

Human Manipulative Behavior in the Central European Late Eneolithic and Early Bronze Age: Humeral Bilateral Asymmetry

Vladimír Sládek,^{1,2*} Margit Berner,³ Daniel Sosna,¹ and Robert Sailer³

¹*Katedra antropologie, Fakulta filozofická, Západočeská univerzita v Plzni, Tylova 18, 30125 Plzeň, Czech Republic*

²*Ústav biologie obratlovců, Akademie věd ČR, Květná 8, 603 65, Brno, Czech Republic*

³*Department of Anthropology, Natural History Museum, Vienna, Austria*

⁴*Department of Information Technology, Natural History Museum, Vienna, Austria*

KEY WORDS cross-sectional geometry; biomechanics; humerus; handedness; Eneolithic; Bronze Age

ABSTRACT It is assumed that the transition from the Late Eneolithic to the Early Bronze Age in Central Europe was associated with substantial changes in subsistence and the perception of gender differences. However, the archeological record itself does not entirely support this model. Alternatively, this transition may be interpreted as a continuous process. We used asymmetry in external dimensions, and asymmetry in size and distribution of cortical tissue of humeri to elucidate the nature of this transition with respect to differences in manipulative behavior. The total sample of 67 individuals representing five archaeological cultures was used. The results indicate that the pattern of asymmetry of the humeral external measurements and the cross-sectional parameters taken at 35% of humeral biomechanical length remain stable during the Late Eneolithic and Early Bronze Age. However, females of both periods show fluctuating asym-

metry for all of the cross-sectional parameters, but directional asymmetry for biomechanical length. Males are nonsignificantly shifted from the line of equivalence for biomechanical length, but exhibit directional asymmetry for the cortical area and polar moment of area. Only distal articular breadth yields fluctuating asymmetry for both females and males in both periods. Thus, the transition from the Late Eneolithic to the Early Bronze Age can be seen as a continuous process that probably affected only a limited part of human activities. We interpret the differences between females and males of both periods as evidence of gender-specific activities; males might have been associated with extra-domestic agricultural labor that resulted in asymmetrical manipulative loading and females with domestic labor with symmetrical manipulative loading in both periods. *Am J Phys Anthropol* 133: 669–681, 2007. ©2007 Wiley-Liss, Inc.

The transition from the Late Eneolithic to the Early Bronze Age (2800–1500, B.C.; see chronological details in Table 1) has been viewed as a significant shift in economic and social organization (Childe, 1930; Gilman, 1981). During the Early Bronze Age the degree of production and distribution of metal increased (Shennan, 1993; Harding, 2000). Exchange networks were extended beyond the regional level and ethnic boundaries (Kristiansen, 1998). It has been suggested that craft specialization emerged to ensure efficient production and distribution of goods (Childe, 1930; Tihelka, 1953; Bátorá, 1991; Shennan, 1995; Kristiansen, 1998). The intensification of production was associated with the activities of individuals who facilitated the exchange of goods and their long-distance transport (Harding, 2000).

It has been argued that in the Central European record the intensification of economy resulted in changes of gender relations (Shennan, 1993) and subsistence strategy (Vencl, 1994; Kadrow, 2001). Based on mortuary evidence, it has been suggested that gender was the dominant structuring principle in the Late Eneolithic, but was overshadowed by hierarchical relationships among males and females in the Early Bronze Age (Shennan, 1993). While orientation of the bodies and associated artifacts were gender-specific in the Late Eneolithic, these distinctions become less rigid in the Bronze Age. Also, it has been argued that mobile subsistence was common in the Late Eneolithic (Vencl, 1994; Kadrow, 2001), while mixed agriculture dominated in the Bronze Age (Neugebauer, 1987; Harding, 2000).

Several authors mentioned that neither the intensification of economy nor subsistence completely restructured the socio-cultural system; instead, the transition was a continuous process (Shennan, 1993; Neustupný, 1997; Harding, 2000; Sládek et al., 2006a). The assumed change in gender relations might be the result of modifications of mortuary rituals, rather than the change of gender roles. Moreover, elaborate burial costumes of adult females and gender symbolism in hoards suggest that gender identity continued to shape social differentiation even during the Early Bronze Age (Shennan, 1975; Neugebauer, 1987).

The impact of economic intensification on subsistence during the Late Eneolithic and Early Bronze Age is subject to discussion. Recent studies have rejected pastoralism as the primary mode of subsistence in the Late Eneolithic and

Grant sponsor: Czech Science Foundation; Grant numbers: GAČR: 206/01/D018; Grant Sponsor: Faculty of Philosophy, University of West Bohemia in Pilsen.

*Correspondence to: Vladimír Sládek, Katedra antropologie, Fakulta filozofická, Západočeská univerzita v Plzni, Tylova 18, 30125 Plzeň, Czech Republic. E-mail: sladekv@yahoo.fr

Received 11 November 2005; accepted 8 November 2006

DOI 10.1002/ajpa.20551

Published online 1 February 2007 in Wiley InterScience (www.interscience.wiley.com).

TABLE 1. The Central European sample composition¹

Period	Culture, dating, and sites	N _F :N _M ⁵
Late Eneolithic (LE)	Bell Beaker (BBC; 2,600–2,000 B.C.) ² : Kněževs (2), Mokrůvky, Tödling (2), Tuchoměřice (BBC). Corded Ware (CWC; 2,900–2,300 B.C.) ² : Blšany, Brozany, Březno (CWC), Čachovice, Franzhausen I (CWC) (3), Kněževs (CWC), Kobylišy, Most, Obrnice, Poplze, Postoloprty, Prosetice, Tuchoměřice (CWC), Veliká Ves, Vikletice (3), Vrbice.	9; 17
Early Bronze Age (EBA)	Únětice (2,200–1,820 B.C.) ² : Bernhardsthal, Groszmuagl, Hobersdorf; Schleimbach; Unterhautzenthall (4), Würnitz Unterwölbling (Unter; 2,020–1,770 B.C.) ³ : Franzhausen I (U) (3), Gemainlebarb F (2), Melk (3) Wieselburger (Wiesl; ~2,000–1,700 B.C.) ⁴ : Hainburg (26).	23; 20

If more than one individual comes from each site, the number of individuals is in parenthesis.

¹ See geographic demarcation and definition of Central Europe in Sládek (2000).

² The radiocarbon dates are given as an estimate of the 68.2% confidence interval from Stadler (1999).

³ The radiocarbon dates are estimated based on the sample of 98 radiocarbon dates from Franzhausen I (U) and is given as the estimate of the 68.2% confidence interval (Stadler, personal communication).

⁴ No radiocarbon dates available yet. The numeric dates are approximated based on relative chronology and archeological context of the Early Bronze Age sites from the Lower Austria (Stadler, personal communication).

⁵ F, Female; M, Male.

have suggested that subsistence and mobility remained stable (see review in Harding, 2000; Sládek et al., 2006a). The continuity of mobility and subsistence during the period has been supported by studies of the cross-sectional properties of lower limb (Sládek et al., 2006a,b). However, both femora and tibiae showed higher (although nonsignificant) resistance to parameters related to a higher level of mobility for Corded Ware group (Late Eneolithic). We argued that this is the result of random impact on a small sample. It is necessary to elucidate the pattern of subsistence differences between the Late Eneolithic and Early Bronze Age using other skeletal features.

There are difficulties in understanding the transition from the Late Eneolithic to Early Bronze Age using only archaeological evidence because of the absence of the settlement features (see review in Sládek et al., 2006a,b). Therefore, reconstruction of life in the Late Eneolithic is based mostly on mortuary evidence that only reflects part of behavioral repertoire (Shennan, 1993). It is surprising how little information has been extracted from human skeletal remains themselves that are intimately related to daily activities.

We assume that social and economic changes during the transition to the Bronze Age would influence behavior of individuals and subsequently the morphology of the upper limb. This influence could be visible in the bilateral asymmetry of those humeral measurements, which are sensitive to mechanical loading. Our assumption is based on the expected differences in the asymmetry of mechanical loading during different physical tasks.

Human dominant limb asymmetry is a primary response to right handedness contralaterally related to a larger left cerebral hemisphere (Falk, 1980; Holloway, 1981; Annett, 1992; LeMay, 1992; White et al., 1994). It has been shown that upper limbs are variably employed during manipulation. Some of the physical activities are expected to affect both arms equally [e.g., maize pounding in prehistoric American Southeast; Bridges (1991); digging activities of San females in Namibia and Botswana; Marshall (1976); Ledger et al. (2000); Lee (1979)] but other habitually produce the pronounced unilateral mechanical loading [e.g., professional tennis-players, Trinkaus et al. (1994); Later Stone Age and Holocene hunters in South Africa, Marshall (1976); Ledger et al. (2000)]. The variability in the asymmetry of humeri has been used to reveal habitual behavioral differences within or between temporal

groups (Bridges, 1985, 1989, 1991; Fresia et al., 1990; Trinkaus et al., 1994; Albert and Greene, 1999; Trinkaus and Churchill, 1999; Ledger et al., 2000; Stock and Pfeiffer, 2001, 2004; Rhodes and Knüsel, 2005), differences in manipulative tasks between males and females (Fresia et al., 1990; Bridges, 1991; Weiss, 2003), age grades (Stirland, 1993; Steele and Mays, 1995), and socially unequal groups (Constandse-Westermann and Newell, 1989).

There are controversies about the relationship between the asymmetry of humeri and behavior when either external upper limb dimensions or geometry of diaphyseal cross-sections are studied. It has been shown that bilateral asymmetry in mechanical loading has a minimum or moderate effect on the length and distal articular breadth of humeri (Trinkaus et al., 1994). Further, it is expected that the length and distal articular breadth of humeri are more ontogenetically constrained and there is little influence induced by differences in behavior and environment (Lieberman et al., 2001; Ruff, 2003). It is supported by studies of tennis players (Haapasalo et al., 1996). Nevertheless, studies of past populations have demonstrated that asymmetry in length and articular breadth of upper limbs can be attributed to the effect of mechanical loading (Steele and Mays, 1995; Mays et al., 1999; Plochocki, 2004) or other environmental but nonmechanically induced factors (Albert and Greene, 1999).

The impact of mechanical loading on bilateral asymmetry in the geometry of cross-sections has been supported by numerous studies (see references above and review in Trinkaus et al., 1994). Any activity-related interpretation of cross-sections expects that the impact of mechanical loading is specific and localized, and that the impact of nonmechanical factors on size and distribution of cortical tissue is minimal. Some of the recent studies questioned these assumptions. Lieberman (1996) has shown that mechanical loading also affects those parts of skeleton that are not directly related to mechanical loading. Lovejoy et al. (2002) argue that activity level is not the primary factor in guiding the morphological formation of cortical tissue. It is assumed that differences in cortical tissue distribution are influenced by endocrinal and genetic factors (see review in Ruff et al., 1993; Trinkaus et al., 1994; Lovejoy et al., 2002; Saxon and Turner, 2005). However, there is extensive clinical, experimental, and bioarcheological evidence that supports the localized and specific effect of mechanical loading (Trinkaus et al., 1994;

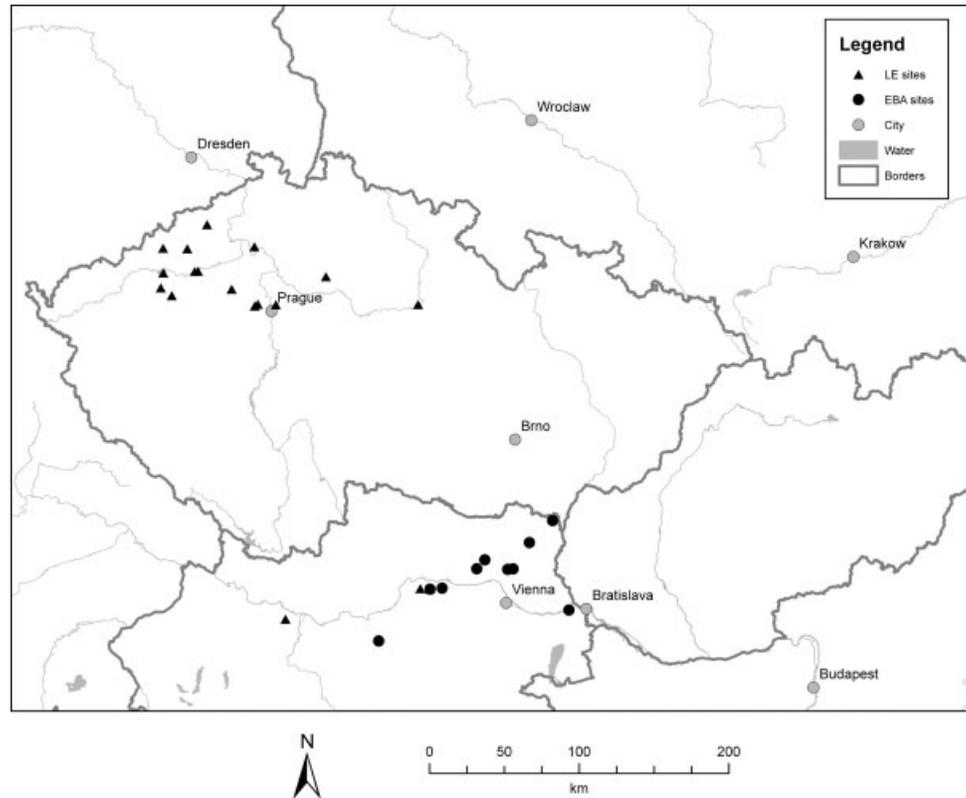


Fig. 1. Map of the Late Eneolithic and Early Bronze Age sites used in the study.

Haapasalo et al., 1996; Larsen, 1999; Ruff, 2000a; Rubin et al., 2001; Holt et al., 2004). Recently, Ruff et al. (2006) reviewed the limits and potential of bone structural analysis and concluded that traditional geometric parameters give the best estimate for mechanical loading studies. Moreover, the advantage of bilateral asymmetry analysis of cross-sections is that both arms approach the same non-mechanical stimuli (Trinkaus et al., 1994; but see Albert and Greene, 1999).

Using asymmetry in external and cross-sectional parameters of humeri, we are concentrated on the nature of the transition from the Late Eneolithic to Early Bronze Age. Two models of the transition can be proposed. First, the transition resulted in substantial changes in the everyday activities of humans. Second, we hypothesize that the transition was rather slow and did not result in substantial changes in the gendered division of activities and subsistence strategy. Such a transition would result in a stable bilateral pattern of mechanical loading in upper limb morphology during the Late Eneolithic and Early Bronze Age. We test the hypothesis via the documentation of humeral asymmetry focusing on humeral length, distal articular breadth, and cross-sectional geometry. We investigate both temporal changes and differences in the bilateral asymmetry between females and males in both periods.

MATERIALS AND METHODS

Sample

A sample of 67 individuals with both right and left preserved humeri was selected from Late Eneolithic and Early Bronze Age skeletal material (Table 1). The Late Eneolithic sample includes sites of the Corded Ware and Bell Beaker cultures, and the Early Bronze Age sample

includes sites of the Únětice, Unterwölbling, and Wieslburger cultures. All of these sites are located in Lower Austria, Moravia, and Bohemia (Fig. 1, see also definitions of the archeological cultures and details about selected sites in Buchvaldek, 1986; Teschler-Nicola, 1992; Shennan, 1993; Neugebauer, 1994).

Since the Central European Late Eneolithic cemeteries are characterized by small numbers of burials, the sample from the Late Eneolithic had to be selected from larger number of sites. We assume that for our purpose the individuals from different Late Eneolithic cemeteries can be studied as one population. The Corded Ware and Bell Beaker groups in Central Europe are considered to be closely related and share similar adaptive strategies and symbolic systems (Neustupný, 1981, 1989; Turek and Peška, 2001). There was also evidence for a certain degree of interaction visible in the temporal overlap of archaeological findings (Dvořák, 1992). Grave goods made from nonlocal materials and variation in ceramic style indicates that commodities were exchanged among communities in Central Europe. Moreover, stable isotope analyses have shown that individuals moved between regions (Price et al., 2004). Therefore, the Late Eneolithic communities in the Czech Republic and Austria were not isolated units.

The age structure of the samples stems from the observation that age is a significant factor that influences cross-sectional morphology (Ruff, 2000a). Only mature individuals were used in this study. The interval for age allocation spans from individuals with complete fusion of long bone epiphyses or closure of the sphenooccipital suture to individuals without marks of advanced degenerative and senescence features, such as tooth loss and significant alteration of articular surfaces. Therefore, these individuals were older than ~20 years at the time of death but younger than 50–60 years at the time of death. The latter

boundary is estimated with a higher degree of uncertainty because there is a low correlation between calendar age-at-death and skeletal traits after the process of ontogeny is completed (see review in Schmitt, 2004). Nonetheless, there is no observed shift in age-at-death among selected samples. Therefore, if any bias appears because of inappropriate older age boundary, it will affect all samples equally.

The sex of the individuals was estimated through assessment of the pelvis, femora, tibiae, and humeri using primary and secondary sex analyses (Murail et al., 1999; see details in Sládek et al., 2006a). The primary sex assessment was done by metric (Novotný, 1975; Brůžek, 1984) and morphological assessment (Bruzek, 2002) of the pelvic bones. Forty-one individuals from the total Late Eneolithic and Early Bronze Age sample ($n_{\text{total}} = 171$) were sexed by means of primary analysis. Fourteen discriminant functions were selected for the secondary sex analysis. The correct classification of the secondary discriminant functions ranges between 89 and 99% of the primary allocated individuals. The final decision for sex allocation was based on the consistency between the results of primary and secondary analyses. If only the data for the secondary discriminant function were available, the allocation was based on the majority of allocations embodied in posterior probabilities of the discriminant functions. If agreement between the selected parameters was not reached, the sex of the individual was allocated as undetermined. Since we are interested in the gender-specific pattern of humeral asymmetry, the undetermined individuals were not used in the study.

Linear and cross-sectional parameters

Distal articular breadth and humeral biomechanical length were used to compare the bilateral asymmetry of external humeral morphology. Distal articular breadth was taken following the standard osteometric approach (Hu4, Bräuer, 1988). The humeral biomechanical length was taken between the most proximal point on the humeral head to the most distal point on the lateral lip of the trochlea (Ruff, 2000b).

Humeral shaft sections were taken at 35% of humeral biomechanical length by CT scan images. Prior to scanning, each bone was oriented in a standardized position with respect to the antero-posterior and medio-lateral planes following an approach specified by Ruff (2000b). The CT scan images were taken by CT HiSpeed Dxi (General Electric, Milwaukee, WI) at 120 kV. Final CT scan images consist of 1-mm-thick slices with a resolution of 512×512 pixels with a pixel dimension of 0.196 mm.

The CT scan images of 35% humeral cross-sections were further processed using the software for digitizing and computing biomechanical parameters previously developed by our team (CT-i software, Sailer et al., 2003). The CT-i software is a Borland Delphi implementation and calculates all biomechanical parameters by manually set points in the periosteal and endosteal contours. These points are free of scanning bias due to the composition and preservation of cortical bone tissues. Furthermore, we have shown that the inter- and intra-observer error that occurs during the manual determination of bone outlines does not significantly affect further computer analysis (Sailer et al., 2003).

Cross-sectional geometry of humeral diaphyses was estimated by CT-i values of areas, second moments of area, and polar moment of area. Cortical area (CA) estimates cross-sectional rigidity in axial compression and tension

(Larsen, 1999; Ruff, 2000a). Maximum second moment of area (I_{max}) and the one perpendicular to it (I_{min}) were used to evaluate resistance to bending rigidity (Larsen, 1999; Ruff, 2000a). Consequently, the polar moment of area (J), as a sum of any two second moments of area perpendicular to each other, was used to estimate torsional rigidity (Levenstone et al., 1994; Larsen, 1999; Ruff, 2000a) and overall bending strength. The polar moment of area has also been shown to be a good estimate of skeletal robusticity (Ruff et al., 1993). Finally, the ratio of $I_{\text{max}}/I_{\text{min}}$ was used to compare diaphyseal shape (Larsen, 1999; Ruff, 2000a).

Humeral asymmetry and statistical treatment

Two patterns of deviation from symmetry were used following Van Valen's (1962) approach: a) directional asymmetry may occur when the normal development of bilateral character is shifted to one side from an expected line of equivalence; b) fluctuating asymmetry may result from stochastic fluctuation of bilateral character around line of equivalence.

Therefore, humeral maximum asymmetry was first computed with respect to the larger side and expressed as a percentage:

$$\text{maximum asymmetry} = [(\text{max} - \text{min})/\text{min}] * 100$$

Max refers to side with maximum value and min to side with minimum value. Zero indicates bilateral symmetry, and an increasing deviation from zero describes the magnitude of bilateral asymmetry. Since the degree of maximum asymmetry is expressed without respect to side, its distribution is skewed (see Trinkaus et al., 1994). Therefore, nonparametric treatment and graphs of medians were used. Medians and 95% confidence intervals of medians were computed using the bootstrap procedure (Resampling Stats for Excel 2.0, Resampling Stats). Nonparametric Mann-Whitney U tests were employed to compare differences between samples both on the inter- and intra-specific level.

Second, humeral standardized asymmetry was computed using following formula and expressed as a percentage:

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

where R refers to the right side and L to the left side. The absolute values of the standardized asymmetry indicate absolute deviation from symmetry. Tendency to the right is expressed in the standardized asymmetry by positive deviation from zero, tendency to the left by negative deviation. Since the distribution of standardized asymmetry is nearly normally distributed, parametric one-sample t tests were used.

Finally, fluctuating and directional asymmetry were visualized and tested also by the bivariate distribution of the right and left character. Since all studied parameters are measured with error, the reduced major axis model was used to compare the bivariate distribution (Kermack and Haldane, 1950; Clarke, 1980; McArdle, 1988; Aiello, 1992). The slope and intercept of the reduced major axis were computed with Software for Reduced Major Axis Regression (Bohonak, 2002) using the pooled Late Eneolithic and Early Bronze Age sample of the respective analysis. In addition to the reduced major axis, the line of expected right and left equivalence (the symmetry line) was projected to each bivariate distribution.

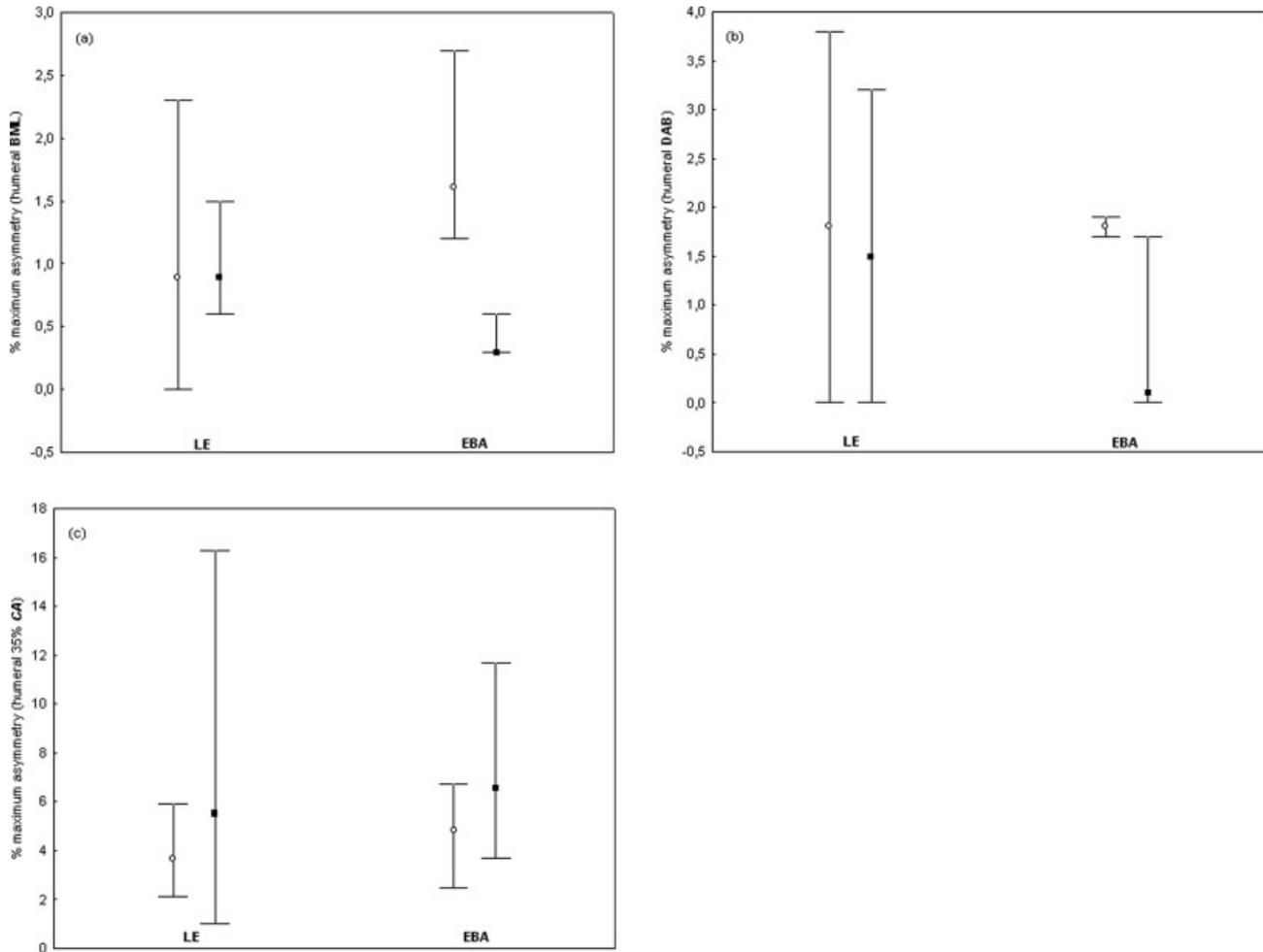


Fig. 2. Median and 95% confidence interval for the percentage maximum asymmetry of humeral biomechanical length (BML) (a), distal articular breadth (DAB) (b), and cortical area (CA) (c) for the Late Eneolithic (LE) and Early Bronze Age (EBA) samples. Open circles: females; filled squares: males.

The Quick Test was employed to compare differences in distribution along the reduced major axis as well as the line of equivalence (Tsutakawa and Hewett, 1977). The Quick test is arranged as Fisher's Exact two-tailed test when the number of individuals above the respective axis is compared with the number of individuals below the axis. The null hypothesis is that either temporal sex-specific groups (interspecific level; comparison between temporal groups) or sex groups in each period (intraspecific level; comparison within temporal groups) have equal distribution along the respective axis. If equal distribution along the reduced major axis is reached, we expect that both groups will not exhibit significant differences in the level of asymmetry (either fluctuating or directional). Further, directional asymmetry was inferred from significant departure from an equal distribution along the line of symmetry. Fluctuating asymmetry was inferred from equal distribution around the line of equivalence.

The data for Fisher's Exact two-tailed test were prepared in Excel tables and further processed with the StatXact 6.1 software (Cytel Software Corporation, 1989–2002). The advantage of StatXact 6.1 software is the computation of exact values instead of an approximation by asymptotic values (Mehta and Patel, 1999). Unless otherwise specified,

Excel 2003 (Microsoft Corporation, 1985–2003) and Statistica 6.0 (StatSoft, 1984–2001) were used for basic computation and statistical treatment.

RESULTS

Temporal differences

Temporal differences between the Late Eneolithic and Early Bronze Age were compared at the interspecific level when both sexes were processed separately. The percentage of maximum asymmetry of humeral external measurements and 35% humeral cross-sectional parameters for the sex-specific samples of the Late Eneolithic and Early Bronze Age are shown in Figures 2 and 3. The resultant *P*-values of the Mann-Whitney *U* test for the interspecific temporal differences are provided in Table 2. The summary for median and 95% confidence interval of percentage asymmetry of I_{\max}/I_{\min} is in Figure 4. The Late Eneolithic and Early Bronze Age females are not significantly different in the percentage maximum asymmetry of the humeral external measurements and 35% humeral cross-sectional parameters including the I_{\max}/I_{\min} ratio. The Late Eneolithic males have a significantly higher

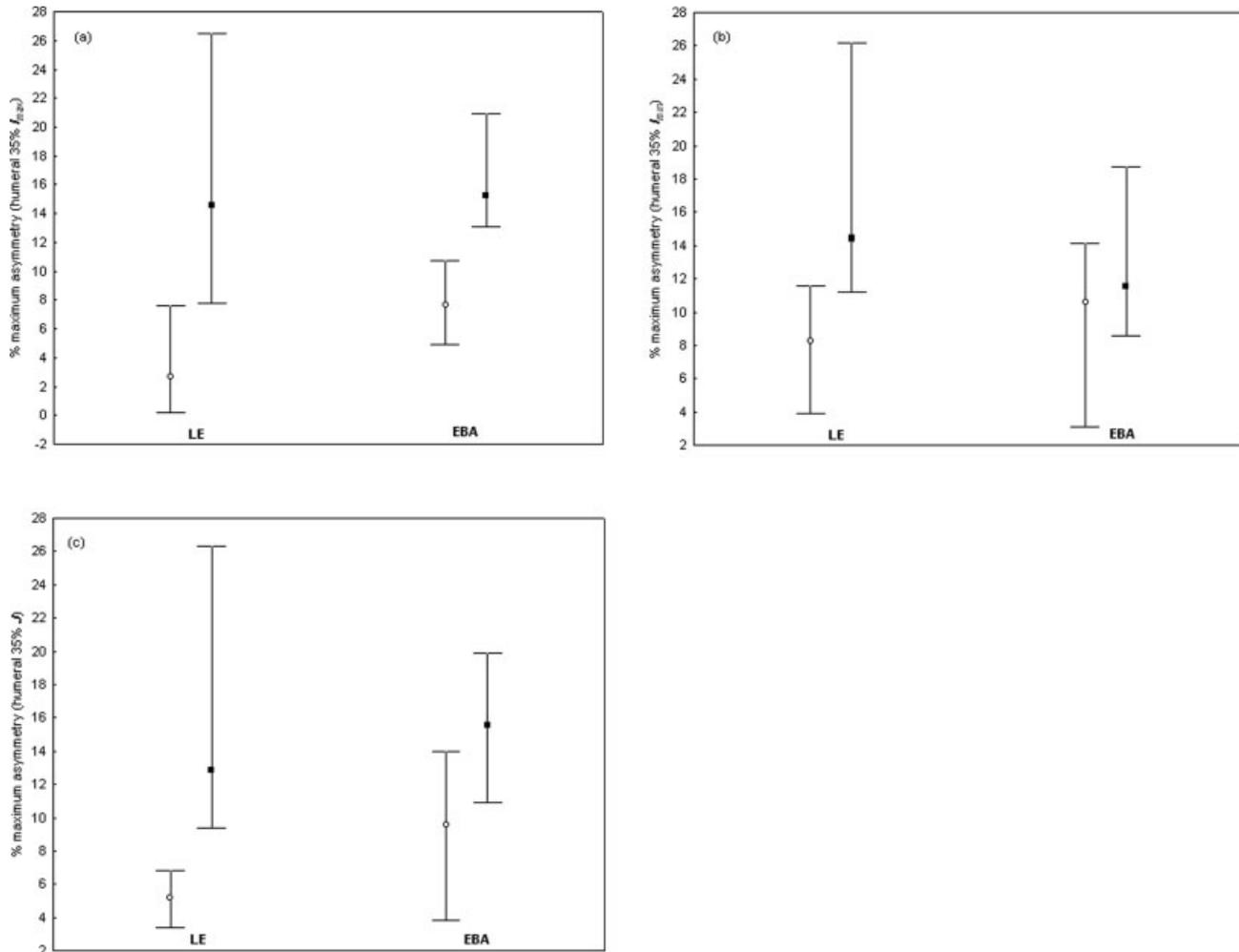


Fig. 3. Median and 95% confidence interval for the percentage maximum asymmetry of maximum second moment of area (I_{max}) (a), minimum second moment of area (I_{min}) (b), and polar moment of area (J) (c) for the Late Eneolithic (LE) and Early Bronze Age (EBA) samples. Open circles: females; filled squares: males.

percentage of maximum asymmetry of humeral biomechanical length in comparison to the Early Bronze Age males. All other parameters including the diaphyseal shape estimate between the male temporal groups remain statistically nonsignificant.

The bivariate distribution of the right and left sides of humeral biomechanical length and 35% humeral cross-sectional parameters, and the results of Quick tests are given in Figures 5–7. Quick tests and temporal comparison is further proceeded using a pooled sample line (the RMA line) and the expected line of symmetry (i.e., the line of the right and left equivalence). As in the previous comparison, the Late Eneolithic and Early Bronze Age distribution of asymmetry remains statistically nonsignificant in comparison to the pooled RMA line. Both female samples have directional asymmetry significantly shifted to the right side in humeral biomechanical length, but fluctuating asymmetry in cortical area and polar moment of area. The comparison based on distal articular breadth also yields fluctuating asymmetry. Similarly, there is not a significant difference in the distribution asymmetry for any external and cross-sectional parameters between the Late Eneolithic and Early Bronze Age males (i.e., RMA comparison). Thus, the Quick test for the RMA analysis

and Mann-Whitney U test produced different results when humeral biomechanical length of male humeri was compared. The male samples have fluctuating asymmetry in humeral biomechanical length and distal articular breadth, but present directional asymmetry to the right side in cortical area and polar moment of area.

We conclude that there are nonsignificant differences between the Late Eneolithic and Early Bronze Age groups in the interspecific comparison. Therefore, the bilateral pattern of manipulative behavior remains stable during both periods. The only contradictory result has been found in the case of the male humeral biomechanical length: the differences between the Late Eneolithic and Early Bronze Age males' yields significant results when Mann Whitney U test is employed but nonsignificant results in the RMA bivariate distribution analysis.

Sex differences

The sex-specific comparison within the Late Eneolithic and Early Bronze Age groups has been applied to reveal differences in sexual dimorphism in the bilateral activities of manipulative behavior. The P -values for the within-

TABLE 2. The *P*-values of Mann-Whitney *U* test for comparisons between the percentage maximum asymmetry distribution for the humeral external measurements and 35% cross-sectional parameters¹

Parameter ²	Temporal differences		Sex dimorphism differences	
	F (LE/EBA)	M (LE/EBA)	LE (F/M)	EBA (F/M)
Hu-BML	0.178	0.013*	0.791	0.001***
Hu-DAB	0.962	0.682	0.666	0.056
CA	0.534	0.616	0.773	0.173
I_{\max}	0.158	0.711	0.028*	0.002**
I_{\min}	0.701	0.444	0.056	0.232
<i>J</i>	0.22	0.913	0.013*	0.015*

¹ See Table 1 for the abbreviations concerning the sample. The significance is indicated by *($P < 0.05$), **($P < 0.01$), ***($P < 0.001$).

² Hu-BML, humeral biomechanical length; Hu-DAB, humeral distal articular breadth; CA, cortical area; I_{\max} , maximum second moment of area; I_{\min} , minimum second moment of area; *J*, polar moment of area. Humeral biomechanical length and distal articular breadth are in mm, bone areas are in mm², and second moments of area are in mm⁴.

group differences in the percentage maximum asymmetry are shown in Table 2. The median and 95% confidence interval for the I_{\max}/I_{\min} and Figure 4. The Late Eneolithic males show greater percentage in maximum asymmetry than females only for maximum second moment of area and polar moment of area. The same comparison in the Early Bronze Age sample has yielded similar results. The Early Bronze Age males show significantly higher percentage in maximum asymmetry than females for maximum second moment of area and polar moment of area. A significantly different percentage of maximum asymmetry has been identified also in humeral biomechanical length between Early Bronze Age males and females. There are no significant differences in 95% confidence interval for median of diaphyseal shape of the I_{\max}/I_{\min} ratio between sex-specific groups.

Differences in sexual dimorphism between the two periods can be revealed also from the RMA bivariate distribution of the humeral biomechanical length and cross-sectional parameters presented in Figures 5–7. In both periods, females show fluctuating asymmetry in all cross-sectional parameters studied. However, both Late Eneolithic and Early Bronze Age females are significantly shifted from the line of symmetry when humeral biomechanical length is compared. Males show fluctuating asymmetry in humeral biomechanical length, but have directional asymmetry shifted to the right for cortical area and polar moment of area in both periods.

The statistically insignificant difference in the pattern of sexual dimorphism between the Late Eneolithic and Early Bronze Age is supported by the bivariate distribution of the mean difference in standardized asymmetry between sexes for each time period shown in Figure 8. Mean difference between males and females was computed by 1,000 iterations of difference between bootstrap means of percentage standardized asymmetry for females and males. The differences between sexes mean difference estimates is not significant when 95% confidence intervals are compared. The Early Bronze Age confidence interval of sex mean difference is shorter mainly in the cortical area and polar moment of area asymmetry, but this may reflect the larger sample size for the Early Bronze Age group. Thus, there is no significant difference between males and females in the selected temporal groups.

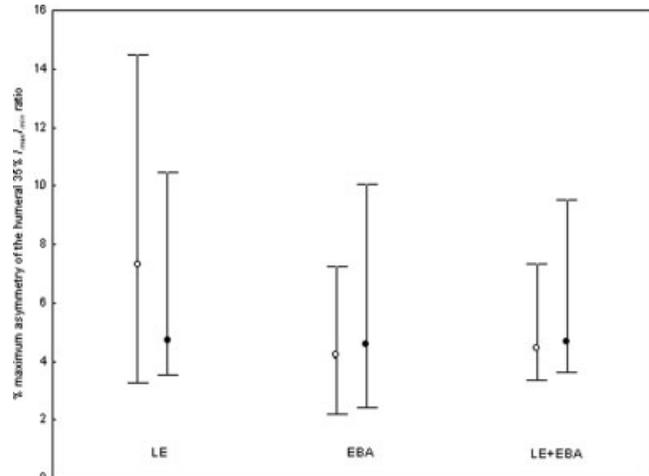


Fig. 4. Median and 95% confidence interval of the percentage maximum asymmetry of the I_{\max}/I_{\min} ratio for the Late Eneolithic (LE), Early Bronze Age (EBA), and combined (LE+EBA) groups. Open circles: females; filled squares: males. Median and confidence intervals of median are given as a bootstrap estimate. See Tables 1 and 2 for the additional abbreviations.

Finally, one-sample *t* tests of mean standardized asymmetry compared to the zero (i.e., symmetry) are provided in Table 3. Females are significantly different from zero in humeral biomechanical length, while males show significant difference from zero in the cross-sectional parameters.

We conclude that females in both periods are characterized by manipulative behavior with equally distributed mechanical loading between the right and left arm but show directional asymmetry in humeral biomechanical length. Manipulative behavior of males in both periods is characterized by higher mechanical loading on the right side while showing fluctuating asymmetry of the external humeral measurements. However, asymmetry in diaphyseal shape remains similar among both males and females.

DISCUSSION

The results indicate that the pattern of asymmetry of the humeral external measurements and 35% of the cross-sectional parameters remain stable during the Late Eneolithic and Early Bronze Age transition. At the same time, the pattern of sexual dimorphism in humeral asymmetry remains stable too. A significant difference was found when the pattern of humeral asymmetry was compared between females and males. Females of both periods have fluctuating asymmetry for all of the cross-sectional parameters, but exhibit directional asymmetry for biomechanical length. Males are nonsignificantly shifted from the line of equivalence for biomechanical length but exhibit directional asymmetry for the cortical area and polar moment of area. Only distal articular breadth yields fluctuating asymmetry for both females and males. Also the measurements of diaphyseal shape (the I_{\max}/I_{\min} ratio) show no significant differences between males and females.

The results demonstrate that the economic and social changes that happened during the transition from the Late Eneolithic to Early Bronze Age (Childe, 1930; Neugebauer, 1994; Harding, 2000; Batora, 2002) had a minor impact on the bilateral asymmetry of manipulative behavior. Given the fact that no significant difference in mechanical loading between the Late Eneolithic and Early Bronze

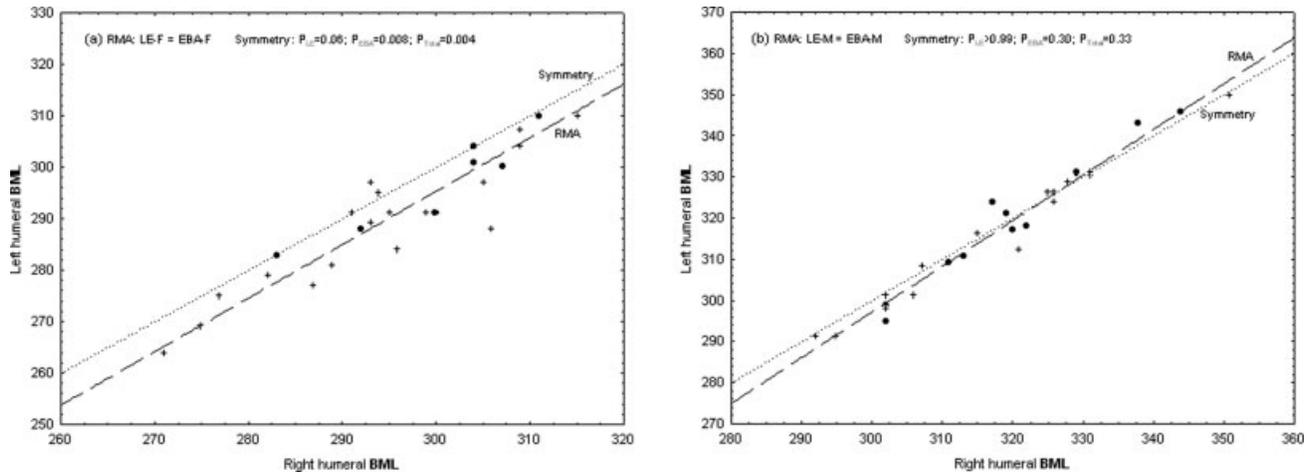


Fig. 5. The bivariate plots of the right versus left humeral biomechanical length (BML) in female (a) and male sample (b). Filled circles: the Late Eneolithic; crosses: the Early Bronze Age group. Reduced major axis (RMA) through the pooled sample and line of expected right and left equivalence (symmetry) presented; results of Quick Test comparisons about both lines shown.

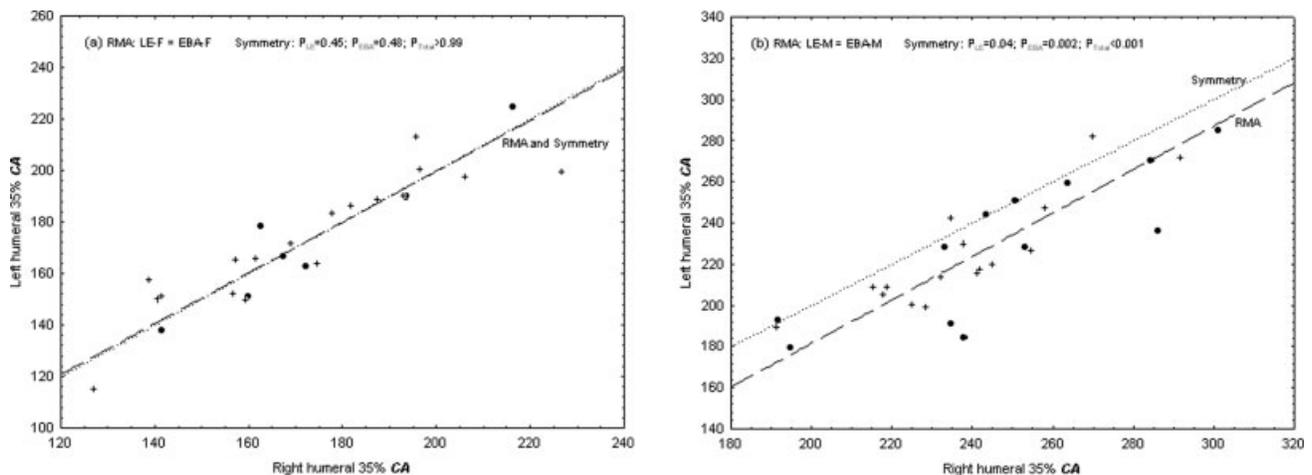


Fig. 6. The bivariate plots of the right versus left 35% humeral cortical area (CA) in female (a) and male sample (b). Filled circles: the Late Eneolithic; crosses: the Early Bronze Age group. See Figure 5 for description and computation details.

Age has been found also when lower limb cross-sections were compared (Sládek et al., 2006a,b), we propose that the transition was rather continuous from the perspective of daily physical activities (i.e., manipulative and locomotor).

The low impact of economic and social changes on bilateral activities in manipulative behavior during the transition from the Late Eneolithic to the Early Bronze Age is also apparent in the pattern of sex differences. During both periods, the sex differences in asymmetry remain identical. The geometric properties of humeri are symmetrical among females but directionally asymmetrical among males. According to the expectations that cross-sectional parameters are highly sensitive to mechanical loading (Trinkaus et al., 1994), we can hypothesize similar gender-specific physical tasks for females and males during both periods.

Similar patterns of gender-specific differences in physical tasks are reported from other archaeological settings. It has been demonstrated (Bridges, 1985, 1989, 1991; Fresa et al., 1990) that directional asymmetry of humeral geometry decreased significantly after the transition to

agriculture in Southeastern United States among females, while directional asymmetry remained relatively unchanged among males. The authors argue that fluctuating asymmetry among females is influenced by female participation in agricultural activities associated with food preparation or other tasks that required the use of both arms. At the same time, the association of directional asymmetry with agriculture among males was questioned. Males were associated with activities, such as hunting, which was practiced even after the transition to food production (see review in Bridges, 1991).

Despite the shared similarities in the distribution of humeral cross-sectional asymmetry between American Southeastern populations at the time of transition to agriculture and the Central European populations at the time of the transition to the Bronze Age, the interpretation of the results must account for the different socio-economic contexts of both phenomena. It is apparent that agriculture in the Late Eneolithic and Early Bronze Age was more developed than the early agriculture in the Southeastern US. Therefore, it remains uncertain whether the

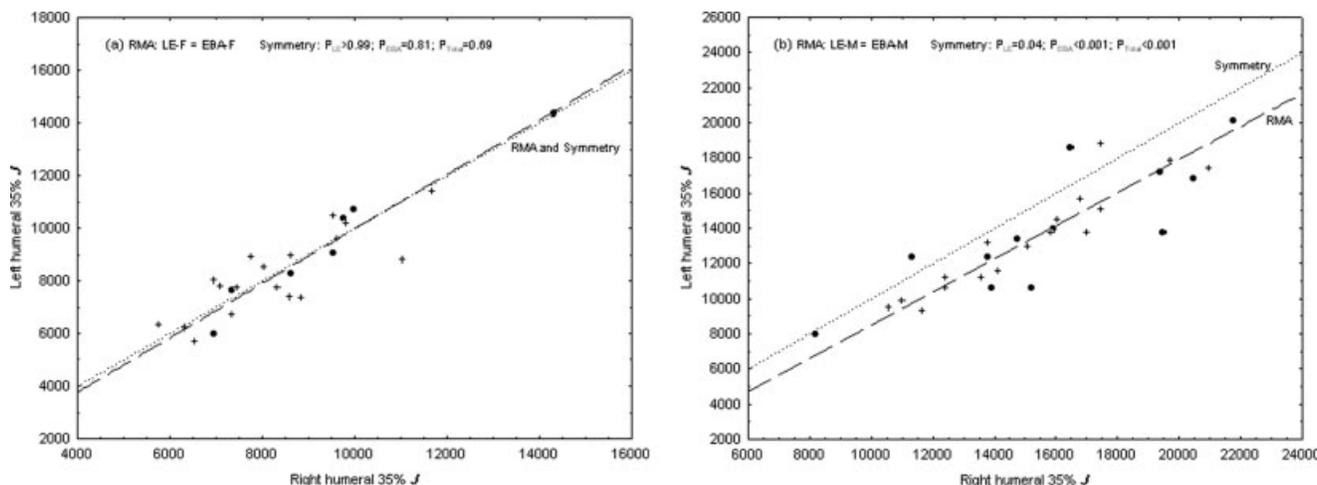


Fig. 7. The bivariate plots of the right versus left 35% humeral polar moment of area (J) in female (a) and male sample (b). Filled circles: the Late Eneolithic; crosses: the Early Bronze Age group. See Figure 5 for description and computation details.

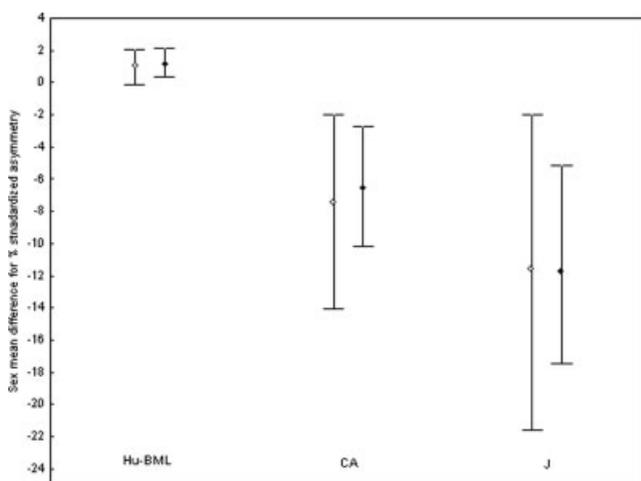


Fig. 8. The sex mean difference and 95% confidence interval for percentage standardized asymmetry differences between the Late Eneolithic and Early Bronze Age. The parameters were estimated using the bootstrap technique (number of iterations = 1,000). Open diamonds: the Late Eneolithic; filled diamonds: the Early Bronze Age. Hu-BML, humeral biomechanical length; CA, cortical area; J, polar moment of area.

Late Eneolithic and Early Bronze Age agriculture had a low impact on the life ways of males, and whether females had to participate more than males in agricultural activities.

The archaeological record in Europe indicates that the Late Eneolithic and Early Bronze Age societies used intensive techniques of farming and that hunting probably played minor role in their subsistence. [Intensive agriculture is understood broadly as any activity that increases yield per hectare (Burton and White, 1984)]. The minor role of hunting is inferred from the low frequency of wild animal remains in the Late Eneolithic and Early Bronze Age (ca. 10–15%, Neustupný, 1969; Furmánek et al., 1991; Harding, 2000). The intensive agriculture is inferred from evidence of wooden yokes from Bronze Age sites (Harding, 2000). Since full pastoralism was rejected in the Late Eneolithic based on the cross-sectional analysis of the lower limbs (Sládek et al., 2006a,b), it is clear that cultivation

was practiced during the Late Eneolithic as well. The use of intensive form of agriculture during the Eneolithic is also supported by evidences of furrows, models of oxen, and buried pairs of oxen (Neustupný, 1969; Sherratt, 1983). Thus, to explain the differences in asymmetry of upper limbs between males and females of the Late Eneolithic and Early Bronze Age, we have to compare differences in gender roles among societies with intensive agriculture.

It has been shown that the participation of females in agriculture decreases with increasing intensification (Boserup, 1970; Martin and Voorhies, 1975; Ember, 1983) because of differential physical abilities for plowing (Murdock and Provost, 1973), incompatibility of plowing with childcare (Brown, 1970), or an increase in the domestic work for females (Ember, 1983; Burton and White, 1984). Based on the differences in gender roles among the ethnographic groups with intensive agriculture and asymmetry in humeral cross-sections we expect that the Late Eneolithic and Early Bronze Age females might have been closely tied to the domestic sphere, while males might have prepared the soil and used animals for traction in the fields. Thus, in the Late Eneolithic and Early Bronze Age males were probably more closely associated with extradomestic agricultural labor that probably resulted in asymmetrical manipulative loading, and females with domestic labor with symmetrical manipulative loading. However, the identification of particular activities responsible for the observed pattern of asymmetry would be speculation at the moment.

Our findings do not support the supposed changes in gender relations during the transition from the Late Eneolithic to the Early Bronze age (Shennan, 1993). It appears more likely that the decrease in gender differences in the Bronze Age, suggested by Shennan (1993), is shaped by the specific nature of the burial record rather than everyday activities in the Early Bronze Age. Relatively weak gender symbolism may reflect ideology inscribed in mortuary rituals and the value that was given to activities performed by men and women. As our results indicate, the activities themselves did not change during the transition.

Distal articular breadth did not show gender specific differences and has fluctuating asymmetry among both females and males. The result was consistent in all performed analyses. Thus, factors that influenced asymmetry in distal articular breadth remain stable during the Late

TABLE 3. Percentage standardized asymmetry for the humeral external measurements and 35% cross-sectional parameters of the combined Late Eneolithic and Early Bronze Age sample¹

Parameter	Females				Males			
	N	Mean	SD	<i>t</i> test ²	N	Mean	SD	<i>t</i> test ²
Hu-BML	24	1.56	1,557	4,900***	26	0.35	1,099	1,643
Hu-DAB	28	-0.16	2,623	-0.321	24	0.73	2,400	1,492
CA	25	-0.05	6,164	-0.044	29	7.01	6,975	5,413***
<i>I</i> _{max}	25	0.39	9,768	0.201	29	13.06	11,911	5,904***
<i>I</i> _{min}	25	1.91	12,960	0.738	29	12.49	11,557	5,820***
<i>J</i>	25	1.06	10,195	0.519	29	12.78	10,833	6,351***

¹ See Table 1 and 2 for the abbreviations.

² One-sample *t* test for sample mean significant difference from zero (i.e. symmetry). The *P*-value significance is indicated by ***(*P* < 0.001).

Eneolithic and Early Bronze Age and the asymmetry in distal articular breadth is not a useful estimate of differences in manipulative loading during the transition. This is in agreement with previous findings of the minimum effect of mechanical loading on the bilateral asymmetry of articular breadth (Trinkaus et al., 1994). In contrast to humeral length, we can expect that ontogenetic formation of distal articular breadth is less environmentally modifiable (Lieberman et al., 2001; Ruff, 2003), which remains stable during the Late Eneolithic and Early Bronze Age transition.

The results of the biomechanical length asymmetry measurements indicate several contradictions. The Late Eneolithic and Early Bronze Age female sample has directional asymmetry for humeral biomechanical length, but males have fluctuating asymmetry. However, it is not easy to interpret behavior from these results as in the case of the biomechanical properties of cross-sections. There are contradictions regarding environmental versus genetic impacts on the length asymmetry. Trinkaus et al. (1994) argued that the mechanical environment would have a low impact on the length asymmetry. Ruff's (2003) study of age changes in humans and baboons showed that changes in length proportions did not reflect behavioral events. In other words, limb length is not affected by the mechanical environment but by genetic factors. On the contrary, Steele and Mays (1995) found that adult humeri present significantly different directional asymmetry to the right in a study of human upper limb asymmetry. They suggest that asymmetry of the upper limb is well explained by the effect of mechanical loading related to handedness.

If mechanical effect is the most parsimonious explanation for length asymmetry differences between males and females, we expect that the mechanical effect would influence other measures of the longitudinal loading. Asymmetry in cortical area can be used to estimate the pattern of longitudinal (i.e., axial) loading.¹ Therefore, the assumption of mechanical impact on length asymmetry must be supported in the Late Eneolithic and Early Bronze Age female sample by directional asymmetry in cortical area. On the other hand, to explain the fluctuating asymmetry

of humeral length in the male sample, we would expect that cortical area also fluctuates around the line of equivalence. The bivariate comparison of right and left cortical area indicates that this is not true for males and females (Fig. 6). The Late Eneolithic and Early Bronze Age females have fluctuating asymmetry in cortical area, but males have directional asymmetry shifted to the right.

The minor effect of mechanical loading on humeral length asymmetry is also supported by the comparison of absolute values between asymmetry of humeral length and cross-sectional parameters (Table 3). The absolute difference between mean standardized asymmetry for humeral length of females and males is about 10 times smaller than the absolute differences between means of cross-sectional parameters. A similar degree of difference has been found when humeral asymmetry was studied after long-term tennis loading both in humeral length and section modulus (Table 5 of Haapasalo et al., 1996). Moreover, the deduced minor effect of mechanical loading is consistent with the nonsignificant difference in the asymmetry of humeral length in long-term tennis players (Haapasalo et al., 1996).

In contrast to our results, Steele and Mays (1995) did not find significant differences between females and males in their comparison of asymmetry of humeral length. On the contrary, Schultz (1937) showed that both females and males are asymmetrical in their humeral length, but that females are more frequently directionally asymmetrical. Given the sex specific differences in humeral length asymmetry for the Late Eneolithic and Early Bronze Age, it is hard to expect that such an inconsistent pattern between fluctuating and directional asymmetry of length is found when only pure genetic control operates.

Therefore, we suggest that length asymmetry in the Late Eneolithic and Early Bronze Age underwent some kind of environmental impact. This environmental impact varied with behavioral differences but was only weakly associated with mechanical loading. We hypothesize that such nonmechanical environmental factors affect growth, as suggested by Albert and Greene (1999). They demonstrated that the overall environmental stress might produce length asymmetry primarily due to the high sensitivity of epiphyseal union. In addition, since Albert and Green (1999) did not find significant differences between females and males, they concluded that this environmental perturbation has similar impact on males and females. Given our results, we expect that at least in the Late Eneolithic and Early Bronze Age, this environmental perturbation was sex-specific. Since little is known about the skeletal features connected with environmental stress and deprivation during ontogeny in the Late Eneolithic and Early Bronze Age, it is difficult to discuss it in more detail here.

¹Cortical area does not seem to be entirely relevant for biomechanical parameters since it is highly influenced by other nonmechanical factors (i.e., aging, diet, etc.) (see review in Larsen, 1999; Ruff, 2000a; Lovejoy et al., 2002). However, these nonmechanical factors are partly adjusted in the asymmetry comparison since they have to operate on both arms equally (Trinkaus et al., 1994). Given the consistent results between cortical area and other relevant biomechanical measures for the asymmetry comparison in the Late Eneolithic and Early Bronze Age female and male samples, the cortical area seems to be a useful parameter in this study for association with axial loading.

CONCLUSION

The following conclusion can be drawn from our results:

1. There is nonsignificant change in the asymmetry of humeral external measurements and geometric properties of humeri between the Late Eneolithic and Early Bronze Age. Therefore, both temporal groups have similar bilateral patterns of manipulative behavior. We assume that the transition between the Late Eneolithic and Early Bronze Age was gradual and probably affected only part of the socio-economic organization.
2. The only exception from the above statement is the result of the asymmetry of the biomechanical length when males of the Late Eneolithic and Early Bronze Age are compared. There is significant difference between the males of both periods when the Mann-Whitney *U* test is used. However, the finding is not supported by Quick test for the RMA analysis and the significance could be influenced by sample size.
3. There are significant differences in the asymmetry of humeral external measurements and geometric properties of humeri when sex is considered. Females and males of the Late Eneolithic and Early Bronze Age exhibit sex specific bilateral activity in manipulative behavior, which indicates continuity from the Late Eneolithic to the Early Bronze Age. This finding does not support temporal shifts in gender relations elucidated using the burial record.
4. Females do not have directional asymmetry in the geometric properties of cross-sections, suggesting that loading was equally distributed between the dominant and nondominant arms. These findings are in agreement with other studies of gender-specific activities during the adoption of agriculture. However, we interpret this result as a reflection of intradomestic activities of females in the Late Eneolithic and Early Bronze Age associated with intensive agriculture.
5. Males have directional asymmetry shifted to the right arm when biomechanical properties of cross-sections are compared. Thus, males continue to perform those physical activities that produce bilateral asymmetry in manipulative behavior. Since hunting is less likely for the Late Eneolithic and the Early Bronze Age, we expect that males of both periods were not excluded from agricultural activities. Given the intensive nature of agriculture for the Late Eneolithic and the Early Bronze Age, males are viewed in the sphere of extra-domestic activities producing bilateral asymmetry of humeral biomechanical parameters.
6. Females have directional asymmetry in biomechanical length of humeri shifted to the right, and males have fluctuating asymmetry without a clear shift to either side. It is difficult to present a behavioral conclusion for the length asymmetry comparison. Given the asymmetry of biomechanical properties of humeri, we assume that mechanical loadings had a minor impact on the variability of asymmetry. However, genetic factors are not clearly supported by our data. Therefore, the length asymmetry can be best explained by either nonmechanical environmental factors or by some kind of relationship between genetic, mechanical, and nonmechanical factors.
7. Comparisons of distal articular breadth did not indicate either temporal or sex specific differences. Therefore, we assumed that the breadth of humeral articular surfaces shows little importance for the reconstruction of behavioral differences in the Late Eneolithic and Early Bronze Age.

ACKNOWLEDGMENTS

We are grateful to Miluše Dobisíková, Maria Teschler-Nicola, and Petr Velemínský for access to the Late Eneolithic and Early Bronze Age samples curated in the Naturhistorisches Museum in Vienna and Národní muzeum in Prague and for their help with several questions concerning the samples. The CT scanning was completed with support of Wolfgang Henninger and Martin Konar from the Institute of Radiology, Veterinärmedizinische Universität Wien. We are grateful to Chris B. Ruff for comments on several parts of the manuscript and Kristin Kozelsky helped with the correction of English manuscript. We would also like to thank Vladimír Blažek, Ivo T. Budil, Michael Estl, Patrik Galeta, Peter Stadler and Jan Zima for their comments.

LITERATURE CITED

- Aiello LC. 1992. Allometry and the analysis of size and shape in human evolution. *J Hum Evol* 22:127–147.
- Albert AM, Greene DL. 1999. Bilateral asymmetry in skeletal growth and maturation as an indicator of environmental stress. *Am J Phys Anthropol* 110:341–349.
- Annett M. 1992. Parallels between asymmetries of *planum temporale* and of hand skill. *Neuropsychologia* 30:624–630.
- Bátora J. 1991. The reflection of economy and social structure in the cemeteries of the Chlopice-Veselé and Nitra Cultures. *Slovenská Archeologia* 39:91–142.
- Bátora J. 2002. Contribution to the problem of craftsmen graves at the end of Aeneolithic and in the Early Bronze Age in Central, Western and Eastern Europe. *Slovenská Archeologia* 50:179–228.
- Bohonak AJ. 2002. RMA: software for reduced major axis regression. San Diego: San Diego State University.
- Boserup E. 1970. Women's role in economic development. New York: St. Martin's.
- Brauer G. 1988. *Antropologie: handbuch der vergleichenden biologie des menschen I*. Stuttgart: Fischer Verlag.
- Bridges PS. 1985. Changes in long bone structure with transition to agriculture: implication for prehistoric activities, Ph.D. thesis, University of Michigan, Ann Arbor.
- Bridges PS. 1989. Changes in activities with the shift to agriculture in the southeastern United States. *Curr Anthropol* 30:385–394.
- Bridges PS. 1991. Skeletal evidence of changes in subsistence activities between the Archaic and Mississippian time periods in northwestern Alabama. In: Powell ML, Bridges PS, Mires AMW, editors. *What mean these bones? Studies in southeastern bioarchaeology*. Tuscaloosa: University of Alabama Press. p 89–101.
- Brown JK. 1970. A note on the division of labor by sex. *Am Anthropol* 72:1073–1078.
- Brůžek J. 1984. Sexual dimorphism of human pelvic bone and hominid ontogeny and phylogeny, Ph.D. thesis, Charles University, Prague.
- Bružek J. 2002. A method for visual determination of sex using the human hip bone. *Am J Phys Anthropol* 117:157–168.
- Buchvaldek M. 1986. *Kultura se šňůrovou keramikou ve střední Evropě*. *Praehistorica* (Univerzita Karlova, Praha) 12:1–160.
- Burton ML, White DR. 1984. Sexual division of labor in agriculture. *Am Anthropol* 86:568–583.
- Childe VG. 1930. *The Bronze Age*. Cambridge: Cambridge University Press.
- Clarke MRB. 1980. The reduced major axis of a bivariate sample. *Biometrika* 67:441–446.
- Constandse-Westermann TS, Newell RR. 1989. Limb lateralization and social stratification in western European Mesolithic societies. In: Hershkovitz I, editor. *People and culture in change: British archaeological report*. (International series, 508). p 405–433.
- Dvořák P. 1992. *Die Gräberfelder der Glockenbecherkultur in Mähren I – Katalog der Funde*. Brno: Petr Dvořák Verlag.
- Ember CR. 1983. The relative decline in women's contribution to agriculture with intensification. *Am Anthropol* 85:285–304.

- Falk D. 1980. Language, handedness, and primate brains: did the Australopithecines sign? *Am Anthropol* 82:72–78.
- Fresia AE, Ruff CB, Larsen CS. 1990. Temporal decline in bilateral asymmetry of the upper limb on the Georgia coast. In: Larsen CS, editor. *The archaeology of Mission Santa Catalina de Guale, Part 2: Biocultural interpretations of a population in transition*. *Anthropological Papers of the American Museum of Natural History* 68. p 121–132.
- Furmánek V, Veliačik L, Vladár J. 1991. Slovensko v dobe bronzovej. Bratislava: Veda.
- Gilman A. 1981. The development of social stratification in Bronze Age Europe. *Curr Anthropol* 22:1–23.
- Haapasalo H, Sievanen H, Kannus P, Heinonen A, Oja P, Vuori I. 1996. Dimensions and estimated mechanical characteristics of the humerus after long-term tennis loading. *J Bone Miner Res* 11:864–872.
- Harding AF. 2000. *European societies in the Bronze Age*. Cambridge: Cambridge University Press.
- Holloway RL. 1981. Volumetric and asymmetry determinations on recent Hominid endocasts—Spy-I and Spy-II Djebel Lhroud-I, and the Sale Homo-Erectus specimens, with some notes on Neandertal Brain Size. *Am J Phys Anthropol* 55:385–393.
- Holt BM, Ruff CB, Trinkaus E. 2004. The Wolff's law debate: throwing out the water, but keeping the baby. *Am J Phys Anthropol* 123:115–116.
- Kadrow S. 2001. U progno nowej epoki: gospodarka i spoleczenstwo wczesnego okresu epoki brazu w Europie Srodkowej. Krakow: Instytut Archeologii i Etnologii Polskiej Akademii Nauk.
- Kermack KA, Haldane JBS. 1950. Organic correlation and allometry. *Biometrika* 37:30–41.
- Kristiansen K. 1998. *Europe before history*. Cambridge, England: Cambridge University Press.
- Larsen CS. 1999. *Bioarchaeology: interpreting behavior from the human skeleton*. Cambridge: Cambridge University Press.
- Ledger M, Holtzhausen L-M, Constatnt D, Morris AG. 2000. Biomechanical beam analysis of long bones from a late 18th century slave cemetery in Cape Town, South Africa. *Am J Phys Anthropol* 112:207–216.
- Lee RB. 1979. *The !Kung San. Men, women, and work in a foraging society*. Cambridge: Cambridge University Press.
- LeMay M. 1992. Left-right dissymmetry, handedness. *AJNR Am J Neuroradiol* 13:493–504.
- Levenstone ME, Beaupré GS, Van Der Meulen MCH. 1994. Improved method for analysis of whole bone torsion tests. *J Bone Miner Res* 9:1459–1465.
- Lieberman DE. 1996. How and why humans grow thin skulls: experimental evidence for systemic cortical robusticity. *Am J Phys Anthropol* 101:217–236.
- Lieberman DE, Devlin MJ, Pearson OM. 2001. Articular area responses to mechanical loading: effects of exercise, age and skeletal location. *Am J Phys Anthropol* 116:266–277.
- Lovejoy CO, Meindl RS, Ohman JC, Heiple KG, White TD. 2002. The Maka femur and its bearing on the antiquity of human walking: applying contemporary concepts of morphogenesis to the human fossil record. *Am J Phys Anthropol* 119:97–133.
- Marshall L. 1976. *The !Kung of Nyae Nyae*. Cambridge, MA: Harvard University Press.
- Martin KM, Voorhies B. 1975. *Female of the species*. New York: Columbia University Press.
- Mays S, Steele J, Ford M. 1999. Directional asymmetry in the human clavicle. *Int J Osteoarchaeol* 9:18–28.
- McArdle BH. 1988. The structural relationship: regression in biology. *Can J Zool* 66:2329–2339.
- Mehta C, Patel N. 1999. *StatXact 4 for Windows*. Cambridge MA: Cytel Software Corp.
- Murail P, Bruzek J, Braga J. 1999. A new approach to sexual diagnosis in past populations. Practical adjustments from Van Vark's procedure. *Int J Osteoarchaeol* 9:39–53.
- Murdock GP, Provost C. 1973. Factors in the division of labor by sex: a cross-cultural analysis. *Ethnology* 9:302–330.
- Neugebauer J-W. 1987. *Die Bronzezeit im Osten Österreichs*. St. Pölten: Niederösterreichisches Presshaus.
- Neugebauer J-W. 1994. *Bronzezeit in Ostösterreich*. St. Pölten – Wien: forschungsberichte der Ur- und Frühgeschichte, Wiss Schriftenreihe Niederösterreichs.
- Neustupný E. 1969. Economy of the corded ware culture. *Archeologické Rozhledy* 21:43–68.
- Neustupný E. 1981. Mobilität der äneolithischen populationen. *Slovenská Archeologia* 29:111–119.
- Neustupný E. 1989. Die Besiedlung Böhmens im Äneolithikum. *Praehistorica Das Äneolithikum und die früheste Bronzezeit (C14 3000–2000 B.C.) in Mitteleuropa: kulturelle und chronologische Beziehungen*. *Acta des XIV. Internationalen Symposiums Prag-Liblice* 20.-24.10.1986 15:81–84.
- Neustupný E. 1997. Šňůrová sídliště, kulturní normy a symboly. *Archeologické rozhledy* 49:304–322.
- Novotný V. 1975. Diskriminantanalyse der Geschlechtsmerkmale auf dem Os coxae beim Menschen. *Papers of the 13th Congress of Anthropologist Czechoslovakia*. Brno: Czech Anthropological Society. p 1–23.
- Plochocki JH. 2004. Bilateral variation in limb articular surface dimensions. *Am J Hum Biol* 16:328–333.
- Price TD, Knipper C, Grupe G, Smerka V. 2004. Strontium isotopes and prehistoric human migration: the Bell Beaker period in Central Europe. *Eur J Archaeol* 7:9–40.
- Rhodes JA, Knüsel CJ. 2005. Activity-related skeletal change in medieval humeri: cross-sectional and architectural alterations. *Am J Phys Anthropol* 128:536–546.
- Rubin C, Turner AC, Bain S, McLeod K. 2001. Low-level mechanical signals augment bone mass and cancellous architecture as dependent on frequency and duration of the stimulus. *J Bone Miner Res (Suppl)*15:427.
- Ruff CB. 2000a. Biomechanical analysis of archeological human skeletons. In: Katzenberg MA, Saunders SR, editors. *Biological anthropology of the human skeleton*. New York: Wiley. p 71–102.
- Ruff CB. 2000b. Body mass prediction from skeletal frame size in elite athletes. *Am J Phys Anthropol* 113:507–517.
- Ruff CB. 2003. Ontogenetic adaptation to bipedalism: age changes in femoral to humeral length and strength proportions in humans, with a comparison to baboons. *J Hum Evol* 45:317–349.
- Ruff CB, Trinkaus E, Walker A, Larsen CS. 1993. Postcranial robusticity in Homo. I. Temporal trends and mechanical interpretation. *Am J Phys Anthropol* 91:21–53.
- Ruff C, Holt B, Trinkaus E. 2006. Who's afraid of the big bad wolff? "Wolff's Law" and bone functional adaptation. *Am J Phys Anthropol* 129:484–498.
- Sailer R, Sládek V, Berner M. 2003. Computer tomography and calculation of bone biomechanics in cross-sections of long bones. *Am J Phys Anthropol* 120:182. (Abstract).
- Saxon LK, Turner CH. 2005. Estrogen receptor [β]: the antimechanostat? *Bone* 36:185–192.
- Schmitt A. 2004. Age-at-death assessment using the os pubis and the auricular surface of the ilium: a test on an identified Asian sample. *Int J Osteoarchaeol* 14:1–6.
- Schultz AH. 1937. Proportions, variability and asymmetries of the long bones of the limbs and the clavicles in man and apes. *Hum Biol* 9:281–328.
- Shennan SJ. 1975. The social organization at Branč. *Antiquity* 49:279–287.
- Shennan SJ. 1993. Settlement and social change in Central Europe. *J World Prehistory* 7:121–161.
- Shennan SJ. 1995. Bronze age copper producers of the Eastern Alps. *Excavations at St Veit-Klinglberg*. Bonn: Habelt.
- Sherratt A. 1983. The secondary exploitation of animals in the Old World. *World Archaeol* 15:90–104.
- Sládek V, Berner M, Sailer R. 2006a. Mobility in Central European Late Eneolithic and Early Bronze Age: femoral cross-sectional geometry. *Am J Phys Anthropol* 130:320–332.
- Sládek V, Berner M, Sailer R. 2006b. Mobility in Central European Late Eneolithic and Early Bronze Age: tibial cross-sectional geometry. *J Archaeol Sci* 33:470–482.
- Steele J, Mays S. 1995. Handedness and directional asymmetry in the long bones of the human upper-limb. *Int J Osteoarchaeol* 5:39–49.
- Stirland AJ. 1993. Asymmetry and activity related change in the male humerus. *Int J Osteoarchaeol* 3:105–114.

- Stock J, Pfeiffer S. 2001. Linking structural variability in long bone diaphyses to habitual behaviors: foragers from the Southern African Later Stone Age and the Andaman Islands. *Am J Phys Anthropol* 115:337–348.
- Stock J, Pfeiffer S. 2004. Long bone robusticity and subsistence behaviour among Later Stone Age foragers of the forest and fynbos biomes of South Africa. *J Archaeol Sci* 31:999–1013.
- Teschler-Nicola M. 1992. Untersuchungen zur Bevölkerungsbiologie der Bronzezeit in Ostösterreich. Phänetische Analyse kontinuierlicher und nichtkontinuierlicher Skelettmerkmale. Habilitationsschrift zur Erlangung der *venia legendi* thesis, Formal- und Naturwissenschaftlichen Fakultät der Universität Wien, Wien.
- Tihelka K. 1953. Moravská Únětická pohřebišť. *Památky archeologické* 44:229–315.
- Trinkaus E, Churchill SE. 1999. Diaphyseal cross-sectional geometry of near Eastern Middle Palaeolithic Humans: the humerus. *J Archaeol Sci* 26:173–184.
- Trinkaus E, Churchill SE, Ruff CB. 1994. Postcranial robusticity in Homo. II. Humeral bilateral asymmetry and bone plasticity. *Am J Phys Anthropol* 93:1–34.
- Tsutakawa RK, Hewett JE. 1977. Quick test for comparing two populations with bivariate data. *Biometrics* 33:215–219.
- Turek J, Peška J. 2001. Bell Beaker settlement pattern in Bohemia and Moravia. In: Nicolis F, editor. *Bell Beakers today. Pottery, people, culture, symbols in prehistoric Europe*. Trento: Proceedings of the International Colloquium Riva del Garda (Trento, Italy), 11–16 May 1998. p 411–428.
- Van Valen L. 1962. A study of fluctuating asymmetry. *Evolution* 16:125–142.
- Vencl S. 1994. K problému sídlišť kultury s keramikou šňůrovou. *Archeologické Rozhledy* 46:3–24.
- Weiss E. 2003. Understanding muscle markers: aggregation and construct validity. *Am J Phys Anthropol* 121:230–240.
- White LE, Lucas G, Richards A, Purves D. 1994. Cerebral asymmetry and handedness. *Nature* 368:196–197.