Mobility in Central European Late Eneolithic and Early Bronze Age: Femoral Cross-Sectional Geometry

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ABSTRACT Some scholars explain the absence of settlements in the Bohemian and Moravian Late Eneolithic (Corded Ware archaeological culture) as a consequence of pastoral subsistence with a high degree of mobility. However, recent archaeological studies argued that the archaeological record of the Late Eneolithic in Central Europe exhibits evidence for sedentary subsistence with mixed agriculture, similar to the subsequent Early Bronze Age. Because the archaeological data do not allow us to address unambiguously the mobility pattern in these periods, we used cross-sectional analysis of the femoral midshaft to test mobility directly on the human skeletal record. The results of femoral midshaft geometry do not support a high degree of mobility in the Late Eneolithic in Central Europe. This conclusion is supported mainly by no significant differences in male groups between the Late Eneolithic and Early Bronze Age in mechanical robusticity and shape of the femoral midshaft, although Corded Ware males still exhibit the highest absolute mean values of the diaphyseal shape (I A-P/I M-L) ratio and antero-posterior second moment of area. However, Late Eneolithic females have significantly higher torsional and overall bending rigidity because of a significantly higher medio-lateral second moment of area. This finding cannot be directly linked with a higher degree of long-distance mobility for these females. A significant difference was also found in overall decrease of size parameters of the femoral midshaft cross section for one of the Early Bronze Age samples, the Wieselburger females. Since the decrease of size and mechanical robusticity for Wieselburger females does not correspond with the parameters of Early Bronze Age females, we can expect a mosaic pattern of changes during the Late Eneolithic and Early Bronze Age period, instead of a simple unidirectional (diachronic) change of the mechanical environment. Am J Phys Anthropol 130:320–332, 2006. ©2006 Wiley-Liss, Inc.
to water sources (Rulf, 1981). Such environmental conditions are well-suited to agriculture. The location of sites does not differ from the environmental condition preferred by other well-documented agricultural groups of the Neolithic and Eneolithic (Rulf, 1981; Turek, 1995; Neustupný, 1997). In addition, evidence of agriculture in the Late Eneolithic is represented by finds of ploughing traces, specialized artifacts associated with agricultural activities, and impressions of cereal grains in the Corded Ware archaeological context (Neustupný, 1997). Finally, according to Neustupný (1997), the Corded Ware culture norm limits secular use of space to the horizontal direction, and uses the vertical axis only for symbolic expression, e.g., burial practices. Given that pits for house construction represent a secular activity, the culture norm generates the invisibility of Corded Ware settlements. However, some authors suggested a technical explanation for missing settlement features, because Corded Ware dwellings were built without the need of elements sunk under the surface (Shennan, 1993).

Given the arguments mentioned above, it seems that the nomadic strategy of the Corded Ware group can be questioned. However, ethnological and archaeological accounts show that the presence of either settlement features or finds usually associated with agricultural activities do not have to be in disagreement with a nomadic-pastoral subsistence and a higher degree of mobility in general (Gribb, 1991; Kelly, 1992; Panja, 2003). Mobility is not just a variable associated with a specific form of subsistence, and does not need to show a constant pattern across cultures and time periods (Kelly, 1992). Also, Gribb (1991) showed that the ethnographic record yields evidence of an association between mobility and agricultural activity, as well as pastoral activity with the sedentary mode.

Multiple archaeological criteria (e.g., settlement distribution, size and shape of houses, substantiality of houses, distribution of artifacts, ecofacts, and debris) are used to give meaning to the archaeological patterning when questions about mobility arise (see reviews and critiques of the archaeological approach to reconstructions of mobility in Wilk, 1983; Rafferty, 1985; Binford, 1987, 1990; Kelly, 1992; Panja, 2003). How can one test the mobility pattern of Late Eneolithic groups using archaeological data, when only the burial record is preserved?

The archaeology of the Late Eneolithic of Central Europe is predominantly based on burial evidence (Shennan, 1993), and reconstruction of life in the past is therefore shifted because of the nature of evidence that reflects a biased form of behavior embodied in mortuary rituals. It is surprising how little information has actually been extracted from human skeletal remains, i.e., evidence which is intimately related to the daily activities of prehistoric people.

It was demonstrated that a bone is a plastic tissue with the capability of adaptive answers to short- and long-term environmental stimuli (reviewed in Larsen, 1999; Katzenberg and Saunders, 2000). Human skeletal remains can be therefore used as a “bridge” between mortuary ritual and the everyday life of Late Eneolithic peoples (Larsen, 1999; Sládek et al., 2003). Central European anthropology of the Late Eneolithic has been traditionally focused more on either pure description or questions of migrations and the origin of racial groups, using a racial and typological approach. Racial and typological studies, however, follow a wrong assumption about the relationships between genetic code and phenotype (Armelagos and Van Gerven, 2003). The alternative approach for testing Late Eneolithic mobility patterns assumes that human behavior plays the role of a filter that limits the amount of those environmental stimuli that will affect bone remodeling. Therefore, behavior is functionally tied to the adaptive “answer” of the skeleton. If the answer of bone is specific and/or localized, the archaeological approach to reconstructions of mobility arises (see reviews and critiques of the archaeological approach to reconstructions of mobility in Wilk, 1983; Rafferty, 1985; Binford, 1987, 1990; Kelly, 1992; Panja, 2003). How can one test the mobility pattern of Late Eneolithic groups using archaeological data, when only the burial record is preserved?

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**TABLE 1. Structure of Central European sample used in study**

<table>
<thead>
<tr>
<th>Culture</th>
<th>Dating and sites</th>
<th>N_T (N_F, N_M)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bell Beaker</td>
<td>(LE; 2600–2000 BC)²</td>
<td>23 (5; 13)</td>
</tr>
<tr>
<td>Corded Ware</td>
<td>(LE; 2900–2300 BC)²</td>
<td>31 (11; 15)</td>
</tr>
<tr>
<td>Černé (CWC); Bělsko (BBC); Bobrov (CWC); Čechovice (Kňaževé); Kohlsý; Kuřín; Liběšice; Malé Březno; Malá Ohrada (CWC); Most; Ohrnice; Pohořelice; Poplice; Postoloprty; Proseč; Rousínov; Široké Třebítce; Tučapy; Tuchoměřice (CWC); Velíká Ves; Vikletice; Vrbice; Výškov</td>
<td>24 (9; 9)</td>
<td></td>
</tr>
<tr>
<td>Unterwołbling</td>
<td>(EBA; 2020–1770 BC)³</td>
<td>42 (16; 14)</td>
</tr>
<tr>
<td>Wieselburger</td>
<td>(EBA; approximately 2000–1700 BC)⁴</td>
<td>31 (16; 12)</td>
</tr>
<tr>
<td>Late Eneolithic</td>
<td>Early Bronze Age</td>
<td>54 (16; 28)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>97 (41; 35)</td>
</tr>
</tbody>
</table>

¹ See geographic demarcation and definition of Central Europe in Sládek (2000). BBC, Bell Beaker culture; CWC, Corded Ware culture.

² Radiocarbon dates are given as estimate of 68.2% confidence interval from Stadler (1999).

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

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

⁵ T, total (indeterminable included); F, female; M, male.
ally associated with the level and pattern of habitual mechanical loading (Bridges, 1985; Larsen, 1999; Ruff, 2000a). Functional comparison of differences in the quantity and distribution of cortical tissue is derived from the biomechanical approach (Ruff, 2000a), when long bones are modeled as engineering beams (Huiskes, 1982). Thus, when using a biomechanical model, the geometric properties of cross sections of long bone (i.e., cross-sectional areas, second moments of area, and polar moment of area) are associated with the amount and pattern of particular mechanical loading (see Materials and Methods, below).

There is an ambiguity about the nature of systemic vs. localized effects on bone structure remodeling when cortical tissue is studied. For example, thicker cortical tissue was localized after an experimental exercise, even in cranial bone that is not directly affected by locomotion (Lieberman, 1996). This finding can question the specific and localized effect of mechanical loading (Lovejoy et al., 2002). However, there are many clinical, experimental, and bioarcheological examples of the localized effects of mechanical loading on the human skeleton (Trinkaus et al., 1994; Haapasalo et al., 1996; Larsen, 1999; Ruff, 2000a; Rubin et al., 2001; Holt et al., 2004). Moreover, the quantity and distribution of cortical tissues in femoral diaphyses were shown to be functionality modeled by mechanical levels induced by variability in locomotion and subsistence, and can therefore be used to study changes in human mobility in the past (Ruff et al., 1984; Trinkaus and Ruff, 1999; Larsen et al., 2001; Stock and Pfeiffer, 2001; Holt, 2003). Thus, changes in torsional rigidity, as well as resistance in antero-posterior loading of the femoral midshaft, induced by differences in mobility between highly mobile preagricultural and sedentary agricultural subsistence, were reported by Bridges (1989). Ruff (1987) also showed that the femora midshafts of mobile groups tend to be less circular in cross section, i.e., the mobility index approaches values larger than 1.0 in antero-posterior second moment area relative to medio-lateral second moment of area of the femoral midshaft cross section.

Given the discussion above, we can expect that mobility vs. sedentism would produce two mutually exclusive patterns in the distribution of cross-sectional geometry of midshaft femora: 1) The absence of Corded Ware settlement structures contrasts with evidence of Early Bronze Age settlements because of different degrees of mobility between those groups (Venč, 1994). In this case, the cross-sectional geometry of the femora midshafts of Corded Ware individuals would show significant differences from the femora of Early Bronze Age sedentary individuals, mainly in a higher level of mechanical robusticity and a less circular outline of the femoral midshaft cross section. 2) The archaeological invisibility of Corded Ware settlements is not a reflection of a high degree of mobility (Neustupný, 1997). We can expect that the cross-sectional geometry parameters of Corded Ware midshaft femora will not show significant differences from Early Bronze Age midshaft femora.

**MATERIALS AND METHODS**

**Sample**

The sample of 151 individuals from five archaeological cultures was selected to address the question of differences in mobility strategies during the Late Eneolithic and Early Bronze Age in Central Europe (Table 1). The sites selected for the study are located in Lower Austria, Moravia, and Bohemia (see definitions of archeological cultures and details about selected sites in Buchvaldek, 1986; Teischler-Nicola, 1992; Shennan, 1993; Neugebauer, 1994). The sample of Bell Beaker individuals was not analyzed separately but pooled together with the Corded Ware group into the category of a combined Late Eneolithic sample because of its poor preservation. Given the fact that the lower limb has nonsignificant and random bilateral asymmetry (Ruff and Jones, 1981; Martorell et al., 1988; Trinkaus et al., 1994), right-side femora were selected for this study when possible, but left femora were used in cases where right femora were not well-preserved.

**Age and sex estimation**

Only Late Eneolithic and Early Bronze Age adults with closed epiphyses were used in this study. Sex of individuals was allocated through the assessment of pelvic, femora, tibiae, and humeri, using primary and secondary sex analyses (Murail et al., 1999). The primary analysis of sex allocation was based on a set of five pelvic measurements and two discriminant function analyses (Novotný, 1975; Brůžek, 1984), as well as on five pelvic morphological features (Brůžek, 2002). Only those individuals with agreement in metric and morphological sex allocation were used as the primary sample. Our primary sample consists of 41 individuals. For the secondary sex allocation, 14 discriminant functions were computed, using different combinations of pelvic, femoral, tibial, and humeral measurements. The correct classification of secondary discriminant functions ranges between 89–99% 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 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, an individual was allocated as indeterminable. Indeterminable individuals were included only in those analyses where the total sample of the Late Eneolithic or Early Bronze Age was used.

Changes in perception of gender in mortuary practices were reported during the Late Eneolithic and Early Bronze Age (Turek and Černý, 2001). We assume that several factors beyond mobility are involved in changes of gender/sexual dimorphism. The control for these factors is beyond the scope of our testing model. Therefore, males and females were further analyzed separately, and mobility was not studied as a phenomenon connected with changes of sexual dimorphism.

**Linear measurements**

Two linear osteometric measurements were used for size and beam-length standardization (see below). Femoral head diameter, used for the estimate of body mass, was taken following the standard osteometric approach (Bräuer, 1988). The definition of femoral biomechanical length as a beam-scaling parameter follows Trinkaus and Ruff (1998), p. 411; see also Ruff and Hayes, 1983).
Diaphyseal sections and computation of cross-sectional parameters

Femoral midshaft sections were taken at 50% of femoral biomechanical length. Each bone was computer-tomography (CT)-scanned by CT HiSpeed Dxi (General Electric, Milwaukee, WI) at 120 kv. Prior to scanning, the femora were oriented in a standardized position with respect to the antero-posterior and medio-lateral planes, following an approach specified by Ruff and Hayes (1983) and Ruff (2000b). Final CT scan images consist of 2-mm-thick slices with a resolution of 512 × 512 pixels, and a pixel dimension of 0.196 mm.

The CT scan images of 50% cross sections were further processed using software for digitizing and computing biomechanical parameters previously developed by us (CT-i software, Sailer et al., 2003). 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 showed that the inter- and intraobserver errors occurring in manually determining bone outlines do not significantly affect further computer analysis (Sailer et al., 2003).

Cross-sectional parameters

Cross-sectional geometry of femoral diaphysis 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). Total area (TA) is the area within the outer subperiosteal boundary. Anatomically oriented second moments of area were used to evaluate resistance to bending rigidity against antero-posterior (I_{A,p}) and medio-lateral (I_{M,l}) loads (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 was also shown to be a good estimate of skeletal robusticity when appropriately scaled by a mechanically relevant measure of body size (Ruff et al., 1993). Finally, the ratio of I_{A,p}/I_{M,l} was used to compare diaphyseal shape (Larsen, 1999; Ruff, 2000a).

Size standardization

It was shown that behaviorally induced differences can be masked by biologically induced differences when body size is not appropriately scaled (Larsen, 1999; Trinkaus and Ruff, 1999; Ruff, 2000a,b). The mechanically relevant measure of body size in axial loading and bending/torsional loading is expected to be body mass (Ruff et al., 1993; Ruff, 2000b).

The estimation of body mass from the skeleton opens up important theoretical issues (Smith, 1996; Ruff, 2002; Auerbach and Ruff, 2004). Only 22% of 151 individuals of the Late Eneolithic and Early Bronze Age sample had preserved bi-iliac breadth to be used for a morphometric (cylindrical model) estimate of body mass (Ruff, 1994). Moreover, the preservation of bi-iliac breadth varied across the sample (e.g., for the Unterwo¨lbling group, only 4.2% individuals had bi-iliac breadth preserved). Therefore, the femoral head estimate of body mass was used (Ruff et al., 1991; Grine et al., 1995). Although femoral head diameter could be partially affected by variation in mechanical loading other than body mass per se (i.e., behavior), it is still a good parameter for estimation of body mass in skeletal samples of fossil hominins (McHenry, 1992; Ruff et al., 1994, 1997; Trinkaus et al., 1994; Grine et al., 1995; Lieberman et al., 2001; Auerbach and Ruff, 2004). Moreover, morphometric and mechanical estimation of body mass often yields similar results when applied to recent as well as Pleistocene hominins (Ruff et al., 1997; Auerbach and Ruff, 2004). Thus, the cross-sectional parameters of Late Eneolithic and Early Bronze Age femora were scaled to body mass estimated from the femoral head diameter by the following equations:

\[
BM = 2.239 \times FHB - 39.9 \quad (\text{McHenry, 1992}) \quad (1)
\]

\[
BM = 2.268 \times FHB - 36.5 \quad (\text{Grine et al., 1995}) \quad (2)
\]

where BM is body mass in kg, and FHB is femoral head diameter in mm. The measurements are raw (not logged) data. The arithmetic mean from equations (1) and (2) was used as a final body mass estimate (for details, see Ruff et al., 1997).

In addition to body mass, moment arm length must be also included in the size standardization when considering bending and torsional loading (Currey, 1984; Ruff et al., 1993; Ruff, 2000a). Moment arm length is based on the relevant biomechanical length of the respective long bones, and we used femoral biomechanical length for this study (Ruff and Hayes, 1983).

In conclusion, cross-sectional areas were scaled using body mass estimated from femoral head diameter. Second and polar moments of area were adjusted by body mass times femoral biomechanical length.

Statistical treatment

Statistica 6.0 (StatSoft, 1984–2001) and Excel 97 (Microsoft Corp., 1985–1997) were used for the basic statistical treatment. Two-way analysis of variance (ANOVA), with sex and culture as grouping variables, was used to test the effect of these variables on biomechanical parameters of selected samples. Post hoc Bonferroni and Fisher LSD tests were employed to compare individual post hoc differences among sex/cultural means of samples. The diaphyseal shape of the midshaft cross section was studied by the bootstrap mean of the I_{A,p}/I_{M,l} index and 95% confidence interval for the mean, using Resampling Stats for Excel 2.0 (Resampling Stats, Inc.) and Excel 97 (Microsoft Corp., 1985–1997). Since the scaling of cross-sectional parameters is based on continuous variables such as body mass and body mass times femoral biomechanical length, and all these parameters are measured with error, the reduced major-axis model was used to compare bivariate distribution (Kermack and Haldane, 1950; Clarke, 1980; McArdle, 1988; Aiello, 1992). Reduced major axis was computed by Software for Reduced Major Axis Regression (Bohonak, 2002). The slope and intercept 95% confidence intervals were estimated using a bootstrap technique. Quick Test was employed to compare distribution differences along the reduced major axis between selected samples (Tsutakawa and Hewett, 1977). This test is arranged as Fisher’s exact two-tailed test when the number of individuals above the reduced major axis is compared with the number of individuals below a reduced major-axis regression through the pooled sample. Data for Fisher’s
TABLE 2. Descriptive sample characteristics of femoral biomechanical length, body mass, and midshaft femoral cross-sectional properties for combined samples of Late Eneolithic and Early Bronze Age groups (mean (N) ± SE)

<table>
<thead>
<tr>
<th>Parameter1</th>
<th>Females (LE)</th>
<th>Females (EBA)</th>
<th>B2</th>
<th>LSD2</th>
<th>Males (LE)</th>
<th>Males (EBA)</th>
<th>B</th>
<th>LSD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fe-BML</td>
<td>390.1 (14) ± 3.66</td>
<td>393.0 (38) ± 3.03</td>
<td>431.6 (23) ± 4.22</td>
<td>429.3 (33) ± 3.62</td>
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</tr>
<tr>
<td>Body mass</td>
<td>56.9 (16) ± 0.85</td>
<td>55.7 (41) ± 0.48</td>
<td>69.0 (28) ± 0.94</td>
<td>70.4 (32) ± 0.77</td>
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</tr>
<tr>
<td>TA adj</td>
<td>814.2 (14) ± 16.00</td>
<td>762.4 (34) ± 12.81</td>
<td>*</td>
<td>840.1 (23) ± 13.69</td>
<td>801.0 (30) ± 11.97</td>
<td></td>
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</tr>
<tr>
<td>CA adj</td>
<td>594.1 (14) ± 13.60</td>
<td>562.4 (34) ± 8.81</td>
<td>613.9 (23) ± 11.87</td>
<td>605.8 (30) ± 8.87</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MA adj</td>
<td>220.1 (14) ± 16.10</td>
<td>200.0 (34) ± 7.35</td>
<td>226.2 (23) ± 11.30</td>
<td>195.4 (30) ± 9.76</td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>IM-L adj</td>
<td>688.1 (14) ± 21.17</td>
<td>628.7 (34) ± 23.89</td>
<td>*</td>
<td>879.8 (23) ± 28.00</td>
<td>819.9 (30) ± 23.34</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IM-M adj</td>
<td>755.4 (14) ± 30.01</td>
<td>632.5 (34) ± 19.99</td>
<td>*</td>
<td>817.4 (23) ± 28.40</td>
<td>799.5 (30) ± 27.03</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>J adj</td>
<td>1,441.4 (14) ± 43.2</td>
<td>1,261.2 (34) ± 40.1</td>
<td>*</td>
<td>1,697.2 (23) ± 46.1</td>
<td>1,619.5 (30) ± 39.5</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1Fe-BML, femoral biomechanical length; BM, body mass; TA, total subperiosteal area; CA, cortical area; MA, medullary area; IA-P, antero-posterior second moment of area; I M-L, medio-lateral second moment of area; J, polar moment of area; adj, adjusted; LE, Late Eneolithic; EBA, Early Bronze Age. Femoral biomechanical length is in mm, body mass in kg, bone areas in mm², and second moments of area in mm⁴. Body areas are size-standardized by body mass * 100; second moments of area are size-standardized by body mass * femoral biomechanical length, and multiplied by 1,000.

2ANOVA post hoc tests: B, Bonferroni post hoc test; LSD, Fisher’s LSD post hoc test.

*P < 0.05.
**P < 0.01.

exact two-tailed test were prepared in Excel tables and further proceeded in StatXact 6.1 software (Cytel Software Corp., 1989–2002). StatXact 6.1 software has an advantage in that exact values instead of approximation by asymptotic values are computed (Mehta and Patel, 1999).

RESULTS

Femoral length and body mass

Subsistence strategy plays an important role in adult body size, including adult stature and body mass (Larsen, 1999). Variation in subsistence strategy produces different stresses, especially in terms of different nutrition. Those groups that ensure adequate nutrition during childhood tend to reach the maximum of their genetic growth potential (e.g., Yagi et al., 1989; Boldsen, 1995; Steckel, 1995). Changes of stature caused by change in subsistence strategy were demonstrated, for example, in the transition to agriculture in the New World and South Asia (Larsen, 1999). However, body-size parameters do not have to be sensitive to every change in nutrition and, as documented for the difference between premodern (1675–1879) and modern (1950–1975) periods in the US (Angel, 1976; Larsen et al., 1995). Formicola and Giannecchini (1999) also showed that the decrease in stature in Western Europe did not occur with subsistence changes between the Upper Paleolithic and Neolithic, but 10,000 years before, at the Late Glacial Maximum. Similarly, subsistence changes, which include the adoption of agriculture, do not affect stature, as documented in temporal archaeological groups in Ontario, the Northern Great Plains, Peru, and Chile (Allison, 1984; Katzenberg, 1992; Cole, 1994).

Body-size parameters of Late Eneolithic and Early Bronze Age groups were estimated using femoral biomechanical length (i.e., a longitudinal parameter highly correlated with stature) and body mass. Results of the comparison are shown for the combined Late Eneolithic and Early Bronze Age sample in Table 2, and for the separate samples in Table 3. None of the combined Late Eneolithic and Early Bronze Age mean comparison of body mass and femoral biomechanical length was significant (Table 2). Comparing the separate samples, the maximum difference in femoral biomechanical length was found between Corded Ware males and Wieselburger males (3% difference, P-value (two-tailed t-test) = 0.12), and the maximum for females was between the Bell Beakers and Unterwo¨lbling sample (1.8% difference, P-value (two-tailed t-test) = 0.58) (Table 3). Given the fact that the comparison between maximal and minimal values was post hoc planned, the values will not reach significance after the Bonferroni correction for multiple comparisons. Similarly, ANOVA post hoc Fisher LSD and Bonferroni tests produced a nonsignificant difference in femoral biomechanical length between the selected samples. The means of body mass reached similar values between the selected samples, and none of the groups was significantly different in ANOVA post hoc analysis (Table 3).

The nonsignificant difference of selected body-size parameters between the Late Eneolithic and Early Bronze Age groups indicates that there were no substantial differences in those subsistence factors which would cause differences in femoral biomechanical length and body mass.

Relative cortical bone

When groups of the genus Homo during their Pleistocene and Holocene evolution were compared, it was shown that cortical area vs. total area (percentage cortical area; %CA) decreased as part of a general evolutionary trend between archaic and recent humans (Ruff et al., 1993). Recent human samples exhibit a high degree of variation in %CA, which also encompasses the variation of archaic humans (Ruff et al., 1993). Later studies also showed that %CA has a poor discriminatory value when femoral midshaft is compared among Late Pleistocene and recent humans (Trinkaus, 1997; Trinkaus and Ruff, 1999). This phenomenon exists, among other reasons, because %CA has no intrinsic biomechanical significance, although it is a useful morphological parameter (Ruff et al., 1993; Larsen, 1999).

The bivariate distribution of cortical area against total area and the results of Quick Tests are shown in Figure 1. Only males of the combined Late Eneolithic group exhibit a significant shift toward lower values. This shift is caused by Bell Beaker males rather than Corded Ware males. In comparison to total area, Bell Beaker males have a lower amount of cortical area not only relative to Early Bronze Age individuals, but also to the separate Corded Ware individuals (for Bell Beakers, 9 individuals...
### TABLE 3. Descriptive sample characteristics (mean (N) ± SE) and post hoc ANOVA test comparison of separate groups of Late Eneolithic and Early Bronze Age

<table>
<thead>
<tr>
<th>Parameter^1 (T)</th>
<th>Bell Beaker (1)</th>
<th>Corded Ware (2)</th>
<th>Únětice (3)</th>
<th>Unterwölbung (4)</th>
<th>Wieselburger (5)</th>
<th>Bonferroni^2</th>
<th>Fisher LSD^2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fe-BML</td>
<td>418.4 (19) ± 5.79</td>
<td>414.5 (25) ± 5.58</td>
<td>413.2 (24) ± 5.18</td>
<td>415.4 (35) ± 4.15</td>
<td>403.3 (31) ± 4.37</td>
<td>1/5*, 4/5^*</td>
<td></td>
</tr>
<tr>
<td>Body mass</td>
<td>64.7 (23) ± 1.51</td>
<td>64.2 (31) ± 1.47</td>
<td>63.6 (23) ± 1.68</td>
<td>62.1 (37) ± 1.25</td>
<td>61.3 (31) ± 1.31</td>
<td>1/5^*</td>
<td></td>
</tr>
<tr>
<td>TA adj</td>
<td>828.9 (19) ± 15.26</td>
<td>814.1 (25) ± 13.25</td>
<td>793.8 (22) ± 16.54</td>
<td>803.4 (26) ± 12.58</td>
<td>746.1 (30) ± 12.52</td>
<td>1/5**, 2/5, 4/5^*</td>
<td>1/5,*** 2/5,*** 3/5, 4/5^*</td>
</tr>
<tr>
<td>CA adj</td>
<td>597.2 (19) ± 13.04</td>
<td>610.8 (25) ± 10.45</td>
<td>593.4 (22) ± 10.20</td>
<td>588.4 (26) ± 9.60</td>
<td>570.7 (30) ± 11.12</td>
<td>2/5^*</td>
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<tr>
<td>MA adj</td>
<td>231.7 (19) ± 13.57</td>
<td>203.3 (25) ± 10.55</td>
<td>200.4 (22) ± 13.22</td>
<td>215.0 (26) ± 9.44</td>
<td>175.3 (30) ± 5.99</td>
<td>1/5**, 4/5^*</td>
<td>1/5,*** 2/5, 4/5^*</td>
</tr>
<tr>
<td>l_{AP} adj</td>
<td>797.4 (19) ± 35.60</td>
<td>779.2 (25) ± 29.70</td>
<td>735.2 (22) ± 36.71</td>
<td>739.0 (26) ± 22.97</td>
<td>671.1 (30) ± 33.52</td>
<td>1/5, 2/5^*</td>
<td>1/5,*** 2/5**</td>
</tr>
<tr>
<td>l_{ML} adj</td>
<td>791.3 (19) ± 25.98</td>
<td>771.7 (25) ± 27.79</td>
<td>762.9 (22) ± 34.86</td>
<td>726.3 (26) ± 26.27</td>
<td>647.2 (30) ± 28.34</td>
<td>1/5, 2/5, 3/5, 4/5^*</td>
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<td>J adj</td>
<td>1,588.8 (19) ± 55.47</td>
<td>1,550.9 (25) ± 48.2</td>
<td>1,498.2 (22) ± 60.21</td>
<td>1,465.2 (26) ± 44.67</td>
<td>1,324.3 (30) ± 58.43</td>
<td>1/5, 2/5**</td>
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<th>Parameter (F)</th>
<th>Bell Beaker (1)</th>
<th>Corded Ware (2)</th>
<th>Únětice (3)</th>
<th>Unterwölbung (4)</th>
<th>Wieselburger (5)</th>
<th>Bonferroni</th>
<th>Fisher LSD</th>
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<td>Fe-BML</td>
<td>387.9 (4) ± 8.98</td>
<td>391.0 (10) ± 4.00</td>
<td>392.6 (9) ± 6.76</td>
<td>394.0 (13) ± 5.26</td>
<td>392.5 (16) ± 4.70</td>
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<tr>
<td>Body mass</td>
<td>54.6 (5) ± 1.31</td>
<td>57.9 (11) ± 0.97</td>
<td>55.9 (9) ± 1.11</td>
<td>55.0 (16) ± 0.60</td>
<td>56.3 (16) ± 0.88</td>
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<tr>
<td>TA adj</td>
<td>849.4 (4) ± 16.56</td>
<td>800.2 (10) ± 20.12</td>
<td>786.0 (8) ± 29.40</td>
<td>805.8 (11) ± 17.95</td>
<td>712.7 (15) ± 12.59</td>
<td>1/5, 4/5^*</td>
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<td>CA adj</td>
<td>599.5 (4) ± 18.03</td>
<td>592.0 (10) ± 18.14</td>
<td>584.9 (8) ± 20.35</td>
<td>591.5 (11) ± 14.07</td>
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<td>MA adj</td>
<td>249.9 (4) ± 18.59</td>
<td>208.2 (10) ± 20.56</td>
<td>211.1 (8) ± 18.83</td>
<td>224.3 (11) ± 12.33</td>
<td>176.2 (15) ± 9.24</td>
<td>1/5, 4/5^*</td>
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<tr>
<td>l_{AP} adj</td>
<td>708.4 (4) ± 40.24</td>
<td>679.9 (10) ± 25.77</td>
<td>672.5 (8) ± 60.74</td>
<td>704.8 (11) ± 36.19</td>
<td>549.5 (15) ± 23.54</td>
<td>1/5, 2/5, 3/5, 4/5^*</td>
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<tr>
<td>l_{ML} adj</td>
<td>766.0 (4) ± 31.58</td>
<td>748.3 (10) ± 40.97</td>
<td>718.2 (8) ± 51.13</td>
<td>661.6 (11) ± 28.80</td>
<td>565.4 (15) ± 18.90</td>
<td>1/5^*</td>
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<td>J adj</td>
<td>1,474.5 (4) ± 35.19</td>
<td>1,428.2 (10) ± 59.5</td>
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<td>1,366.4 (11) ± 57.32</td>
<td>1,114.9 (15) ± 37.28</td>
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<th>Parameter (M)</th>
<th>Bell Beaker (1)</th>
<th>Corded Ware (2)</th>
<th>Únětice (3)</th>
<th>Unterwölbung (4)</th>
<th>Wieselburger (5)</th>
<th>Bonferroni</th>
<th>Fisher LSD</th>
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<td>Fe-BML</td>
<td>428.0 (11) ± 6.69</td>
<td>434.8 (12) ± 5.39</td>
<td>433.9 (9) ± 6.38</td>
<td>433.4 (12) ± 5.87</td>
<td>421.6 (12) ± 6.29</td>
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<tr>
<td>Body mass</td>
<td>68.6 (13) ± 1.34</td>
<td>69.4 (15) ± 1.36</td>
<td>70.0 (9) ± 1.99</td>
<td>71.8 (11) ± 1.17</td>
<td>69.4 (12) ± 0.92</td>
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<tr>
<td>TA adj</td>
<td>840.5 (11) ± 21.59</td>
<td>839.7 (12) ± 18.36</td>
<td>802.2 (9) ± 24.73</td>
<td>802.7 (9) ± 22.76</td>
<td>796.7 (12) ± 18.10</td>
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<tr>
<td>CA adj</td>
<td>596.9 (11) ± 20.18</td>
<td>622.4 (12) ± 12.42</td>
<td>594.9 (9) ± 15.47</td>
<td>594.7 (9) ± 15.19</td>
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<tr>
<td>MA adj</td>
<td>243.6 (11) ± 18.24</td>
<td>210.3 (12) ± 12.80</td>
<td>207.4 (9) ± 23.38</td>
<td>208.0 (9) ± 19.15</td>
<td>176.9 (12) ± 8.83</td>
<td>1/5^*</td>
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<tr>
<td>l_{AP} adj</td>
<td>858.5 (11) ± 51.66</td>
<td>899.1 (12) ± 26.65</td>
<td>767.9 (9) ± 53.84</td>
<td>816.9 (9) ± 23.59</td>
<td>861.3 (12) ± 36.95</td>
<td>1/5, 2/5, 3/5, 4/5^*</td>
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<tr>
<td>l_{ML} adj</td>
<td>823.6 (11) ± 39.92</td>
<td>811.7 (12) ± 41.93</td>
<td>824.2 (9) ± 60.13</td>
<td>796.6 (9) ± 41.60</td>
<td>782.3 (12) ± 42.79</td>
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<tr>
<td>J adj</td>
<td>1,682.4 (11) ± 83.2</td>
<td>1,710.8 (12) ± 48.6</td>
<td>1,592.1 (9) ± 84.30</td>
<td>1,613.5 (9) ± 53.81</td>
<td>1,644.5 (12) ± 68.50</td>
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</table>

^1 See Tables 1 and 2 for abbreviations and computation details.

^2 Numbers indicate pair significance between respective groups.

* P < 0.05.

** P < 0.01.

*** P < 0.001.
below pooled reduced major axis/2 individuals above the axis; see data of distribution for the Corded Ware group in Fig. 1.

It is unclear how to interpret the differences and similarities between the Late Eneolithic and Early Bronze Age groups in %CA. Relative thickness of cortical bone might be interpreted as either expansion of periosteal surface or decrease of medullar cavity, or both (Ruff et al., 1993). Furthermore, the relative thickness of cortical bone does not have to be associated with either rigidity or strength of the bone. In fact, a high score of %CA was reported for an agricultural sample from the Georgia coast, designated as “gracile” in other features (Ruff et al., 1984). Moreover, both total area and cortical area can be sensitive to body mass. Thus, the similarity of %CA between the Late Eneolithic and Early Bronze Age groups can be associated with contradictory factors; other comparisons for the description of differences in robusticity are needed.

In conclusion, females in both the combined Late Eneolithic and separate Corded Ware samples are not significantly different in the portion of cortical area relative to total area. In contrast, Late Eneolithic males have lower values of cortical area compared to the amount of total area.

Cortical area and axial robusticity

The amount of adjusted cortical area in the femoral midshaft exponentially declines across the Pleistocene and Holocene samples (Ruff et al., 1993). Such a reduction of adjusted cortical area was interpreted as a decline of bone rigidity in compressive loading, related to changes of physical environment and behavioral changes in subsistence strategy (Ruff et al., 1993; Ruff, 2000a). Therefore, differences in adjusted cortical area between the Late Eneolithic and Early Bronze Age groups are a reflection of behavioral changes related to axial robusticity.

A nonsignificant difference between the combined Late Eneolithic and Early Bronze Age groups both for males and females was found when the mean of adjusted cortical area was compared (Table 2). In analyses of separate means of adjusted cortical area, only the values for Wieselburger females significantly decreased compared to the other Late Eneolithic and Early Bronze Age groups in Fisher’s LSD post hoc test (Table 3). The decrease of Wieselburger females probably reflects the general decrease of size and robusticity of femoral midshafts, because the means of adjusted total area and second and polar moments of area also indicate a significant reduction (see below). The absence of significance between the separate samples of males and females of the Late Eneolithic and the majority of Early Bronze Age samples is also supported by reduced major-axis comparisons (Fig. 2). Both females and males of the Late Eneolithic and Early Bronze Age have similar distribution above and below the pooled reduced major axes. Therefore, we can conclude that if there is any behavioral difference in mechanical environment between the Late Eneolithic and Early Bronze Age, it does not affect the axial rigidity of femoral midshafts.

Polar moment of area and torsional robusticity

In absolute values, the male and female samples of the combined Late Eneolithic have higher polar moments of area than males and females of the combined Early Bronze Age groups (Table 2). A significant mean decrease of polar moment of area is reached only for the females in ANOVA Fisher’s LSD post hoc comparisons (Table 2). Average differences for polar moment of area are nonsignificant for separate male samples, although Corded Ware males exhibit the highest level of torsional robusticity (Table 3). The difference in the mean of polar moment of area between the Corded Ware and Early Bronze Age males is striking, especially for the Unetice males. Given the chronology of Corded Ware and Unetice (Table 1), the decline in torsional robusticity may be an effect of the reduction of mechanical loading between the Late Eneolithic and Early Bronze Age. However, since the mean difference is not significant, we consider the divergence between Corded Ware and Unetice males to be a result of sampling error. In contrast, the decline of polar moment area among Early Bronze Age females can be seen even when separate groups are considered.
(Table 3). Both the Bell Beaker and Corded Ware females have the highest values for female mean difference of polar moment of area. The difference is significant in comparison to the Wieselburger female sample. However, Wieselburger females show the lowest value significant in Fisher’s LSD post hoc test, not only for the comparison with Late Eneolithic females, but also with the other Early Bronze Age female groups.

The bivariate distribution of femoral midshaft polar moment of area against femoral length and body mass is shown in Figure 3. The Late Eneolithic females and separate distribution of Corded Ware females are above the pooled reduced major axis, and therefore the groups exhibit a significantly higher level of torsional robusticity when scaled to body size and moment arm length. Moreover, all Bell Beaker females are arranged above the reduced major axis for the pooled Late Eneolithic and Early Bronze samples. However, because of the small sample size of Bell Beaker females (n = 4), any inference must be cautious. Late Eneolithic males are evenly distributed around the reduced major axis, but Early Bronze Age males are distributed slightly below the axis (Fig. 3). However, the distribution is not significant in Quick Test analysis.

Thus, the Late Eneolithic females have a significantly higher torsional rigidity of the femoral midshaft than the Early Bronze Age female groups in reduced major-axis analysis. The trend is also supported by ANOVA analysis of the combined female samples. However, on average, the separate female samples are significantly higher than the Wieselburger females only. In contrast, the Late Eneolithic males do not exhibit any distinction in torsional rigidity in comparison to Early Bronze Age males.

**Second moment of area comparison and diaphyseal shape**

The comparison of bootstrap means of the $I_{A-P}/I_{M-L}$ ratio (i.e., the mobility index) for the Late Eneolithic and Early Bronze Age groups indicates that 95% confidence intervals overlap between the studied samples (Table 4). The combined Late Eneolithic females and separate Corded Ware female sample have the lowest absolute values for the $I_{A-P}/I_{M-L}$ ratio when compared to the Early Bronze Age females. On the contrary, the Corded Ware males reach the largest values among the studied samples. The distribution of Late Eneolithic and Early
Bronze Age females around the pooled reduced major axis is not significantly shifted for any of the studied samples (Fig. 4). The graph shows that Late Eneolithic females are slightly more shifted below the axis. Late Eneolithic males are distributed more above the axis; nonetheless, the trend is nonsignificant.

The pattern of bending rigidity distribution was further evaluated comparing individual second moments of area. Descriptive characteristics of antero-posterior and medio-lateral second moments of area are shown for the combined Late Eneolithic and Early Bronze Age sample in Table 2, and for the separate samples in Table 3.

On average, the combined Late Eneolithic female sample, in medio-lateral second moments of area, is significantly higher than the Early Bronze Age groups in ANOVA post hoc Bonferroni and Fisher LSD tests (Table 2). In contrast, antero-posterior second moments of area are not significant between the combined Late Eneolithic and Early Bronze Age females. A slightly different picture appears when the separate means of female samples are compared (Table 3). Only the Early Bronze Age Wieselburger females exhibit a consistent pattern of a significantly lower degree of antero-posterior as well as medio-lateral second moments of area regarding not only Late Eneolithic females but also Early Bronze Age females. Thus, the differences between the Wieselburger females and Early Bronze Age samples are associated with size rather than diaphyseal shape. The separate Late Eneolithic female samples (BBC and CWC), in general, differ significantly only from the Wieselburger females, but not from the rest of the Early Bronze Age groups.

Means of antero-posterior and medio-lateral second moments of area of the combined Late Eneolithic and Early Bronze Age male samples are not significantly different (Table 2). The Corded Ware males have a significantly higher mean of antero-posterior second moment of area than the Uněticě sample (Table 3).

The bivariate distribution of antero-posterior and medio-lateral second moments of area relative to the product of body mass and femoral biomechanical length is given in Figures 5 and 6. Late Eneolithic females are significantly shifted above the pooled reduced major axis in the medio-lateral second moment of area, but with nonsignificant distribution along the axis in the antero-posterior second moment of area, in comparison with Early Bronze Age females. Also, Corded Ware females are significantly shifted above the pooled reduced major axis ($P = 0.008$) of the medio-lateral second moment of area, but equally distributed on the antero-posterior second moment of area ($P = 0.48$), compared to the other groups that were studied.

The combined Late Eneolithic males are not significantly different in antero-posterior and medio-lateral second moments of area distribution in comparison to the pooled reduced major axis. However, Corded Ware males are partly shifted above the pooled reduced major axis of the antero-posterior second moment of area ($P = 0.10$), but equally distributed in the medio-lateral second moment of area ($P = 0.99$). Bell Beaker males show a
clear shift in neither antero-posterior nor medio-lateral second moment of area comparison.

In conclusion, the significantly higher polar moment of area of the Late Eneolithic females is affected by higher resistance in the medio-lateral second moment of area, but without differences in the antero-posterior second moment of area, in comparison to the Early Bronze Age females. The Late Eneolithic males are significantly different neither in bending/torsional robusticity nor in diaphyseal shape. However, the Corded Ware males are partly shifted to a higher antero-posterior bending resistance, which may indicate a shift to a higher degree of mobility (although not significant).

**DISCUSSION**

The Central European Late Eneolithic and Early Bronze Age femoral midshaft cross sections should be considered similar with respect to mobility. There are significant differences in neither diaphyseal robusticity nor diaphyseal shape between the Corded Ware males and other male samples. However, the Corded Ware males still show the highest mean values for polar moment of area, antero-posterior second moment of area, and \( I_{A-P}/I_{M-L} \) ratio. These parameters are associated with a higher degree of mobility. Therefore, elucidation of the nonsignificant trend, which may represent either sampling error or some biomechanical meaning, must be confirmed by larger samples and/or other analyses focused on other skeletal parts associated with mobility changes.

The Late Eneolithic females are significantly different in torsional and overall bending robusticity of the femoral midshaft in comparison to the Early Bronze Age. The significant differences are caused by medio-lateral second moment of area rather than the expected antero-posterior second moment of area. Thus, the differences between the Late Eneolithic and Early Bronze Age in torsional and overall bending robusticity cannot be explained by a higher degree of long-distance mobility with antero-posterior loading, but with some movements which employ muscle groups that produce higher medio-lateral loading.

It is difficult to find a behaviorally induced difference in the medio-lateral loading movement for the Late Eneolithic and Early Bronze Age groups. Therefore, it is more likely that the medio-lateral bending resistance can be produced by body-shape differences.

The only exception to the female pattern differences described above is for the Wieselburger females, which
are significantly different in all size parameters of cross sections, overall bending, and torsional robusticity, and in the shape of the diaphyseal midshaft cross section. The decrease of cortical area could be explained by the impact of the taphonomic and postdepositional processes, but this is not the case for the Wieselburger sample. The group of Wieselburger females was sampled from the Hainburg cemetery, where the preservation of bones was the best among the studied groups, with intact periosteoal and endosteal surfaces. Moreover, the decrease of cortical area of the Wieselburger females contrasts with the nonsignificant difference in biomechanical length and body mass. Therefore, this decrease cannot be explained by biological impact. We can expect that the Wieselburger group had a different social/subsistence pattern from that of the Early Bronze Age and Late Eneolithic females. However, this prediction must be further tested using tibiae and humeri to obtain a more appropriate picture of biomechanical pattern among the Late Eneolithic and Early Bronze Age groups.

Any behavioral consequences of the presented analyses should take into consideration that only two extreme levels of mobility were compared: fully mobile groups (Late Eneolithic groups) and fully sedentary groups (Early Bronze Age groups). Such a model is not entirely realistic. We can expect that the Late Eneolithic and especially Early Bronze Age groups are characterized by combined mobile and sedentary subsistence activities (e.g., Harding, 2000). Therefore, our results seem to reject the fully mobile subsistence for the Late Eneolithic in Central Europe, but do not answer questions about the proportion of mobile/sedentary subsistence activities during the Late Eneolithic and Early Bronze Age. Moreover, our biomechanical analysis was designed solely to study the general pattern of biomechanical differences within females and males, which were pooled without respect to subgroup differences such as differences associated with age or social status. We can therefore conclude that the Central European Late Eneolithic period shows a general pattern of mechanical loading similar to the Early Bronze Age, but individual subgroup differences may be obscured in our analysis, mainly because of the small sample size.

The results also question the impact of a unidirectional (diachronic) pattern of transition between the Central European Late Eneolithic and Early Bronze Age on mechanical loading of the femoral midshaft. Based on the femoral data, we infer that the transition between the Late Eneolithic and Early Bronze Age did not bring a complete substantial unidirectional change in mechanical loading. Instead of the complete unidirectional transition between the Late Eneolithic and Early Bronze Age, we can expect that the mechanical environment was affected by an increase in social differentiation and subsistence specialization operating during the Late Eneolithic and Early Bronze Age as a mosaic across time periods and between/within cultures. Such a mosaic pattern of changes may explain, for example, the significant difference in femoral cross-sectional size and shape in Wieselburger females in comparison to Early Bronze Age females.

**CONCLUSIONS**

A biomechanical analysis of femoral midshaft cross sections indicates no clear differences between Late Eneolithic and Early Bronze Age groups. Therefore, if some differences in mobility and subsistence strategy between the Late Eneolithic and Early Bronze Age existed, those activities did not produce significantly distinct patterns of mechanical loading on the femoral midshaft. It is highly likely that other explanations than the traditional mobile pastoralist model must be employed to explain the invisibility of Central European Corded Ware settlements and the Late Eneolithic in general.

This conclusion is supported by no significant differences among male samples. However, given that the means of Corded Ware males reach their highest values in I₄₉,/I₄₉L ratio and torsional and overall bending robusticity (although not significant), our results and eventual conclusion must be verified at least on tibia cross-sectional data and/or in other samples from the period.

On the other hand, Late Eneolithic females show a significantly stronger femoral midshaft cross section for bending in the mediolateral plane compared to Early Bronze Age females. The difference cannot be associated with a higher degree of long-distance mobility, but must be explained by other movement patterns. The Wieselburger females of the Early Bronze Age have a significantly small size and rounder shape of femoral midshaft cross sections. Thus, Wieselburger females contrast not only with the Late Eneolithic but with other Early Bronze Age groups. Therefore, we can expect that the transition of mechanical loading between the Late Eneolithic and Early Bronze Age did not approach a simple diachronic direction (unidirectional pattern) between those two periods. We expect that changes in mechanical environment during the Late Eneolithic and Early Bronze Age followed a mosaic pattern associated with changes between time periods and between/within cultures, both in social stratification and in subsistence specialization. However, the association between changes in cross-sectional geometry of the femoral midshaft and social differentiation and subsistence specialization cannot be proved because of the nature of the samples used in this study. Other analyses are needed.

**ACKNOWLEDGMENTS**

We are grateful to Maria Teschler-Nicola, Miluše Dobišková, and Petr Velemínský for access to the Late Eneolithic and Early Bronze Age samples stored in the Naturhistorisches Museum in Vienna and Národní Muzeum in Prague, and for their help with several questions concerning the samples. CT scans were undertaken with the support of Wolfgang Henninger and Martin Konar from the Institute of Radiology, Veterinární medicínske Universita Wien. Daniel Soesa and Tanja Pabsits helped with correction of the English-language manuscript, and Christopher B. Ruff and Brigitte M. Holt helped with editing the final version of the manuscript. We also thank Vladimir Blážek, Ivo T. Budíl, Viktor Černý, Michael Estl, Patrik Galeta, Petr Krístuf, Erik Trinkaus, Jan Turek, Gabriela Macho, Karin Wiltschek-Schrotta, Peter Stadler, and Jan Zima for comments and other help.

**LITERATURE CITED**


