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Craniofacial morphology in Austrian Early Bronze Age populations reflects sex-specific migration patterns

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Summary - *The Early Bronze Age (2.300-1.500 BC) in lower Austria consists of three synchronous regional manifestations (Únětice, Unterwölbling, and Wieselburg cultures). The bearers of these cultures inhabited a relatively small geographic area and shared similar ecological conditions, but previous studies revealed population differences in skeletal morphology. We analyzed the cranial morphology of 171 individuals of these populations with a geometric morphometric approach in order to compare different migration scenarios. We find significant mean form differences between populations and between sexes. In a principal component analysis, the Wieselburg population, located southwest of the Danube, largely separates from the Únětice population north of the Danube, whereas the southwestern Unterwölbling group, which played a central role in trading bronze objects, overlaps with both. The Böheimkirchen group, inhabiting the southwestern Danubian area in the later phase of the Early Bronze Age, differs from the chronologically older Unterwölbling group. Geographic distance between six sites and position relative to the river Danube accounted for 64% of form distance variation; the effect of the river Danube was considerably larger than that of geographic distance per se. As predicted for a patrilocal system in which females have a larger marriage domain than males, we found that female mean forms are more similar to each other than male mean forms. Geographic conditions explained more than twice as much variation in females as in males, suggesting that female migration was more affected by geographical constraints than male migration was.*

Keywords - *Bronze Age, Migration, Morphological variation, Procrustes form space.*

Introduction

For a century, Austria's Bronze Age populations (2300-800 BC) have been the subject of intensive investigation. Their archaeological and biological features have been examined in large collections from numerous funeral sites and settlement pits. In particular, the skeletal populations recovered from Early Bronze Age sites of eastern Austria play a key role in the investigation of Bronze Age societies, not only because of the abundance of available material but also because of the extent of cultural segmentation within so small a territory.

It has been known since the turn of the 20th century that the Early Bronze Age of eastern Austria does not present a cultural unity (Reinecke, 1899; Hoernes, 1903; Menghin, 1913, 1915; Willvonseder, 1935, 1963/1968; see in particular Pittioni, 1937, 1954). It differs across three regional manifestations according to material culture (ceramics, metal objects such as dress pins, arm rings, and torques), burial rites (orientation), and other features. North of the

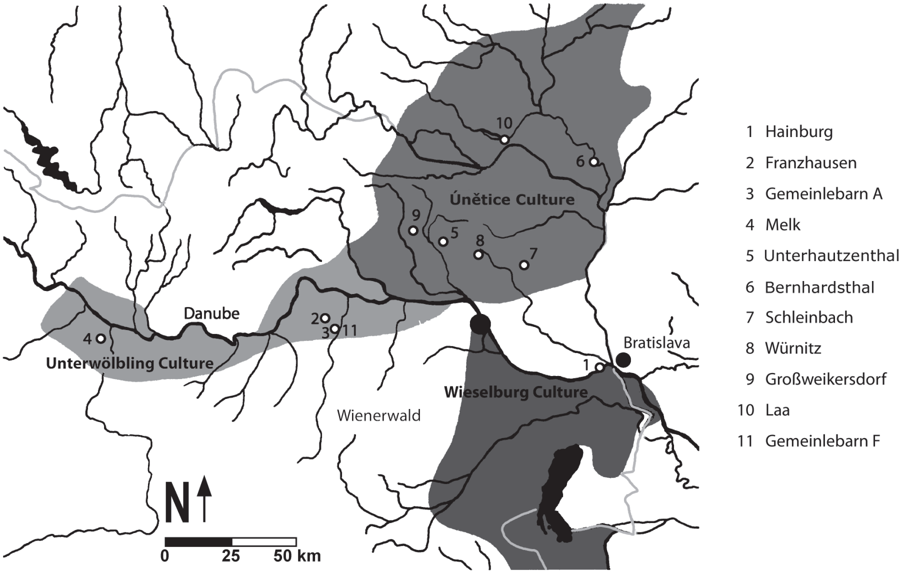

Fig. 1 - Spread of cultural groups of the Early Bronze Age (2300-1500 BC) in Lower Austria. The numbers 1 through 11 indicate the sites included in this study.

Danube, in the Weinviertel, between Kamptal in the west and the river March in the east, lay the domain of the Únětice culture; in the southern region of the Danube Alps foreland, between the river Enns and the Wienerwald, especially along the tributary streams of the Danube, was the area of the Unterwölbling culture. The third regional manifestation was the Wieselburg or Gata group, which lay south of the Danube and east of the Wienerwald, as well as in northern Burgenland (Fig.1). Our study is based on finds obtained by rescue excavations of the Federal Bureau of Preservation of Archaeological Monuments and other institutions (Leeb, 1987; Neugebauer, 1991, 1994; Trnka, 1993/1994; Krenn-Leeb, 1994, 2006, 2008; Lauermann, 1995; 2003; Neugebauer & Neugebauer, 1997; Neugebauer & Blesl, 1998; see also Sprenger, 1996; Lippert *et al*., 2001; Blesl, 2005a, b, c).

Anthropological investigations have addressed these Early Bronze Age populations in many ways. Early studies were mostly descriptive and focused on metrical and morphological parameters (Szombathy, 1934; J. Weninger, 1954; M. Weninger, 1954; Ehgartner, 1959), while more recent studies address pathological and demographical issues to reconstruct the living conditions of these populations (Teschler-Nicola, 1982-85; Teschler-Nicola, 1988, 1989; Heinrich & Teschler-Nicola, 1991; Schultz & Teschler-Nicola, 1989; Ziemann-Becker, 1992; Pirsig *et al.*, 1992; Teschler-Nicola & Prossinger, 1992, 1997; Kneissel *et al*., 1994; Teschler-Nicola & Gerold, 2001; Novotny, 2005). In a morphometric study of the Early Bronze Age skeletal collection stored at the Natural History Museum Vienna, Teschler-Nicola (1992a) found significant mean differences among the members of the three archaeologically distinct areas. She interpreted this finding as a genetic consequence of geographical barriers, such as the river Danube and the Wienerwald.

Despite these studies, relatively little is known about the migration pattern of these populations and the degree of genetic isolation or population admixture. In the present paper we investigate the craniofacial morphology of the east Austrian Early Bronze Age populations by including newly excavated remains and by the use of geometric morphometric methods. We compute morphological distances among population-, site-, and sex-specific average forms and shapes, and examine how they reflect possible migration scenarios.

Given the clear geographical separation of the populations and the resulting restrictions on migration, we expect that morphological distances should express geographic distances to some degree. In particular, as the river Danube presents a barrier for migration, we expect relatively large morphological distances between populations from opposite sides of the Danube. Archaeological findings (Grupe *et al.*, 1997) substantiate the presence of a patrilocal system characterized by higher mobility of females than of males. Thus we would expect female population mean forms to be more similar than male mean forms, but female migration should increase within-population variability of females.

Materials and Methods

Material

The sample comprises 171 crania of adult individuals dated to the Early Bronze Age (ca. 2300-1500 BC) and includes four different cultural groups. The southeastern Danubian Wieselburg group includes the necropolis of Hainburg (N=49); the southwestern Danubian Unterwölbling group consists of the sites Franzhausen I, Gemeinlebarn A and Melk (N=78); and the northern Únětice group includes the sites Unterhautzenthal, Bernhardsthal, Schleinbach, Würnitz, Großweikerdorf, and Laa (N=43). These three groups belong to the middle phase of Early Bronze Age, namely the "Gemeinlebarn II" stadium. The Böheimkirchen group of the Věteřov Culture (N=10) represents a later manifestation ("Gemeinlebarn III" stadium) of the cultural groups located in the southwestern Danubian area and includes only the site Gemeinlebarn F. All specimens are stored in the Department of Anthropology at the Natural History Museum of Vienna.

The specimens are a representative sample of the geographic range and age distribution of each population, with males and females approximately equally distributed (Tab. 1). Adulthood was assessed by closure of the spheno-occipital synchondrosis. Sex was taken from previous studies (Heinrich & Teschler-Nicola, 1991; Teschler-Nicola, 1992a; Berner & Wiltschke-Schrotta, 1992; for the Hainburg sample we used data obtained by Novotny *et al.*, unpublished) based on a large range of skeletal traits, among which the pelvic bone was given the largest weight (Ferembach *et al.*, 1979). In addition, archaeological data, such as orientation of the individual in the grave, side position, and grave goods (Neugebauer, 1994), which are considered to be very conservative indicators in Early Bronze Age societies, were taken into account for sex determination.

Data acquisition

To capture overall craniofacial morphology, a total of 58 ectocranial three-dimensional landmarks on the viscerocranium, neurocranium and basicranium were digitized using a Microscribe 3DX (Fig. 2). The landmarks were digitized by A.P. in two separate sessions per skull and were fitted together by a least-squares superimposition of five fiducial points located in both sessions.

Measurement error in landmark acquisition was assessed by digitizing six different specimens on five different occasions. Shape variation across the six skull means was 17.4 times larger than the pooled variation across the repeats. Furthermore, in a principal component analysis the repeated specimens clustered closely together and for all configurations the closest neighbor was a repeat of the same skull. Measurement error thus is negligibly small as compared to the variation between specimens.

Only relatively well-preserved specimens were digitized, but for several individuals it was not possible to measure all landmarks. When landmarks were missing on one side of the cranium only, they were estimated by reflecting the preserved landmarks across the midplane. Landmarks missing on both sides were estimated by warping the average of the complete specimens of the corresponding population to the partially preserved specimens using a thin-plate spline interpolation (Gunz *et al.*, 2004, 2009).

Tab. 1 - Number of specimens for each cultural group, necropolis and sex.

CULTURAL GROUP	NECROPOLIS	CHRONOLOGICAL ATTRIBUTION[1]	N° MALE	N° FEMALE
Wieselburg	Hainburg	Gem II	22	27
	Franzhausen	Gem II	19	25
Unterwölbling	Gemeinlebarn A	Gem II	9	8
	Melk	Gem II	5	3
	Unterhautzenthal	Gem II	8	9
	Bernhardsthal	Gem II	9	4
Únětice	Schleinbach	Gem II	2	1
	Würnitz	Gem II	3	0
	Großweikersdorf	Gem II	3	2
	Laa	Gem II	1	1
Böheimkirchen	Gemeinlebarn F	Gem III	7	3
Total			88	83

[1] Gem = Gemeinlebarn; Early Bronze Age in Austria is chronologically divided into three stages: Gemeinlebarn I (approximately 2300-1800 BC), Gemeinlebarn II (approximately 1800-1600 BC), and Gemeinlebarn III (approximately 1600-1500 BC).

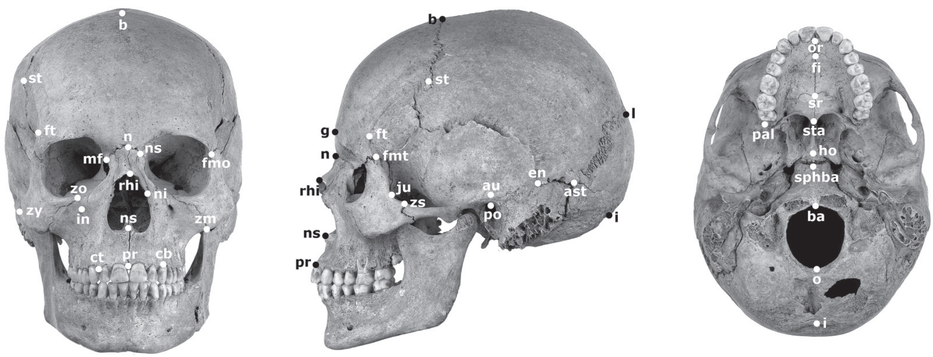

Fig. 2 - Anatomical landmarks digitized on the crania. Bilateral points were taken on both sides. pr = Prosthion; ns = Nasospinale; rhi = Rhinion; n = Nasion; g = Glabella; b = Bregma; l = Lambda; i = Inion; o = Opisthion; ba = Basion; sphba = Sphenobasion; ho = Hormion; sta = Staphylion; sr = Staurion; fi = Foramen incisivum; or = Orale; cb = Canine base; ct = Canine tip; ni = Nasale inferius; ns = Nasale superius; mf = Maxillofrontale; zo = Zygoorbitale; fmo = Frontomalare orbitale; zm = Zygomaxillare; st = Stephanion; ft = Frontotemporale; fmt = Frontomalare temporale; ju = Jugale; zs = Zygotemporale superior; zy = Zygion; au = Auriculare; po = Porion; ms = Mastoidale; in = Infraorbitale; ast = Asterion; en = Entomion; pal = Postalveolare.

Analysis of size and shape

Shape coordinates of the landmark configurations were computed by a Generalized Procrustes Analysis (Rohlf & Slice, 1990; Bookstein 1996; Rohlf, 1999; Zollikofer & Ponce de Leon, 2002; Mitteroecker & Gunz, 2009). Most geometric morphometric analyses are based on shape variables only, but the statistical separation of groups is more effective when based on both shape and size. The specimens were thus ordinated with a relative warp analysis in Procrustes form space (Dryden & Mardia, 1998; Mitteroecker *et al.*, 2004, 2005), which is a principal component analysis (PCA) of the matrix of shape coordinates augmented by one single additional column for the natural logarithm of Centroid Size (logCS). In biological data, where allometry is present, log CS typically has the largest variance of any column of this matrix, and thus allometric shape and geometric size are expressed in a single size-shape component, the first principal component of that space (Mitteroecker *et al.,* 2004; Schaefer *et al.*, 2004). A PCA of Procrustes shape space is given in the supplementary online material.

The statistical significance of mean form differences and of differences in total form variation was computed by permutation tests (5000 random permutations). To assess the association of mean form differences with the geographic distribution of the sites, we regressed Procrustes form distances on geographic distances and on a dummy variable that is 0 when both sites are on the same side of the river Danube and 1 when they are on opposite sides. All analyses were performed in Morpheus (Slice, 2008), Morphologika 2.5 (O'Higgins & Jones, 2006) and Mathematica 7.0 (Wolfram Research).

Results

Figure 3 shows a scatterplot of the first two principal component scores, accounting for 34.1% of form variation. Males and females differ along the first PC whereas the populations differ mainly but not exclusively along PC 2. The remaining PCs do not substantially contribute to group separation and have a smooth eigenvalue distribution (the first eigenvalues are 0.261, 0.086, 0.049, 0.036, 0.034, 0.031, 0.029, …). In the first two components, the southern Wieselburg group and the chronologically younger Böheimkirchen group are partly separated from the Únětice group north of the Danube. The Unterwölbling group is more intermediate and overlaps with the others. While most individuals from the Wieselburg Culture have positive PC 2 scores, eight individuals (5 females and 3 males recovered from the Hainburg site) have negative PC 2 scores and overlap with the northern Danubian groups. Interestingly, all eight specimens have been associated with objects (ceramics and metal grave goods) typical for the Únětice Culture (Krenn-Leeb, personal communication). Apart from these specimens the Wieselburg group largely separates from the northern populations in the PC plot.

Form variation along the first two principal components is visualized in Figures 4 and 5 as deformations of a polyhedral surface representation of the average landmark configuration. PC 1, which represents allometric form variation within the sample, comprises changes in the relative size of the viscerocranium and neurocranium along with differences in the protrusion of glabella and the nasal bone as well as in maxillary and zygomatic breadth. High scores along PC 2 correspond to relatively broad and short crania, while low scores are associated with relatively narrow and elongated crania.

Pairwise permutation tests indicate significant differences between the population mean forms ($P<0.0004$ for each of the six tests based on all Procrustes shape coordinates). Male and female mean forms significantly differ within each population ($P<0.0006$ for each of the four tests).

In the PCA shown in Figure 3, males appear to be more variable than females. Also, males have more variance than females in full form space (0.00473 vs. 0.00400, significant at $P<0.005$) and likewise in shape space (0.00400 vs. 0.00341, $P<0.002$). Indeed, males have a larger variance of population mean forms as compared to females (0.00108 vs. 0.00073) as well as

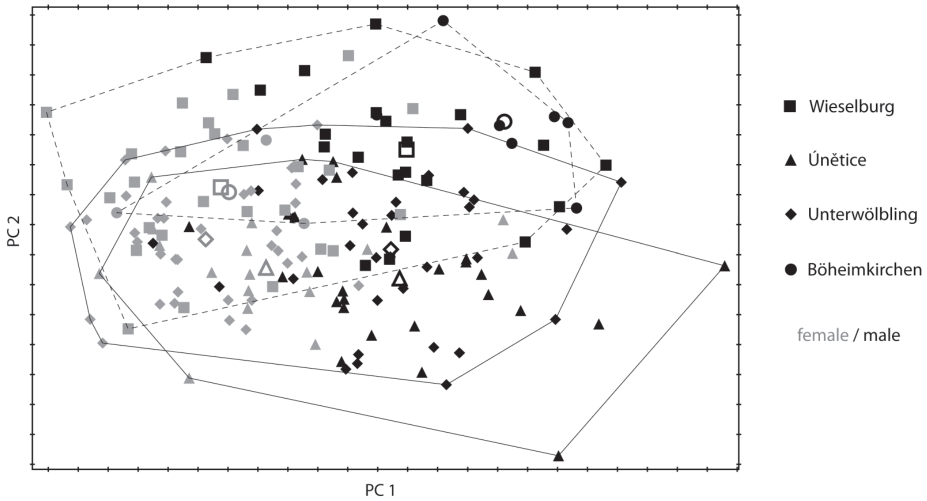

Fig. 3 - Principal components (PCs) in Procrustes form space for the full sample. Black symbols represent male individuals, gray symbols females. The large open symbols are the sex-specific population group means. The convex hulls of the Wieselburg group and the Böheimkirchen group are shown as dashed lines, those of the Unterwölbling group and the Únětice group as solid lines. The corresponding shape variation is visualized in Figures 4 and 5.

a larger within-population variance (0.00415 vs. 0.00366).

Figure 6 shows a PCA of the sex-specific and site-specific group mean forms. In the northern Únětice group we included just the sites of Unterhautzenthal and Bernhardsthal because of the small sample size of the other groups. The ordination of the site mean forms resembles the geographic distribution of the groups, and again the female mean forms are more similar to each other than the male mean forms are. Procrustes distances between the site mean forms are given in Table 2.

We regressed Procrustes form distances between site means on geographic distances and on a dummy variable encoding the location relative to the river Danube. We did not include Gemeinlebarn F in these calculations as it is from a later period than the other sites. Geographic distance explains 14.4 % of form distance variation, whereas the Danube explains 55.4%. Computed separately for each sex, the model explains 18% of form distance variation in males and 43% in females; the effects of geographic distances and of the river Danube are both larger in females than in males. The same pattern results when using shape distances instead of form distances, but the fractions of explained variances are generally lower. Log transformation of morphological and geographic distances did not substantially change the results.

Discussion

According to its archaeological, geographical, and temporal characteristics, our sample of Bronze Age populations from Lower Austria has been divided into four main groups: the Únětice group (north of the Danube), the Unterwölbling group (southwest of the Danube), the Wieselburg group (southeast of the Danube), and the Böheimkirchen group of the so-called "Věteřov Culture", which represents a later manifestation of the Early Bronze Age (transition to the Middle Bronze Age) located in the southwestern Danubian area. Confirming previous results (Teschler-Nicola, 1992a), we found significant differences in cranial form between populations and between sexes. The pattern of morphological differences is shown by the ordination analysis of Procrustes form distances (Figs. 3, 4, 5). The first PC represents overall size along with allometric shape variation within the sample and separates males from females. This pattern is in agreement with many other studies showing that sexual dimorphism in the human cranium consists to a large extent of allometric differences (e.g., Shea, 1986; Rosas & Bastir, 2002; Schaefer *et al.*, 2004; Bulygina *et al.*, 2006). The second component corresponds to relatively broad and short crania versus relatively narrow and elongated crania. This classical component of 'brachycephaly' versus 'dolichocephaly', apparently unrelated to sexual dimorphism, also involves variation in maxillary prognathism and nasal bone morphology as well as changes in the cranial base angulation (compare, e.g., Rosas & Bastir, 2002; Bookstein *et al.*, 2003; Bastir & Rosas, 2004; Mitteroecker & Bookstein, 2008).

In the PCA, the Wieselburg population, located southest of the Danube, separates almost completely from the Únětice population north of the Danube. This supports previous findings that those groups were culturally and phenotypically distinct (Neugebauer, 1994; Teschler-Nicola, 1992a). Yet eight individuals buried in the Wieselburg territory match morphological and archaeological attributes of the Únětice group. This is supported by archaeological findings (metal typology) suggesting an affinity to the Únětice-Wieselburg mixed (cultural) group of SW Slovakia (Schubert, 1973; Leeb, 1987, p.67).

The Unterwölbling group, spreading over the southwestern Danubian area, overlaps with both the Wieselburg and the Únětice group. The exceptional wealth of the recovered grave goods in Franzhausen I and the location of the site as a "crossing point" between N-S and E-W trading routes suggest that the Unterwölbling population played a key role in trading bronze objects, knowledge, and maybe experts (Neugebauer 1994; Sprenger, 1996). The overlap of this population with the other groups in form space may reflect the larger degree of admixture due to the population's central role in an early socio-economic network.

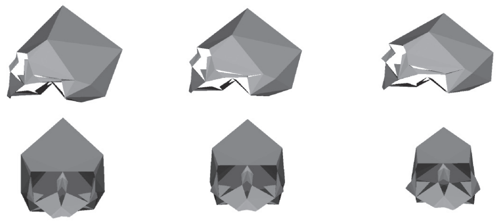

Fig. 4 - Visualization of the shape variation along the first principal component in form space as deformations of a polyhedral surface representation of the average cranium (middle shapes). The left shapes correspond to negative PC scores, the right shapes to positive scores (three standard deviations from the mean). Positive scores are associated with a large viscerocranium relative to the neurocranium, along with a pronounced glabella and nasal bone.

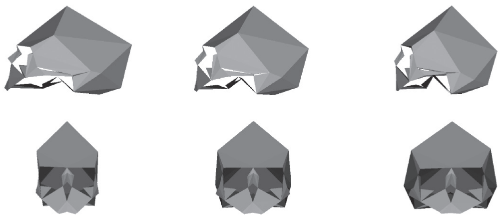

Fig. 5 - Visualization of the shape variation along the second principal component in form space. Positive scores are associated with a short and broad cranium together with a flat occipital region and retrognathic alveolar and nasal bones.

The Böheimkirchen group (Gemeinlebarn F) inhabiting the southwestern Danubian area in the later phase of the Early Bronze Age differs morphologically from the chronologically older Unterwölbling group. This is especially apparent when comparing the mean forms of Gemeinlebarn A and Gemeinlebarn F, which differ temporally by only a few decades. There is evidence that life conditions changed during the early Bronze Age (Teschler-Nicola & Prossinger, 1992, 1997; Teschler-Nicola & Gerold, 2001) and these changes could have affected cranial morphology. Morphological changes in humans induced by environmental changes have been documented in

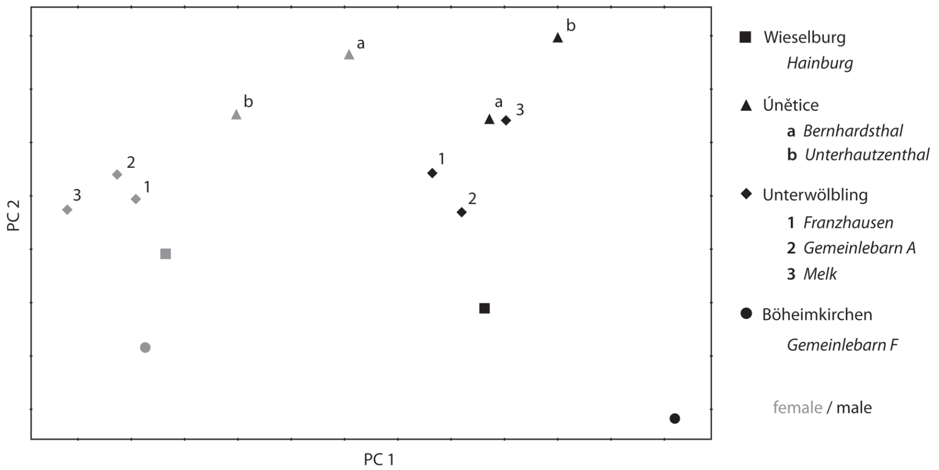

Fig. 6 - Principal components (PC) of the sex-specific and site-specific mean configurations in Procrustes form space.

Tab. 2 - Procrustes form distances between male group mean configurations (bold) and between female group mean configurations.

	WIES	BÖHE	UNTW			ÚNĚ	
	Hain	**Gem F**	**Fran**	**Gem A**	**Melk**	**Unth**	**Bern**
Hain	-	0.044	0.027	0.044	0.035	0.036	0.051
Gem F	**0.047**	-	0.041	0.042	0.048	0.051	0.061
Fran	**0.040**	**0.061**	-	0.037	0.028	0.033	0.048
Gem A	**0.044**	**0.055**	**0.032**	-	0.043	0.046	0.056
Melk	**0.045**	**0.062**	**0.035**	**0.040**	-	0.046	0.060
Unth	**0.051**	**0.065**	**0.044**	**0.047**	**0.044**	-	0.036
Bern	**0.041**	**0.058**	**0.036**	**0.042**	**0.037**	**0.035**	-

Wies - Wieselburg
Hai - Hainburg
Böhe - Böheimkirchen
Gem F - Gemeinlebarn F

Untw - Unterwölbling
Fran - Franzhausen
Gem A - Gemeinlebarn A
Melk - Melk

Úně - Únětice
Unth - Unterhautzenthal
Bern - Bernhardsthal

a large range of secular trend studies (e.g., Boas, 1912; Hunter & Garn, 1969; Smith, *et al*., 1986; Buretic-Tomljanovic *et al*., 2003; Jantz & Jantz, 2000; Wescott & Jantz, 2005). Also, analyses of metal objects recovered from Wieselburg sites suggest an intensification of trading and an exchange of knowledge at the transition between the Early and Middle Bronze Age (Duberow *et al*., 2009). While Early Bronze Age artifacts correspond in their lead isotope ratios to Slovakian deposits (in the east), the ratios for objects from the Middle Bronze Age lie within the range of the ore field of the Mitterberg (in the west), indicating an increase in mobility between settlement areas in the east (Wieselburg group) and the west (Böheimkirchen group). Thus, in addition to secular changes, the morphological difference between the two populations Gemeinlebarn A and F may have partly been a result of gene flow. The smaller Procrustes distance between males of these groups than between females leads to speculations about higher male migration rates in response to intensified trading. Further investigations might elucidate these complex issues of cultural alteration as a biological phenomenon.

As predicted for a patrilocal system in which females have a larger marriage domain than males, we found that female mean forms have less variance than male mean forms. Contrary to our expectation, females also have less within-population variance. But males typically are more variable than females – they grow longer and faster, leading to a larger and more variable adult size. Similarly, Teschler-Nicola (1992a) found a higher variability of average craniometrical traits in males than in females. Archaeological evidence such as the small settlement sizes, demographic parameters (Heinrich & Teschler-Nicola, 1991; Teschler-Nicola, 1992a; Novotny, 2005) and sex- and culture-specific grave goods ("foreign women"), suggest that a patrilocal system was widespread in Early Bronze Age societies. Also, Grupe *et al.* (1997), using archaeometric methods, found a high number of immigrating females among the Bell Beaker people in Central Europe.

A linear model including geographic distance and position of the site relative to the river Danube accounted for 64% of form distance variation across site means; the effect of being north or south of the Danube was much larger than that of geographic distance per se. This reflects isolation by distance, which is found to be a common pattern among human populations (e.g., Relethford 2004, 2008). When computed separately for each sex, the model explained more than twice as much variation in females as in males. This again indicates that females had a higher migration rate and that female migration was more affected by geographical constraints than male migration.

In summary, cranial morphology reflects social, geographic, and temporal relationships among these Early Bronze Age populations, even though they inhabited a relatively small geographic area and shared similar ecological conditions. Smaller variation across female mean forms and a stronger influence of geographical distances as compared to males indicate a patrilocal system with larger female marriage domains.

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