The impact of subsistence changes on humeral bilateral asymmetry in Terminal Pleistocene and Holocene Europe

Vladimír Sládek ^{a,*}, Christopher B. Ruff ^b, Margit Berner ^c, Brigitte Holt ^d, Markku Niskanen ^e, Eliška Schuplerová ^a, Martin Hora ^a

^a *Department of Anthropology and Human Genetics, Faculty of Science, Charles University, Prague, Czech Republic*

^b *The Center for Functional Anatomy and Evolution, Johns Hopkins University, Baltimore, USA*

^c *Department of Anthropology, Natural History Museum, Vienna, Austria*

^d *Department of Anthropology, University of Massachusetts, Amherst, USA*

^e *Department of Archaeology, University of Oulu, Oulu, Finland*

***Corresponding author:**

E-mail address: sladekv@yahoo.fr (V. Sládek)

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Abstract

Analyses of upper limb bone bilateral asymmetry can shed light on manipulative behavior, sexual division of labor, and the effects of economic transitions on skeletal morphology. We compared the maximum (absolute) and directional asymmetry in humeral length, articular breadth, and cross-sectional diaphyseal geometry (CSG) in a large ($n > 1200$) European sample distributed among 11 archaeological periods from the Early Upper Paleolithic through the 20th century. Asymmetry in length and articular breadth is right-biased, but relatively small and fairly constant between temporal periods. Females show more asymmetry in length than males. This suggests a low impact of behavioral changes on asymmetry in length and breadth, but strong genetic control with probable sex linkage of asymmetry in length. Asymmetry in CSG properties is much more marked than in length and articular breadth, with sex-specific variation. In males, a major decline in asymmetry occurs between the Upper Paleolithic and Mesolithic. There is no further decline in asymmetry between the Mesolithic and Neolithic in males and only limited variation during the Holocene. In females, a major decline occurs between the Mesolithic and Neolithic, with resulting average directional asymmetry close to zero. Asymmetry among females continues to be very low in the subsequent Copper and Bronze Ages, but increases again in the Iron Age. Changes in female asymmetry result in an increase of sexual dimorphism during the early agricultural periods, followed by a decrease in the Iron Age. Sexual dimorphism again slightly declines after the Late Medieval. Our results indicate that changes in manipulative behavior were sex-specific with a probable higher impact of changes in hunting behavior on male asymmetry (e.g., shift from unimanual throwing to use of the bow-and-arrow) and food grain processing in females, specifically, use of two-handed saddle querns in the early agricultural periods and one-handed rotary querns in later agricultural periods.

Introduction

It is likely that human manipulative behavior changed significantly through the Terminal Pleistocene and Early Holocene in response to changes in foraging strategy (Binford, 1968, 1984; Flannery, 1969; Shott, 1993; Wright, 1994), the adoption of agriculture in the Early Holocene (Bender, 1978; Clark and Brandt, 1984; Wright, 1994; Larsen, 1995; Price, 2000; Milisauskas, 2002; Robb, 2013; Smith et al., 2015), and the intensification of agriculture during the Middle Neolithic and Copper Age (Sherratt, 1981, 1983; Milisauskas and Kruk, 2002; Greenfield, 2010). Other subsequent technological and social changes may also have affected behavioral use of the upper limb, including increasing urbanism (Schaub, 1982; Finkelstein, 1992; Issar and Zohar, 2004; Kristiansen and Larsson, 2005) and the beginning of metal ore mining and metallurgy (Craddock, 1995; Golden et al., 2001; Haaland, 2004; Johnston, 2008; Amzallag, 2009; Radivojević et al., 2010), as well as an increase in social complexity and occupational specialization (Clark and Parry, 1990; Cipolla, 1994; Johnson and Earle, 2000).

One clue to human manipulative behavior in the past can be derived from assessments of handedness and upper limb bone bilateral asymmetry (e.g., Bridges, 1985, 1989, 1991; Constandse-Westermann and Newell, 1989; Fresia et al., 1990; Trinkaus et al., 1994; Churchill et al., 1996; Albert and Greene, 1999; Trinkaus and Churchill, 1999; Ledger et al., 2000; Stock and Pfeiffer, 2001, 2004; Weiss, 2003; Rhodes and Knüsel, 2005; Auerbach and Ruff, 2006; Marchi et al., 2006; Sládek et al., 2007; Kujanová et al., 2008; Stock et al., 2013; Macintosh et al., 2014; Sparacello et al., 2015). Bilateral skeletal asymmetry in the upper limb bones is significant among past and recent humans because the upper limb is directly influenced by the lateralized effect of manipulation and is free from the relatively symmetrical loading of the lower limbs associated with bipedal locomotion (Auerbach and Ruff, 2006).

Bilateral asymmetry in the upper limb long bones has been found to be more pronounced in humeri than in ulnae and radii (Watson, 1974; Trinkaus et al., 1994; Bridges et al., 2000; Auerbach and Ruff, 2006). Upper limb bone lengths and articular breadths are less asymmetrical than diaphyseal breadths and measures of skeletal strength (i.e., cross-sectional geometric properties [CSG]; Ruff, 2008), possibly because they are less developmentally plastic (Jones et al., 1977; Ruff et al., 1994; Trinkaus et al., 1994; Sládek et al., 2007). In fact, it has been shown that CSG properties directly correspond with bilateral asymmetry in mechanical loading of the upper limbs, especially marked in athletes with different patterns of asymmetry in upper limb use (Jones et al., 1977; Roy et al., 1994; Ruff et al., 1994; Kontulainen et al., 2002; Shaw and Stock, 2009; Shaw, 2011). Moreover, studying bilateral skeletal asymmetry in CSG properties has other advantages for reconstructing manipulative behavior: comparing the right and left sides minimizes the effect of systemic non-mechanical factors such as diet, as well as variation in body size.

Bilateral asymmetry in the upper limb skeleton is shaped, at least in part, by handedness—that is, by the effect of the systematic preference of one hand for a particular task, where the dominant hand is associated with higher dexterity and skill acquisition (Perelle and Ehrman, 1994; Trinkaus et al., 1994; Steele, 2000; Raymond and Pontier, 2004; McManus, 2009; Shaw, 2011). Human handedness is strongly right-biased, with the proportion of left handers ranging from 1–11% based on certain behavioral measures such as different hand skill (Hardyck and Petrinovich, 1977) to 4–28% based on a more generalized motor skill test (Perelle and Ehrman, 1994: Table 1). It has also been shown that there is culturally mediated handedness variation influenced by factors such as gender differences (Perelle and Ehrman, 1994), education and socio-economic status (Leiber and Axelrod, 1981; Annett and Kilshaw, 1983; Perelle and Ehrman, 1994; Raymond and Pontier, 2004), as well as the negative perception of left-handedness (Wile, 1934; Hardyck and Petrinovich, 1977).

However, handedness is not the only factor involved in the asymmetric use of the upper limb because maximum load is not always directly imposed on the dominant hand, i.e., the side with the greater degree of motor control. There are highly unilateral activities that directly subject the dominant hand to the highest mechanical loading, such as professional tennis playing (Jones et al., 1977; Kontulainen et al., 2002), and woodworking and warfare-related weapons training (Rhodes and Knüsel, 2005; Sparacello et al., 2011, 2015). However, there are also activities that employ both hands equally without respect to the dominant hand, such as grain grinding using a saddle quern (Sládek et al., unpublished results) and digging activities (Marshall, 1976; Lee, 1979; Ledger et al., 2000). Finally, there are activities involving reduced loading of the dominant hand because the dominant hand is used for better skill control compared to the non-dominant limb, which is used for stabilization (e.g., see the distribution of maximum muscle activity between the right and left hand during underhand spear thrusting in Shaw et al., 2012).

Based on the recent frequency of right-handedness and high frequency of right-handed individuals in the Upper Pleistocene (see review about bilateral asymmetry among Neanderthals and Early Upper Paleolithic humans in Trinkaus et al., 1994; Churchill and Formicola, 1997), we can expect that right-biased bilateral hand asymmetry dominated Terminal Pleistocene and Holocene Europe. However, the degree of bilateral asymmetry need not have been constant or always different from zero, especially when the separate subsistence roles of males and females are considered. Changes in hunting strategy observed during the Terminal Pleistocene; e.g., from "short-distance" to "long-distance" killing, and including more exploitation of small game and other local resources (Flannery, 1969; Binford, 1984; Churchill, 1993; Churchill et al., 1996; Churchill and Rhodes, 2009); might be expected to result in a more significant change in upper limb use among males than among females, given that hunting was primarily a male activity (Bridges, 1985; Binford, 2001; Kelly, 2013;

Sadvari et al., 2015). The adoption and intensification of agriculture affected female intra-domestic activities, such as food preparation and grinding by either two-handed saddle querns introduced in the early Neolithic or one-handed rotary querns introduced in the Iron Age (Mauldin, 1993; Wright, 1994; Adams, 1999; Holodňák, 2001; Watts, 2014). In contrast, changes in bilaterally asymmetric use of the upper limbs during the Holocene among males may not have been so pronounced, for two reasons. First, the major change in subsistence-related activities for males may have occurred in conjunction with the reduction of hunting after the Upper Paleolithic. Second, unilateral activities associated with hunting may have been replaced, in part, by other activities with similar unilateral loading patterns, such as the crafting of stone hatchets and woodworking (Sparacello et al., 2011), metallurgy (Macintosh et al., 2014), and warfare (Sparacello et al., 2015). The increased reliance on agricultural subsistence during the Holocene was accompanied by other processes, such as economic specialization and increased social complexity. Manipulative tasks could reflect opposing processes associated with higher unilateral loading related to gender-specific and non-agricultural activities (e.g., emergence of elites and daily uni-manual weapons training of the warrior class; Sparacello et al., 2011). Industrialization may also have affected patterns of bilateral asymmetry by reducing the sexual dimorphism of occupational activities (Auerbach and Ruff, 2006) and possibly introducing technological factors promoting use of one hand over the other (McManus, 2009).

The goal of this study is to assess how humeral bilateral asymmetry varies with respect to Terminal Pleistocene and Holocene changes in subsistence and socio-economic organization within Europe. To help interpret the bilateral asymmetry results, we also include a separate analysis of right and left humeral variation. Our analyses concentrate on asymmetries in humeral length, articular breadth, and CSG properties across sex, temporal, and regional subdivisions. We expect greater variation in asymmetry in CSG properties than

in length and articular breadth. We also expect sex differences in asymmetry to vary temporally, in accordance with the differential effects of technological and social change at subsistence transitions on males in the Terminal Pleistocene and females in the early agricultural Holocene, as well as in accordance with later changes in food processing (mainly grinding technology) and increases in social complexity.

Materials and methods

Sample

Skeletal material was obtained from museums and other osteological collections throughout Europe, as part of another larger study (Ruff et al., 2012, 2015). Table 1 shows the composition of the present study sample as well as the temporal period abbreviations used in this study and details of dating. A total of 1508 right humeri and 1494 left humeri divided across 11 time periods were examined. For asymmetry analyses, only paired samples are used, with a total of 1227 matched pairs. Sex was determined using standard osteological features of the pelvis and skull (Buikstra and Ubelaker, 1994; Bruzek, 2002). There is a slight predominance of male humeri both for individual right and left sides and in the matched pairs. Sample sizes for particular features vary due to differential preservation (see individual results tables for details on the sample size in each analysis). The skeletal samples were divided into seven European regions: Britain, Scandinavia, North-Central Europe, France, Italy, the Iberian Peninsula, and the Balkans (Fig. 1). Individual sites are given in the Supplementary Online Materials (SOM) Table S1.

The pooled pan-European sample includes three pre-agricultural groups (EUP–Meso) and eight agricultural groups (Neol–Recent), with a calibrated C¹⁴ BP range for the pre-agricultural groups of 33 kyr to 6 kyr BP and for the agricultural groups of 7 kyr BP to the 20th century (Table 1). The main criterion for individual/site classification was based on the archaeological culture (Milisauskas, 2011), with the exception of the early Copper Age sample from Fontenoce Recanati, Italy (5,450 cal. BP). This sample is included in the Neolithic so as not to confuse the early Copper Age with developed Later Copper Age groups of the Corded Ware and Bell Beaker cultures, which belong to our Copper Age sample. Finally, the recent group includes individuals from the pre-industrial 17th century through the industrial 19th and 20th centuries. This combines “Early Modern” and “Very Recent” groups used in some other analyses of this sample (Ruff et al., 2012, 2015). Given that the recent pre-industrial and industrial samples are non-significantly different in asymmetry variables (Sladek et al., in prep; see also the Discussion below), we combine all the recent groups into one period for the present study. For some analyses, we separate the total agricultural sample into early agricultural (Neol–BA) and late agricultural periods (IA–Recent). We also use “agricultural Holocene” to separate agricultural groups from Holocene foragers. To simplify descriptions, for these analyses the entire recent sample is treated as falling into the late agricultural period.

Measurements and CSG properties

Table 2 summarizes details of the linear measurements and CSG properties used in the present study. Linear osteometric measurements included maximum humeral length (HML) and humeral head superoinferior breadth (HHDSI), taken following the standardized techniques described in Bräuer (1988). Cross-sectional properties—humeral cross-sectional

area (HCA) and polar section modulus (HZp)—were measured according to the standard protocol described in Ruff (2002) and Trinkaus (1997). Bones were oriented relative to anatomical antero-posterior (A-P) and medio-lateral (M-L) axes, and humeral cross-sectional contours were obtained at 35% of humeral biomechanical length (see Table 2) from the distal end, either by computed tomography (Sládek et al., 2006, 2010) or external molding combined with biplanar radiography to determine approximate endosteal contours (i.e., "Latex Cast Technique;" Trinkaus and Ruff, 1989; Stock, 2002; O'Neill and Ruff, 2004; Sylvester et al., 2010). Structural properties were derived from CT scans using either manually digitized periosteal and endosteal contours by CTi software (Sailer et al., 2003; Sládek et al., 2006, 2010) or by the semi-automated MomentMacro procedure (<http://www.hopkinsmedicine.org/fac/mmacro.htm>). Structural properties from the Latex Cast Method were obtained using ImageJ (Abràmoff et al., 2004) with MomentMacro implementation (Sylvester et al., 2010). It has been shown that CSG properties derived from the Latex Cast Method accurately represent true CSG properties (O'Neill and Ruff, 2004; Sylvester et al., 2010). In this study we examined two CSG parameters: cross-sectional area (HCA), which is a measure of the contribution of bone geometry to axial rigidity and strength, and the polar section modulus (HZp), which is a measure of the contribution of bone geometry to average bending and torsional strength (Ruff, 2008).

For comparisons involving separate right and left humeri, CSG properties were standardized for body size by dividing CA by body mass (and multiplying by 100) and dividing Zp by body mass $\times$ biomechanical length (and multiplying by 10000; Ruff, 2000). Body mass was estimated from either bi-iliac breadth and stature (58% of the total sample) (Ruff et al., 2005) or from femoral head breadth using a technique developed for European samples based on stature/bi-iliac breadth body mass estimates (see review of body mass technique in Ruff et al., 2012). Stature was estimated using either the anatomical method with

age term (39% of the total sample; Raxter et al., 2006, 2007) or from long bone lengths (Ruff et al., 2012) with a preference for the techniques based on femoral + tibial or femoral length.

Computation of asymmetry

Maximum (absolute) asymmetry (MaxA; [%]) was used to express the overall amount of asymmetry without respect to side as follows:

$$1) \text{ MaxA} = [(\text{max} - \text{min})/((\text{max} + \text{min})/2)] * 100,$$

where “max” is the side with the larger value and “min” is the side with the smaller value. A value of zero indicates bilateral symmetry, and deviation from zero describes the magnitude of asymmetry.

Directional asymmetry (DirA; [%]) describes the magnitude of laterality and was calculated as follows:

$$2) \text{ DirA} = [(R - L)/((R + L)/2)] * 100,$$

where “R” is the right side and “L” is the left side. Asymmetry favoring the right side is expressed as a positive value, and asymmetry favoring the left side is expressed as a negative value, with values near zero indicating the absence of directional asymmetry (Auerbach and Ruff, 2006).

Statistical treatment

Summary statistics for MaxA and DirA are expressed as the median and bootstrap $\pm 95\%$ CI of the median. The bootstrap CIs were computed using a macro developed for Visual Basic in Excel 2010 following the approach described in Manly (2006). We applied

1,000 replications of bootstrap samples, and the $\pm 95\%$ CIs were constructed using the bootstrap-t technique (see Manly [2006:65] for further details). In addition to the bootstrap $\pm 95\%$ CI of the median, the following nonparametric tests were employed to assess the statistical significance of maximum and directional asymmetry variation: the multiple-group Kruskal-Wallis test to assess significance of between-period differences within sex, the Mann-Whitney U test for two independent samples to test for significant sexual dimorphism, and the one-sample Wilcoxon Signed-Rank test for testing the significance of directional asymmetry against $H_0 = 0$ (i.e., against the absence of directional asymmetry). Comparisons using individual right and left humeral CSG properties were carried out using a two-way ANOVA with sex, period, and interaction of sex*period. Distance-weighted LS regressions against $\log_{10}$ (years BP) were used to assess the general pattern of variation through the Terminal Pleistocene and Holocene in right and left humeral polar section modulus, within sex.

The tables, raw data preparation, and bootstrap calculations were produced and performed using Excel Microsoft Office Professional 2010 (Microsoft Corporation, 2010). All other tests were computed in Statistica for Windows 12 (64 bits; StatSoft, Inc. 1984–2013).

Results

Maximum asymmetry

The medians and bootstrap $\pm 95\%$ CIs of maximum asymmetry, by period and sex, are given for humeral maximum length and articular breadth in Table 3, and for CSG properties in Table 4. Figure 2 shows the temporal distribution of median maximum asymmetry in

humeral length, articular breadth, and HZp. The lowest magnitude and range of variation is observed in length (range of the medians 0.3–2.91%) and breadth (range of the medians 0.95–2.93%) and the largest in HZp (range of the medians 5.69–47.06%). Maximum asymmetry in humeral length remains unchanged between the Terminal Pleistocene and early Holocene, but maximum asymmetry in the polar section modulus strongly decreases by approximately 35% between the Early Upper Paleolithic and Neolithic in males, and by approximately 6% between the Late Upper Paleolithic and Copper Age in females. Paired data for articular breadth in the EUP and LUP samples are available only for males ($n = 4$); however, among males maximum asymmetry in breadth remains very similar between the Terminal Pleistocene and Holocene.

Directional asymmetry

Table 3 shows the medians and bootstrap $\pm 95\%$ CIs for directional asymmetry in humeral length and articular breadth. Directional asymmetry in humeral length and breadth is significantly different between periods in the nonparametric multiple-group Kruskal-Wallis test ($p < 0.001$) in both sexes and in all post-hoc tests except the EUP, LUP, and Meso samples. However, directional asymmetry in length and breadth is relatively small ($< 3\%$) compared to CSG properties, and there is no clear temporal pattern through our entire Terminal Pleistocene and Holocene sample.

Table 4 shows the medians and bootstrap $\pm 95\%$ CIs for directional asymmetry in CSG properties. All directional asymmetries are significantly right-biased both in male and female HCA and HZp except the LUP males and females¹ and early agricultural females. Figure 3 plots the directional asymmetry in the humeral polar section modulus by temporal

period and sex. Overall temporal variation in directional asymmetry in cortical area and polar section modulus is significant in the nonparametric multiple-group Kruskal-Wallis test ($p < 0.001$) in both sexes, and both CSG properties show similar patterns of overall temporal change. Average directional asymmetry in HZp in males decreases between the Early Upper Paleolithic and Mesolithic from close to 40% to close to 10% (Mann-Whitney U test $p < 0.01$), but temporal change in males between the Mesolithic and Neolithic is absent (Mann-Whitney U test $p = 0.22$) and after the Neolithic is relatively minor, varying by only about $\pm 5\%$. For the Early Upper Paleolithic, there is no female sample available, and only a limited sample is available for the Late Upper Paleolithic. However, there is no evidence for a change in directional asymmetry of CSG properties between the LUP and Mesolithic in females (Fig. 3). Females do show a later significant decrease in asymmetry at the beginning of the Holocene, between the Mesolithic and Neolithic (approximately 16% in HZp; Mann-Whitney U test $p < 0.05$). Directional asymmetry in the humeral polar section modulus in females declines further in the Neolithic to close to zero, and remains close to zero in the subsequent Copper and Bronze Ages. After the early agricultural Holocene, females again show significant directional asymmetry in HZp during the Iron Age (about 6%; Wilcoxon Signed-Rank test $p < 0.01$), with little change thereafter. The increase from the pooled early agricultural groups is near-significant in the Iron Age (Mann-Whitney U test $p = 0.068$) and significant in the Roman period (Mann-Whitney U test $p = 0.019$). Thus, a major reduction in directional asymmetry among females appears during the Neolithic, whereas in males, this decline appears prior to the adoption of agriculture and never reaches levels as low as those of Neolithic to Bronze Age females. Moreover, male directional asymmetry in the humeral polar section modulus remains relatively unchanged during the late agricultural periods, whereas females are more affected by technological shifts beginning during the Iron Age (see Discussion).

Figure 4 shows boxplots of directional asymmetry in HZp for the early agricultural Holocene periods (Neol, BA, CopA) and the late agricultural Holocene periods (Roman, EMed, LMed, Recent) by sex and seven major European regions. Males show a significant p -value in the one-sample Wilcoxon Signed-Rank test (i.e., against $H_0 = 0$; no directional asymmetry) in all the early and late agricultural Holocene regions. In contrast, the absence of right-dominated activity in females during the early agricultural Holocene is supported by the nonsignificant difference in directional asymmetry in HZp from 0 in the early agricultural Holocene in all available regions except Britain (Britain $p = 0.042$). However, females increase in directional asymmetry between the early and late agricultural Holocene, except in Italy (Italy $p = 0.26$; but see the large number of strongly left-dominant females in the Italy sample). Thus, within-region comparisons of directional asymmetry in the humeral polar section modulus support the general pan-European pattern of temporal variation presented in Figure 3, i.e., the absence of the right-dominated directional asymmetry in females during early agricultural periods. Moreover, the common patterns of variation across regions provide strong evidence that changes in directional asymmetry among females associated with the adoption of agriculture in the Neolithic and technological progress during the Iron Age/Roman period are a global reflection of subsistence effects on CSG properties, apparent across the majority of European regions. Our results for the regional analyses also indicate that the reduction of directional asymmetry in the female sample during the early agricultural Holocene can be seen as a specific skeletal feature associated with early agricultural subsistence throughout most of Europe.

Sexual dimorphism in asymmetry

Tables 3 and 4 summarize the results of the Mann-Whitney U test for sexual dimorphism in directional asymmetry in humeral length, articular breadth, and CSG properties. Figure 5 shows sexual dimorphism in directional asymmetry for humeral length, breadth, and HZp. Sexual dimorphism in humeral articular breadth asymmetry is nonsignificant in all temporal periods, but asymmetries in humeral length and CSG properties are significant in the majority of periods. Sexual dimorphism in length is much less than that in CSG properties, and is also relatively consistent across periods, with females showing more asymmetry (longer on the right side). Cross-sectional geometric properties show a higher level of directional asymmetry in males (larger on the right side), but with more variation between periods. Sexual dimorphism in CSG asymmetry is high in the LUP and declines in the Mesolithic (although sample sizes are small in both periods), then increases in the early agricultural Holocene, mostly due to the decrease in directional asymmetry in females. It is less pronounced during the later Holocene due to the subsequent increase in directional asymmetry during the Iron Age in females, and it continues to decline through the recent period.

Right and left humeral CSG variation

Figure 6 summarizes temporal variation in the right and left humeral polar section moduli relative to body size plotted by $\log_{10}$ (years BP) for each individual (see range of log years BP for each period in Table 1). In males, the decrease in directional asymmetry observed between the Early Upper Paleolithic and Mesolithic is due to the large increase in humeral strength on the left side, whereas right humeral strength remains essentially unchanged. After the Mesolithic (about 3.9 log Years BP), temporal changes in right and left humeral strength in males approximately parallel each other. Therefore, directional asymmetry remains relatively unchanged from the Neolithic to the recent period despite the

fact that humeral strength decreases toward the Neolithic, increases slightly during the Iron Age and Roman period, and decreases again toward the recent period. In females, both right and left humeral strength increase between the Upper Paleolithic and Mesolithic; however, right humeral strength subsequently decreases, whereas left humeral strength continues to increase. Thus, females increase loading during the Terminal Pleistocene and early Holocene mostly on the left side but decrease loading on the right side, resulting in almost equivalent strengths on both sides by the Neolithic. Both sides show a parallel decline between the Neolithic and the Bronze Age (about 3.8 to 3.5 log years BP). After the Bronze Age, females begin to reduce loading more on the left side, which explains why directional asymmetry increases again during the later Holocene periods. Relative humeral strength declines on both sides throughout the Holocene in females.

Discussion

Our results indicate that the overall magnitude of maximum bilateral asymmetry is larger in humeral CSG properties than in humeral lengths and articular breadth over the entire Terminal Pleistocene and Holocene. Asymmetry in CSG properties also shows a greater range of variation between temporal periods, especially in the major behavioral transition between the Upper Paleolithic and Neolithic, whereas asymmetry in humeral length and articular breadth remains virtually unchanged over this time span. Other temporally later changes in CSG asymmetry, for example, the decline and then increase among females from the Copper Age through the Iron Age, are also not paralleled by similar changes in length and articular breadth asymmetry. Thus, our results support the suggestion that bilateral asymmetry in lengths and breadths is more closely related to non-behavioral factors, such as genetic and

hormonal influences (Trinkaus et al., 1994; Auerbach and Ruff, 2006; Sládek et al., 2007), whereas asymmetry in CSG properties is more induced by differences in mechanical loading (e.g., Trinkaus et al., 1994). Our results also demonstrate that these differences between skeletal dimensions are not specific to a particular period but can be seen as a general feature of human postcranial variation in bilateral skeletal asymmetry.

Similarities in the general magnitude of asymmetry between humeral length and articular breadth do not necessarily indicate that they are controlled by the same biological processes, however, because sexual dimorphism in asymmetry was found to be significant in humeral length (females greater) but nonsignificant in articular breadth. Greater bilateral asymmetry in humeral length among females has been observed in other studies (Schultz, 1937; Auerbach and Ruff, 2006; Sládek et al., 2007; Macintosh et al., 2014), and suggests possible sex-linkage (Auerbach and Ruff, 2006), although environmental influences (Steele and Mays, 1995; Sládek et al., 2007) cannot be ruled out.

Our results for CSG properties indicate that a major shift in maximum and directional asymmetry occurs between the Terminal Pleistocene and Holocene; however, the timing of the shift is sex-specific. In males, the shift in asymmetry in CSG properties occurs mainly between the Upper Paleolithic and Mesolithic, and is mostly due to increases on the left side. There is no further decrease in asymmetry between the Mesolithic and Neolithic in males, as well as in the subsequent Holocene. In contrast, females decrease in directional asymmetry in CSG properties later, during the Mesolithic-Neolithic transition, mainly because of an increase in strength on the left side, but also a decrease on the right side. In females, average directional asymmetry declines to close to zero in all the early agricultural groups but increases again in the subsequent Iron Age.

Our observed decrease of directional asymmetry between the Upper Paleolithic and Mesolithic in males may reflect changes in hunting strategy observed in the archaeological

record during the Terminal Pleistocene and Mesolithic (Binford, 1968; Flannery, 1969; Shott, 1993), although stochastic effects due to the relatively small samples cannot be ruled out. Human groups intensified "killing at distance" hunting strategies (Binford, 1984) during the Upper Paleolithic (see review in Churchill, 1993; Schmitt et al., 2003; Churchill and Rhodes, 2009). At the same time they experienced an increase in reliance on "low ranking" resources such as small game in the Terminal Pleistocene and the Mesolithic (Binford, 1968; Flannery, 1969; see also review in Zeder, 2012). This trend also resulted in changes in weapon technology mainly through the introduction of the bow-and-arrow, possibly beginning in the middle of the Upper Paleolithic but becoming more commonly employed in the later Upper Paleolithic and Mesolithic (see review in Bergman, 1993; Churchill, 1993; Cattelain, 1997; Knecht, 1997; Nassaney and Pyle, 1999; Pétilion et al., 2011). In fact, the increase in use of the bow-and-arrow may be one of the key factors responsible for increasing loading on the left arm and subsequently decreasing directional asymmetry between the Upper Paleolithic and Mesolithic (Knüsel, 2000), as inferred also, for example, from the increase of humeral external dimensions on the left side in the medieval sample of military archers from the *Mary Rose* (Stirland, 1993, 2013). In contrast, the greater asymmetry in Early Upper Paleolithic males compared to the Late Upper Paleolithic and Mesolithic is likely to be caused by habitual employment of spear thrusting (Schmitt et al., 2003), unimanual throwing (Shaw and Stock, 2009), and possibly other activities such as scraping tasks (Shaw et al., 2012). The changes in weaponry technology indicated by the decrease of directional asymmetry during the Terminal Pleistocene may be a broader reflection of the shift in hunting distances from closer range in the Early Upper Paleolithic to more flexible long distance hunting, especially at the end of the Late Upper Paleolithic and subsequent Mesolithic.

Because hunting is not the key subsistence activity for females (Kelly, 2013), their relatively stable directional asymmetry in the Upper Paleolithic and Mesolithic may reflect

the fact that food gathering induced a similar loading regime on the upper limbs, regardless of changes in overall foraging strategy during the Terminal Pleistocene and Mesolithic.

However, females experienced significant change when Neolithic groups began to be fully dependent on domestic cereals and especially on food processing of the grains. Although some grinding was present even during the Upper Paleolithic and Mesolithic (see review in Crombé and Robinson, 2014), grain grinding began to be intensively used in the early Neolithic (Lynch and Rowland, 2005; Watts, 2014). Moreover, the first grinding technology is associated with a two-handed saddle quern (i.e., using a ground stone and hand stone; see Fig. 7A), which is expected to produce a highly symmetrical pattern of loading on the upper limbs (Watts, 2014; Sládek et al., unpublished results). It is likely that this technological transition and reliance on grinding is also reflected in a decrease in directional asymmetry.

The sex-specific response to changes in subsistence between the Terminal Pleistocene and early Holocene is also supported by the assessment of regional variation. The decrease in directional asymmetry in females is not specific to only one particular region but, with the exception of Britain, was found in all analyzed European regions in our study. In contrast, males show a low level of directional asymmetry in the Neolithic only in France, but this value is still significantly different from an absence of directional asymmetry. The regional decrease of directional asymmetry in early agricultural females has been also reported in the Central European Holocene (Sládek et al., 2007; Macintosh et al., 2014) and Italy (Marchi et al., 2006; Sparacello and Marchi, 2008; Sparacello et al., 2011), and outside of Europe in the southeastern United States (Bridges, 1989; Hogue and Dongarra, 2002) and at the Neolithic Çatalhöyük site in southern Anatolia (Sadvari et al., 2015). The decrease of directional asymmetry observed among early agricultural females was interpreted as a result of the higher reliance of females on intra-domestic tasks (Sládek et al., 2007; Sparacello and Marchi, 2008), for example in grain grinding (Marchi et al., 2006; Sparacello et al., 2011) and particularly in

maize processing (Bridges, 1989; Hogue and Dongarra, 2002), or as the result of more gender conservative ideology (Sparacello and Marchi, 2008). However, our study shows in a broader European context that the decrease of directional asymmetry and higher loading on the left arm observed in females is a characteristic of the entire early agricultural setting, and in fact is one of the key humeral features that can be associated with early agricultural subsistence.

An impact of technological change associated with food processing can also be detected in the increase in directional asymmetry during the Iron Age found in all of our regional female samples. The Iron Age is associated with an important technological improvement for food processing—the appearance of rotary querns (see Fig. 7B; Watts, 2014). As indicated from direct measurements of muscular activity (Sládek et al., unpublished results), use of the rotary quern produces unilateral loading of the dominant upper limb, compared to bilateral loading produced by the two-handed saddle quern. This impact may account for the increase in average directional asymmetry during the Iron Age (HZp) and Roman period (HCA, HZp) in females. However, the variation in female values observed in the Iron Age and Roman period may also indicate that the shift between the saddle quern and rotary quern was not abrupt but that bimanual saddle querns remained an alternative for grain grinding even during later Holocene periods. In fact, saddle querns are reported not only from the Iron Age but also from later Holocene periods (e.g., Lynch and Rowland, 2005; Alonso et al., 2011), albeit with low rates of frequency. Thus, our results may support the view that saddle querns began to be less frequently incorporated into intra-domestic female activities after the Bronze Age than rotary querns and that the appearance of saddle querns in the archaeological record after the Iron Age may be a reflection of the complementary practice of grinding with saddle querns in addition to the generally more frequent use of rotary querns.

The directional asymmetry in CSG properties remains somewhat variable even among late agricultural groups. After the Iron Age, directional asymmetry in humeral strength

generally declines slightly in males toward the most recent period. Females show very little if any change in average directional asymmetry during these periods. The sex-specific changes in directional asymmetry in humeral strength result in a decrease of sexual dimorphism from about 9.5% observed in the Iron Age to 1.6% in the recent period. This may reflect a greater decline among males in unilateral tasks in more recent times, possibly associated with a decrease in sexual division of labor that accompanied more urbanized living and the Industrial Revolution. Auerbach and Ruff (2006) also found a decline in sexual dimorphism of bilateral asymmetry in upper limb bone diaphyseal breadths in industrial versus pre-industrial samples from Europe. These results are consistent with temporal trends in the lower limb bones, in which sexual dimorphism in cross-sectional geometric shape declines in more recent populations (Ruff, 1987), most likely linked to mobility changes and again, reduction in sexual division of labor.

Our Holocene temporal variation does not clearly support a significant impact of the origin of metallurgy on humeral directional asymmetry in males as suggested in Macintosh et al. (2014). In fact, asymmetry in HZp remains similar in males between the Neolithic and the first metallurgy groups in the Copper as well as Bronze Ages. There is a slight increase in directional asymmetry among males in HZp between the Bronze and Iron Age that could be related to the intensification of metallurgy and adoption of iron observed during the European Iron Age (Craddock, 1995; Milisauskas, 2011). However, we might expect that other factors played a role in the increase of asymmetry among Iron Age males, such as the progress in organization of military systems occurring during this time period (Collis, 2003).

Reconstruction of CSG properties for Iron Age elite militia shows that they had relatively large directional asymmetry in humeral torsional rigidity as expected from pre- and peri-adolescent weapon training (Sparacello et al., 2015). Thus, the slight increase of humeral strength asymmetry observed in our pan-European Iron Age sample may indicate that warrior

activities played a more prominent role in manipulative behavior among Iron Age males; however, this must be tested on larger and more structured samples from the Iron Age.

Conclusions

Our comparisons of humeral bilateral asymmetry in a very large sample of European skeletons extending from the Upper Paleolithic through the 20th century shed light on both general trait and sex-specific differences in asymmetry, as well as behavioral effects on asymmetry. Asymmetry in humeral length and articular breadth, favoring the right side, is relatively small and consistent between temporal periods, and thus does not reflect any of the behavioral changes occurring over this time span. This suggests a strong genetic component to asymmetry in these characteristics. Females have more asymmetry in humeral length but nonsignificant asymmetry in articular breadth, indicating possible sex-linkage of asymmetry in length.

Bilateral asymmetry in humeral diaphyseal strength is much more marked and shows strong, sex-specific temporal variation. Both males and females decline in strength asymmetry following the Pleistocene, but the decline occurs earlier in males, at the Upper Paleolithic-Mesolithic transition, and later in females, between the Mesolithic and Neolithic. The decline in males is caused mainly by an increase in strength on the left side, while strength remains unchanged on the right side, possibly corresponding to a change in hunting strategy, e.g., use of the bow-and-arrow rather than unimanual throwing behavior. The later decline in asymmetry in females, also largely related to an increase on the left side but accompanied by a decrease on the right side, appears correlated with new food processing techniques in the Neolithic involving use of two-handed grinding implements (saddle querns). Average

directional asymmetry in humeral strength is close to zero among early agricultural females of the Neolithic through Bronze Ages. It then increases in the Iron Age, possibly corresponding to the replacement of bimanual with unimanual (rotary quern) and other food grinding techniques. Thus, our observed overall trend supports the view that changes in hunting strategy during the Terminal Pleistocene had a greater effect on asymmetry in male manipulative tasks, whereas the adoption of agriculture had a greater effect on asymmetry in female manipulative tasks.

Our results indicate that the adoption of agriculture increases sexual dimorphism in manipulative loading mainly because of a decrease of asymmetry in females. However, sexual dimorphism in manipulative loading subsequently decreases in the Iron Age and remains relatively constant thereafter. There is a slight decline in asymmetry among males leading to less sexual dimorphism in the most recent (post-Medieval) period, which may reflect a reduction in sex-specific manipulative behaviors.

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Footnotes

¹The directional asymmetry in CSG properties in the Late Upper Paleolithic is not found to be significantly different from zero in the Wilcoxon Signed-Rank test (p -values: HCA = 0.17; HZp = 0.33) but is found to be significant by bootstrap CIs (i.e., 0 is not included in the $\pm 95\%$ CIs for LUP) in the male LUP sample. In females, the absence of directional asymmetry in both CSG properties is supported by the nonsignificant Wilcoxon Signed-Rank test (p -values: HCA = 0.22; HZp = 0.08) and by the nonsignificant bootstrap CIs. In part, this contradiction may be the result of the stochastic effect of the small sample size, especially the female Late Upper Paleolithic sample. It may also highlight the fact that the effect of strongly right- and left-handed individuals is more pronounced and stochastic in such small samples; therefore, estimates of asymmetry from Upper Paleolithic and Mesolithic samples must be interpreted with a higher level of caution than those from larger Holocene samples. In contrast, the observed absence of directional asymmetry in CSG properties in the early agricultural group in females is supported not only by correspondence between the nonsignificant one-sample Wilcoxon Signed-Rank test and $\pm 95\%$ CIs, but also by the low range of $\pm 95\%$ CIs.

Figure legends

Figure 1. Map of the sites used in the study.

Figure 2. A summary of the median maximum asymmetry in humeral properties ($\pm 95\%$ CIs of the median are shown in Tables 3 and 4; see abbreviations for humeral properties in Table 2).

Figure 3. Asymmetry in humeral polar section moduli (median $\pm 95\%$ CI; filled = males, open = females; Kruskal-Wallis ANOVA is significant for median directional asymmetry HZp in males and females when $p < 0.01$, in both Pleistocene-Holocene and agricultural Holocene comparison).

Figure 4. Directional asymmetry in polar section modulus in the early agricultural Holocene (A, C) and late agricultural Holocene (B, D) by region and sex (males [A-B], females [C-D]); Median, Upper, and Lower Quartile, Non-outlier range; dots represent the distribution of individual values; ns = not significant, * $p < 0.05$, ** $p < 0.01$, N/A sample for this particular analysis is not available).

Figure 5. Percentage sexual dimorphism for directional asymmetry in humeral maximum length (HML), articular breadth (HHDSI), and section modulus (HZp) by temporal periods.

Figure 6. Scatterplots of right (solid) and left (dashed) humeral section moduli by sex (size standardized values are shown; lines are distance-weighted LS regression fittings against mid-logarithmic years BP; mean ANOVA is significant for right and left HZpstd in males and females when $p < 0.01$, in both Pleistocene-Holocene and agricultural Holocene; see Table 1 for the range of the minimum and maximum log years BP dating of temporal periods).

Figure 7. Experimental grinding with saddle quern (A) and rotary quern (B).

Table 1. Summary of the study sample by temporal period and sex^a

	Abbrv.	C ¹⁴ BP ^b	logYearsBP ^c	Males ^d			Females ^d			Total ^d		
				Right	Left	Paired	Right	Left	Paired	Right	Left	Paired
Early Upper Paleolithic	EUP	33,400–26,400	4.52-4.42	8	10	8	5	8	5	13	18	13
Late Upper Paleolithic	LUP	21,900–11,350	4.34-4.06	12	12	10	5	6	5	17	18	15
Mesolithic	Meso	10,500–6,050	4.02-3.77	24	25	20	14	18	11	38	43	31
Neolithic	Neol	7,300–4,600	3.86-3.66	77	77	61	54	54	47	131	131	108
Copper Age	CopA	4,600–3,950	3.66-3.60	42	47	31	30	28	22	72	75	53
Bronze Age	BA	4,350–2,950	3.64-3.47	102	98	79	82	87	71	184	185	150
Iron Age	IA	2,250–1,700	3.35-3.23	64	64	45	63	55	50	127	119	95
Roman	Roman	1,900–950	3.28-3.22	39	38	32	40	37	32	79	75	64
Early Medieval	EMed	1,300–950	3.13-2.98	142	133	111	95	90	73	237	223	184
Late Medieval	LMed	925–550	2.97-2.74	204	211	172	187	175	146	391	386	318
Recent	Recent	320–10	2.51-1.00	129	135	115	90	86	81	219	221	196
Total				843	850	684	665	644	543	1508	1494	1227

^a The number of individuals indicates the maximum individuals preserved in each period. The number of individuals varies according to preservation of the respective parameter. The final number of individuals used in each analysis is provided in the results and summary tables. For details about sample sizes and sites and European regions by temporal periods included in the studied sample see Table S1.

^b Range of the maximum and minimum calibrated C¹⁴ BP date for period.

^c Range of the minimum and maximum natural logarithm of the C¹⁴ BP date.

^d Maximum number for right humerus (Right), left humerus (Left) and individuals with both right and left sides preserved (Paired) by sex.

The preservation is given as the number of total preserved individuals with HML.

Table 2. Summary of linear osteometric and CSG measurements and asymmetry calculation used in the present study

Measurements	Abbrev.	Description ^a
Humeral maximum length	HML	Distance parallel to the long axis of the humeral shaft from the most superior point on the head of the humerus to the most inferior point on the trochlea. [mm] (M[Hu]#1).
Humeral head S-I breadth	HHDSI	Direct distance between the most superior and inferior points on the border of the articular surface on humeral head [mm] (M[Hu]#10).
Humeral cortical area	HCA	Humeral axial rigidity and strength at 35% of biomechanical length (length from proximal surface of humeral head to distal edge of lateral lip of trochlea) [mm ²].
Humeral polar section modulus	HZp	Humeral torsional and average bending strength at 35% of biomechanical length [mm ⁴].

^a "M" refers to Martin numbers of osteometric measurements (Bräuer, 1988).

Table 3. Maximum and directional asymmetry in humeral length (HML) and articular breadth (HHDSI) by sex and temporal period
(Median [*N*; $\pm 95\%$ CI])

Period ^a	Males		Females	
	MaxA	DirA	MaxA	DirA
Humeral maximum length (HML)				
EUP	0.72 (8; 0–1.36)	<u>0.56 (8; -0.35–1.28)</u>	0.65 (5; 0–1.93)	<u>0.30 (5; -1.88–1.24)</u>
LUP	0.62 (10; 0–2.28)	<u>0.30 (10; -1.84–1.35)</u>	1.74 (5; 0–4.46)	<u>1.72 (5; -0.53–4.41)</u>
Meso	0.30 (20; 0–0.68)*	<u>0.00 (20; -0.23–0)*</u>	0.36 (11; 0–0.39)*	<u>0.36 (11; -1.1–1.07)*</u>
Neol	0.97 (61; 0.66–1.23)*	0.90 (61; 0.54–1.19)*	1.80 (47; 1.17–2.15)*	1.78 (47; 1.17–2.14)*
CopA	0.91 (31; 0.53–1.28)	0.63 (31; 0.24–1.17)*	1.64 (22; 1.4–2.17)	1.63 (22; 1.37–2.23)*
BA	1.53 (79; 1.26–1.89)*	1.49 (79; 1.27–2.02)*	1.91 (71; 1.38–2.2)*	1.89 (71; 1.37–2.2)*
IA	1.82 (45; 1.44–2.24)	1.81 (45; 1.44–2.26)	2.13 (50; 1.65–2.61)	2.11 (50; 1.61–2.6)
Roman	2.12 (32; 1.86–2.44)	2.09 (32; 1.82–2.51)	2.91 (32; 2.29–3.72)	2.87 (32; 2.3–3.71)
EMed	1.28 (111; 1.06–1.4)*	1.17 (111; 0.92–1.41)*	1.84 (73; 1.57–2.02)*	1.82 (73; 1.56–1.99)*
LMed	1.35 (172; 1.21–1.5)	1.23 (172; 1.05–1.32)	1.56 (146; 1.4–1.77)	1.49 (146; 1.31–1.66)
Rec	0.96 (115; 0.8–1.23)*	0.93 (115; 0.84–1.23)*	1.41 (81; 1.21–1.7)*	1.33 (81; 1.11–1.6)*
Humeral head S-I breadth (HHDSI)				
EUP	0.95 (4; 0.95–2.07)	0.95 (4; 0.95–2.07)	-	-
LUP	1.43 (7; 0–4.04)	1.43 (7; -0.42–4.75)	-	-

Meso	1.10 (6; 0–3.38)	<u>0.64 (6; -1.57–2.3)</u>	-	-
Neol	1.59 (46; 1.22–2.3)	1.01 (46; 0.16–1.69)	1.49 (34; 0.86–2.02)	<u>0.63 (34; -0.3–1.88)</u>
CopA	2.00 (15; 1.72–3.7)	<u>0.00 (15; -1.74–1.67)</u>	1.50 (11; 0.6–2.59)	<u>0.00 (11; -1.62–1.66)</u>
BA	2.17 (61; 2.11–2.89)	1.98 (61; 1.77–3.16)	2.44 (49; 2.44–3.59)	<u>0.00 (49; -1.59–0)</u>
IA	2.93 (39; 1.81–4.22)	2.48 (39; 1.17–3.6)	2.32 (34; 2–3.36)	1.65 (34; 0.68–2.39)
Roman	1.90 (26; 1.12–2.71)	<u>0.79 (26; -0.47–2.02)</u>	1.67 (20; 0–3.48)	<u>0.25 (20; -3.11–0.77)</u>
EMed	2.08 (87; 1.9–2.21)	0.23 (87; -1.38–0.47)	2.39 (54; 2.23–2.85)	1.69 (54; 0.92–3.34)
LMed	2.00 (163; 1.92–2.38)	0.79 (163; 0.56–1.41)	2.22 (148; 2.07–2.68)	0.96 (148; 0.71–1.78)
Rec	1.53 (91; 1.1–1.85)	0.45 (91; -0.25–0.7)	1.87 (73; 1.25–2.46)	<u>0.00 (73; -0.75–0.29)</u>

^a See Table 1 for abbreviations.

All male and female multiple Kruskal-Wallis comparisons between periods significant at $p < 0.05$.

* Mann-Whitney U test for sexual dimorphism significant at $p < 0.05$.

Underlined values indicate one-sample Wilcoxon Signed-Rank test for asymmetry not significant.

Table 4. Maximum and directional asymmetry in humeral CSG properties by sex and temporal period (N ; $\pm 95\%$ CI) ¹

Period ^a	Males		Females	
	MaxA	DirA	MaxA	DirA
Humeral cortical area (HCA)				
EUP	29.57 (5; 0–54.72)	25.76 (5; -2.48–44.62)	-	-
LUP	25.30 (10; 20.4–33.77)*	<u>22.98 (10; 8.56–53.53)</u>	8.16 (5; 0–31.01)*	<u>7.84 (5; -6.36–29.36)</u>
Meso	11.31 (16; 8.34–14.39)	10.7 (16; 7.75–13.69)	10.66 (5; 3.81–23.17)	10.12 (5; 0.09–21.42)
Neol	7.84 (66; 4.74–9.38)*	6.97 (66; 3.97–9.24)*	4.64 (44; 2.88–6.86)*	<u>0.12 (44; -1.7–2.2)*</u>
CopA	9.65 (32; 7.19–14)*	8.75 (32; 6.53–13.77)*	4.31 (21; 0.7–6.82)*	<u>1.18 (21; -0.42–5.02)*</u>
BA	9.51 (70; 7.37–11.76)*	9.04 (70; 7.13–11.13)*	5.60 (57; 4.46–7.69)*	<u>-0.11 (57; -3.52–2.15)*</u>
IA	10.82 (54; 9.69–13.04)*	10.00 (54; 8.79–12.93)*	7.81 (54; 6.25–12.03)*	<u>2.64 (54; 0.04–5.36)*</u>
Roman	6.71 (33; 3.03–9.61)	5.33 (33; 2.34–8.2)	5.04 (34; 1.91–6.73)	2.88 (34; 0.27–5.65)
EMed	7.78 (104; 6.21–10.13)*	5.53 (104; 3.38–7.33)*	4.98 (73; 3.49–6.1)*	1.78 (73; -0.16–3.17)*
LMed	7.42 (122; 5.32–8.42)*	6.25 (122; 4.65–7.71)*	4.57 (103; 3.92–5.2)*	3.91 (103; 3.04–4.95)*
Rec	5.47 (114; 4.53–6.17)	4.10 (114; 3.05–5.5)	6.25 (77; 5.03–7.64)	4.55 (77; 2.76–5.29)
Humeral polar section modulus (HZp)				
EUP	47.06 (5; 0.00–111.5)	38.1 (5; 11.35–73.37)	-	-
LUP	30.35 (10; 20.45–36.99)	<u>26.23 (10; 15.64–64.23)</u>	16.18 (5; 0.00–40.37)	<u>14.97 (5; -5.1–38.1)</u>
Meso	15.36 (16; 13.8–21.11)	10.48 (16; 4.55–23.13)	16.32 (5; 6.1–33.71)	15.09 (5; 6.12–29.2)
Neol	12.34 (66; 5.39–16.3)	10.49 (66; 3.8–13.66)*	10.34 (44; 8.2–13.74)	<u>-0.6 (44; -7.23–3.35)*</u>

CopA	15.7 (32; 11.57–21.85)*	13.41 (32; 8.27–20.53)*	5.69 (21; 4.28–10.31)*	<u>-0.78 (21; -6.61–2.67)*</u>
BA	12.32 (70; 8.51–15.55)*	11.15 (70; 7.48–13.87)*	5.9 (57; 4.49–7.4)*	<u>-0.34 (57; -2.53–1.78)*</u>
IA	17.55 (54; 13.34–21.54)*	15.66 (54; 11.63–20)*	10.67 (54; 8.26–14.4)*	6.15 (54; 2.02–11.18)*
Roman	9.13 (33; 4.12–11.37)	8.02 (33; 4.85–12.58)	10.36 (34; 1–15.78)	6.70 (34; 0.09–13.18)
EMed	14.31 (104; 11.92–16.22)*	12.91 (104; 10.63–14.3)*	6.93 (73; 3.76–8.42)*	5.85 (73; 3.14–9.05)*
LMed	11.11 (122; 9.19–13.11)*	8.85 (122; 6.5–10.1)*	6.48 (103; 4.45–7.5)*	5.05 (103; 4–5.95)*
Rec	10.68 (114; 9.38–12.16)	8.82 (114; 7.4–10.2)	9.24 (77; 5.36–11.18)	7.23 (77; 4.41–9.21)

^a See Table 1 for abbreviations.

All male and female multiple Kruskal-Wallis comparisons between periods significant at $p < 0.05$.

* Mann-Whitney U test for sexual dimorphism significant at $p < 0.05$.

Underlined values indicate one-sample Wilcoxon Signed-Rank test for asymmetry not significant.

Figure 1

Figure 2

(A) Males

(B) Females

Figure 3

Figure 4

Figure 5

Figure 6

(A) Males

(B) Females

(A) Saddle Quern

(B) Rotary Quern