









## Supplementary Information 1

Pairwise comparisons of data presented in **Figures 2, 3, and 5** using Wilcoxon rank sum test with Holm's P-Value correction method.<sup>1,2</sup> Light shading indicates not significant at .05 level. Heavy shading indicates not significant at .10 level.

**Figure 2:**

LSI	Atij	Bana.	Domuz.	Haci.	Hal.C.	Jarmo	Leilan	Mash.	Raqai	Um.Q	Cay.
Bana.	<.0001										
Domuz.	<.0001	.0001									
Haci.	.1496	<.0001	<.0001								
Hal.C.	<.0001	<.0001	<.0001	<.0001							
Jarmo	<.0001	<.0001	<.0001	<.0001	<.0001						
Leilan	.0633	<.0001	<.0001	1.000	<.0001	<.0001					
Mash.	.0014	.6086	1.000	.0007	.0003	.1117	.0007				
Raqai	.6502	.0132	<.0001	1.000	<.0001	<.0001	1.000	.0087			
Um.Q	<.0001	1.000	.0013	<.0001	<.0001	<.0001	<.0001	.9228	.0032		
Cay.	<.0001	<.0001	<.0001	<.0001	.0012	<.0001	<.0001	.0012	<.0001	<.0001	
Ziyad.	.0004	1.000	.0013	.0005	<.0001	<.0001	.0009	.5929	.1276	1.000	<.0001

**Figure 3:**

M <sub>1</sub> WA	Mod. WB	11 <sup>th</sup> Mill.	9-8 <sup>th</sup> Mill.	8-7 <sup>th</sup> Mill.	6 <sup>th</sup> Mill.	5 <sup>th</sup> Mill.	4 <sup>th</sup> Mill.
11 <sup>th</sup> Mill.	1.000						
9-8 <sup>th</sup> Mill.	1.000	1.000					
8-7 <sup>th</sup> Mill.	.0162	.2267	.0314				

6 <sup>th</sup> Mill.	<.0001	.0002	<.0001	.0003			
5 <sup>th</sup> Mill.	.0099	.0562	.0128	.0759	1.000		
4 <sup>th</sup> Mill.	<.0001	.0004	<.0001	<.0001	.0004	.06443	
3 <sup>rd</sup> Mill.	<.0001	<.0001	<.0001	<.0001	<.0001	.0512	1.000

<b>M<sub>2</sub> WA</b>	Mod. WB	11 <sup>th</sup> Mill.	9-8 <sup>th</sup> Mill.	8-7 <sup>th</sup> Mill.	6 <sup>th</sup> Mill.	5 <sup>th</sup> Mill.	4 <sup>th</sup> Mill.
11 <sup>th</sup> Mill.	1.000						
9-8 <sup>th</sup> Mill.	1.000	1.000					
8-7 <sup>th</sup> Mill.	.0691	.1006	.0856				
6 <sup>th</sup> Mill.	<.0001	.0002	<.0001	.0042			
5 <sup>th</sup> Mill.	.0991	.1006	.0720	.1687	1.000		
4 <sup>th</sup> Mill.	<.0001	.0001	<.0001	.0013	.0014	.1006	
3 <sup>rd</sup> Mill.	<.0001	<.0001	<.0001	.0042	.0207	.2337	1.000

<b>Astragalus GLI</b>	Mod. Wild Boar	9-8 <sup>th</sup> Mill.	8-7 <sup>th</sup> Mill.	6 <sup>th</sup> Mill.
9 <sup>th</sup> -8 <sup>th</sup> Mill.	<.0001			
8 <sup>th</sup> -7 <sup>th</sup> Mill.	.1020	<.0001		
6 <sup>th</sup> Mill.	.0250	<.0001	.9723	
3 <sup>rd</sup> Mill.	<.0001	<.0001	<.0001	<.0001

<b>Tibia Bd</b>	Mod. Wild Boar	9-8 <sup>th</sup> Mill.	8-7 <sup>th</sup> Mill.	6 <sup>th</sup> Mill.
9 <sup>th</sup> -8 <sup>th</sup> Mill.	.1726			
8 <sup>th</sup> -7 <sup>th</sup> Mill.	.0009	<.0001		
6 <sup>th</sup> Mill.	.0101	<.0001	.02791	
3 <sup>rd</sup> Mill.	<.0001	<.0001	<.0001	.01123

**Figure 5:**

<b>M<sub>2</sub> Centroid</b>	11 <sup>th</sup> Mill.	8-7 <sup>th</sup> Mill.	6 <sup>th</sup> Mill.	5 <sup>th</sup> Mill.	4 <sup>th</sup> Mill.	3 <sup>rd</sup> Mill.
8 <sup>th</sup> -7 <sup>th</sup> Mill.	.2647					
6 <sup>th</sup> Mill.	.0336	.0150				
5 <sup>th</sup> Mill.	.5333	.4762	1.000			
4 <sup>th</sup> Mill.	.0280	.0107	.2647	.2647		
3 <sup>rd</sup> Mill.	.0088	.0023	.0479	.2647	.7139	
Modern Wild Boar	1.000	.0280	<.0001	.1667	<.0001	<.0001

<b>M<sub>3</sub> Centroid</b>	11 <sup>th</sup> Mill.	8-7 <sup>th</sup> Mill.	6 <sup>th</sup> Mill.	5 <sup>th</sup> Mill.	4 <sup>th</sup> Mill.	3 <sup>rd</sup> Mill.
8 <sup>th</sup> -7 <sup>th</sup> Mill.	1.000					
6 <sup>th</sup> Mill.	.0006	.2637				
5 <sup>th</sup> Mill.	.1697	1.000	1.000			
4 <sup>th</sup> Mill.	.0026	.3556	.2828	.9333		
3 <sup>rd</sup> Mill.	.0002	.2476	.0553	.2637	1.000	
Modern Wild Boar	1.000	1.000	.0019	.2637	.0107	.0014

M <sup>2</sup> Centroid	11 <sup>th</sup> Mill.	8-7 <sup>th</sup> Mill.	6 <sup>th</sup> Mill.	4 <sup>th</sup> Mill.	3 <sup>rd</sup> Mill.
8 <sup>th</sup> -7 <sup>th</sup> Mill.	.5714				
6 <sup>th</sup> Mill.	.1765	1.000			
4 <sup>th</sup> Mill.	.1818	.0607	.0392		
3 <sup>rd</sup> Mill.	.1029	.0049	.0005	1.000	
Modern Wild Boar	1.000	.0100	.0004	.0003	>.0001

M <sup>3</sup> Centroid	11 <sup>th</sup> Mill.	8-7 <sup>th</sup> Mill.	6 <sup>th</sup> Mill.	5 <sup>th</sup> Mill.	4 <sup>th</sup> Mill.	3 <sup>rd</sup> Mill.
8 <sup>th</sup> -7 <sup>th</sup> Mill.	.7222					
6 <sup>th</sup> Mill.	.0559	.2118				
5 <sup>th</sup> Mill.	1.000	1.000	1.000			
4 <sup>th</sup> Mill.	1.000	1.000	1.000	1.000		
3 <sup>rd</sup> Mill.	.5000	.2698	.3110	1.000	1.000	
Modern Wild Boar	1.000	.3636	.0007	1.000	.7222	.0505

1. Tests conducted in R Stats package v.3.3.1 using pairwise.wilcox.test() function.

2. Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* **6**, 65–70.

## Supplementary Information 2

Fligner-Killeen tests<sup>1</sup> of homogeneity of variances for astragalus GLI, tibia Bd, M1 WA, and M2 WA data presented in **Table 2** in the text of the manuscript. For the following tests, data were grouped into three categories: Pre-Neolithic (Ksar Akil and Hallan Çemi), Neolithic (Jarmo, Çayönü, Gritille, Mezraa-Teleilat, Banahilk, Umm Qseir, Domuztepe), and Post-Neolithic (Atij, Raqa'i, Leilan, Mozan, Arbid, Hacinebi).

### Astragalus GLI



Fligner-Killeen chi-squared = 35.474, df = 2, p-value = 1.982e-08

**M1 WA**

Fligner-Killeen chi-squared = 18.948, df = 2, p-value = 7.681e-05

**M2 WA**

Fligner-Killeen chi-squared = 30.057, df = 2, p-value = 2.973e-07

**Tibia Bd**

Fligner-Killeen chi-squared = 17.857, df = 2, p-value = 0.0001326

1. Tests conducted in R Stats package v.3.3.1 using `fligner.test()` function: William J. Conover, Mark E. Johnson and Myrle M. Johnson (1981). A comparative study of tests for homogeneity of variances, with applications to the outer continental shelf bidding data. *Technometrics* **23**, 351–361.