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Gábor Holló
László Szathmáry
Antónia Marcsik
Zoltán Barta

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Linear Measurements of the Neurocranium Are Better Indicators of Population Differences than Those of the Facial Skeleton: Comparative Study of 1,961 Skulls

GÁBOR HOLLÓ,[1,2] LÁSZLÓ SZATHMÁRY,[1] ANTÓNIA MARCSIK,[3] AND ZOLTÁN BARTA[1]

Abstract The aim of this study is to individualize potential differences between two cranial regions used to differentiate human populations. We compared the neurocranium and the facial skeleton using skulls from the Great Hungarian Plain. The skulls date to the 1st–11th centuries, a long space of time that encompasses seven archaeological periods. We analyzed six neurocranial and seven facial measurements. The reduction of the number of variables was carried out using principal components analysis. Linear mixed-effects models were fitted to the principal components of each archaeological period, and then the models were compared using multiple pairwise tests. The neurocranium showed significant differences in seven cases between nonsubsequent periods and in one case, between two subsequent populations. For the facial skeleton, no significant results were found. Our results, which are also compared to previous craniofacial heritability estimates, suggest that the neurocranium is a more conservative region and that population differences can be pointed out better in the neurocranium than in the facial skeleton.

The human cranium is a widely studied paleoanthropological subject. It probably constitutes the most complex part of the skeleton, housing the brain and different sense organs (Enlow 1990; Hallgrímsson et al. 2007). The skull is composed of three embryologically distinct portions that follow a morphologically integrated and hence somewhat independent development and variation: the basicranium, the neurocranium, and the facial skeleton (Ackermann 2005; Bastir et al. 2006; Cheverud 1982; González-José et al. 2004; Lieberman et al. 2002).

In the present study we address the question of whether the neurocranium and the facial skeleton, represented here by two sets of selected linear measurements, differ from each other in depicting differences between populations. It is important to emphasize that in this work we do not attempt to estimate degrees of genetic relationships among populations to examine the problem of reconstructing

[1] Department of Evolutionary Zoology and Human Biology, University of Debrecen, P.O. Box 3, Debrecen H-4010, Hungary.
[2] Department of General Psychology, University of Debrecen, P.O. Box 28, Debrecen H-4010, Hungary.
[3] Department of Anthropology, University of Szeged, P.O. Box 660, Szeged H-6701, Hungary.

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genetic relations based on morphological data [see Collard and Wood (2000) and Hlusko (2004) versus Manica et al. (2007), Relethford (2004), Roseman (2004), Roseman and Weaver (2007), and Sparks and Jantz (2002)]. We merely investigate the extent to which the linear measurements of the neurocranium and the facial skeleton are suitable for indicating potential shape differences among the archaeologically well-distinct populations that lived in the territory of the Great Hungarian Plain between the 1st and the 11th centuries A.D.

The neurocranium and the facial skeleton differ from each other functionally and ontogenetically. The neurocranium protects the brain, the center of the nervous system, whereas the facial skeleton holds our most important sense organs as well as the aperture of the alimentary canal. To a certain extent, the evolutionary tracks of the two cranial parts followed different directions from early hominins to the derived modern human (increasing neurocranial globularity vs. facial retraction) (Bookstein et al. 2003; Lieberman et al. 2002). The neurocranium ends its growth and development earlier than the splanchnocranium (facial skeleton) (Bastir et al. 2006, 2007; Bookstein et al. 2003; Kohn 1991; Zollikofer and Ponce de León 2002), and hence it is expected to be under minor influence of environmental effects. Accordingly, the two cranial parts should diverge in reflecting population differences.

Previous studies used the neurocranium to follow population history (Gunz et al. 2009; Harvati and Weaver 2006; Holló et al. 2008), whereas other studies showed that facial measurements were informative markers of genetic distances (Betti et al. 2009; Perez et al. 2007; Schillaci 2008).

During the time span considered in our study, climatic fluctuations in the Carpathian basin were modest (Jakab et al. 2009; Rácz 2001; Sümegi et al. 2009) and probably did not play a special role in differentially affecting the facial skeleton of the population samples used in this study (Bastir and Rosas 2004; González-José et al. 2005; Harvati and Weaver 2006; Kohn 1991; Roseman 2004; Strand Viðarsdóttir et al. 2002). Accordingly, here we test the null hypothesis that, compared to the neurocranium, the facial skeleton is a less sensitive marker of dimensional population differences.

Materials and Methods

We examined skulls from the 1st to the 11th centuries excavated in the Great Hungarian Plain. The region, which forms the western border of the Eurasian steppe, covers an area of approximately 100,000 km^2 and is situated in the Carpathian basin in Central Europe.

The database is from 4,001 adult crania: 1,540 were measured by our research group, and the remaining record is derived from previous publications (see Szathmáry et al. 2008). The material comes from 147 archaeological sites. They are dated to seven chronocultural periods: the Sarmatian period (1st–4th century), the transition period (400–420), the Hun-Gepidic epoch (420–455 and

455–567) (in tables and figure captions, this is simply indicated as Gepidic), the Early Avar age (568–670, ca.), the Late Avar age (about 670–800; later it corresponds to 895), the period of the Hungarian conquest and settlement (895–1000, i.e., the 10th century), and the 11th century, part of the Arpadian age. A more detailed description of the historical background is provided by Holló et al. (2008).

The bones are preserved in museums (Department of Anthropology, Hungarian Natural History Museum, Budapest; Jósa András Museum, Nyíregyháza, Hungary; Hermann Ottó Museum, Miskolc, Hungary; and Vasvári Pál Museum, Tiszavasvári, Hungary) and provisionally at the universities of Debrecen and Szeged, for scientific examinations. Sex was determined according to the method of Acsádi and Nemeskéri (1970). For the definition of adulthood we followed the criteria of Nemeskéri et al. (1960) and Johnston (1961).

Thirteen linear measurements on the skull were analyzed (Martin 1928): maximum cranial length, basion-nasion distance, maximum cranial breadth, minimum frontal breadth, basion-bregmatic height, and porion-bregmatic height on the neurocranium; and bizygomatic breadth, upper facial height (nasion-prosthion distance), orbital breadth, orbital height, nasal breadth, nasal height, and bigonial breadth on the facial skeleton.

In the present work we examined 1,961 skulls, among which 822 crania have no missing values. A further 751 skulls have no missing neurocranial values, whereas 388 have a complete series of facial data. As a whole, 1,573 (822 + 388) and 1,210 (822 + 388) crania have been used in this study to describe the neurocranium and the facial skeleton, respectively.

The means and standard deviations of the measurements are presented in Table 1 (neurocranium) and Table 2 (facial skeleton), and the chronocultural distribution of the material is shown in Table 3. Females and males were analyzed together because of the poor sample size of the facial data set for some early periods (notably, the Sarmatian, transition, and Hun-Gepidic). Therefore the data were standardized (Studentized) in the course of the principal components analysis.

Statistical analyses were carried out in the R interactive statistical environment (R Development Core Team 2008). Principal components analyses were performed by the R function prcomp (R Development Core Team 2008). We analyzed the first two principal components (the eigenvalues of the principal components are reported in Table 4). Linear mixed-effects models were fitted (lmer function of the lme4 package; Bates 2007), where the archaeological sites were entered as a random factor (Reiczigel et al. 2007; Searle 1971). Pairwise multiple comparisons (Hsu 1996; Reiczigel et al. 2007) between the models representing the archaeological periods were done using the glht function of the multcomp package (Hothorn et al. 2008). All the subpopulations (according to archaeological period) were satisfactorily tested for normal distribution (R function qqnorm; R Development Core Team 2008).

Table 1. Means (and Standard Deviations) of the Single Measurements According to Archaeological Period: Neurocranial Dimensions

Archaeological Period	*Maximum Cranial Length (mm)*	*Basion-Nasion Distance (mm)*	*Maximum Cranial Breadth (mm)*	*Minimum Frontal Breadth (mm)*	*Basion-Bregmatic Height (mm)*	*Porion-Bregmatic Height (mm)*
Sarmatian period (1st–4th century)	176.5 (8.6)	101.0 (5.8)	140.2 (7.3)	96.3 (4.9)	134.3 (7.3)	113.7 (6.9)
Transition period (400–420)	179.7 (7.2)	101.8 (5.3)	138.7 (6.8)	96.9 (4.4)	136.4 (6.8)	114.1 (7.2)
Gepidic epoch (420–567)	179.9 (6.8)	101.8 (5.7)	136.7 (5.1)	95.6 (4.5)	134.4 (5.4)	114.1 (4.6)
Early Avar age (568–c. 670)	178.3 (7.4)	98.9 (5.8)	141.7 (6.3)	95.2 (4.7)	129.1 (7.2)	110.4 (6.8)
Late Avar age (c. 670–895)	178.4 (7.4)	98.8 (5.2)	142.0 (6.4)	95.8 (4.7)	128.7 (6.8)	111.9 (6.1)
10th century (895–1000)	179.5 (7.7)	100.5 (5.1)	141.9 (7.0)	96.9 (4.8)	133.0 (5.5)	111.8 (6.1)
11th century	180.7 (7.4)	100.4 (5.2)	138.7 (5.8)	96.5 (4.7)	132.5 (6.4)	111.6 (6.2)

Table 2. Means (and Standard Deviations) of the Single Measurements According to Archaeological Period: Facial Dimensions

Archaeological Period	*Bizygomatic Breadth (mm)*	*Upper Facial Height (mm)*	*Orbital Breadth (mm)*	*Orbital Height (mm)*	*Nasal Breadth (mm)*	*Nasal Height (mm)*	*Bigonial Breadth (mm)*
Sarmatian period (1st–4th century)	130.7 (7.9)	67.3 (6.0)	40.5 (2.5)	32.8 (1.6)	24.4 (1.6)	50.7 (3.7)	100.2 (9.8)
Transition period (400–420)	130.0 (6.9)	69.4 (3.7)	39.4 (2.0)	33.0 (1.7)	23.9 (1.8)	51.3 (3.2)	98.9 (8.7)
Gepidic epoch (420–567)	132.4 (7.0)	70.5 (4.9)	41.5 (1.8)	32.7 (1.7)	24.6 (1.8)	51.4 (3.5)	101.9 (6.4)
Early Avar age (568–c. 670)	131.2 (7.2)	70.0 (5.2)	39.7 (2.5)	33.4 (2.1)	25.5 (2.2)	51.4 (3.7)	100.7 (7.8)
Late Avar age (c. 670–895)	131.2 (7.2)	69.4 (5.2)	40.3 (2.2)	33.4 (2.2)	25.3 (2.0)	51.0 (3.5)	98.6 (7.7)
10th century (895–1000)	132.9 (6.6)	69.3 (4.9)	40.8 (2.3)	33.2 (2.4)	25.3 (2.1)	51.5 (3.5)	101.0 (6.9)
11th century	130.9 (6.8)	70.4 (4.8)	40.0 (2.4)	33.1 (2.3)	24.7 (1.9)	50.9 (3.6)	100.7 (7.1)

Table 3. Number of Skulls of the Three Subsets in Diverse Archaeological Periods

Archaeological Period	*Neurocranium*	*Facial Skeleton*	*Complete Data Subset*
Sarmatian period (1st–4th century)	57	20	19
Transition period (400–420)	53	27	18
Gepidic epoch (420–567)	78	33	26
Early Avar age (568–c. 670)	192	163	103
Late Avar age (c. 670–895)	808	694	482
10th century (895–1000)	192	152	86
11th century	193	121	88
Total	1,573	1,210	822

Results

Neurocranial Measurements. In our previous study (Holló et al. 2008), we made an attempt to explore the correlation between anatomical profiles and cultural changes induced by sequential populations on the basis of the neurocranium, and we used the same database as in the present paper. Thus here we refer only to the statistics of the neurocranial principal components published in that study. The matrix of variable loadings is presented by Table 5.

Figure 1, which shows the means of the principal components in the diverse periods, reveals a possible sudden change between the Gepidic and Avar ages in both PC1 and PC2. Conversely, a tendency in the principal components throughout the entire time span considered in this study cannot be observed. Pairwise tests of the linear mixed-effects models (LMMs) show that in PC1, the overall size factor, there are significant differences between the transition and the Early Avar periods ($z = -3.092$, $p = 0.030$).

Table 4. Eigenvalues of the Principal Components

	Principal Component						
	PC1	*PC2*	*PC3*	*PC4*	*PC5*	*PC6*	*PC7*
Eigenvalue for neurocranium	2.837	1.055	0.840	0.581	0.446	0.242	
Eigenvalue for facial skeleton	3.280	1.080	0.835	0.710	0.500	0.322	0.274
Eigenvalue for neurocranium (822 individuals without missing values)	2.892	1.034	0.845	0.583	0.439	0.208	
Eigenvalue for facial skeleton (822 individuals without missing values)	3.301	1.085	0.820	0.710	0.512	0.305	0.268

Table 5. Matrices of Variable Loadings

Measurement	*PC1*	*PC2*
Neurocranium		
Maximum cranial length	0.426	–0.028
Basion-nasion distance	0.460	0.296
Maximum cranial breadth	0.251	–0.791
Minimum frontal breadth	0.402	–0.348
Basion-bregmatic height	0.456	0.399
Porion-bregmatic height	0.417	0.079
Facial skeleton		
Bizygomatic breadth	0.448	–0.307
Upper facial height	0.433	0.290
Orbital breadth	0.329	–0.118
Orbital height	0.265	0.679
Nasal breadth	0.307	–0.364
Nasal height	0.441	0.279
Bigonial breadth	0.380	–0.370
Neurocranium (822 individuals without missing values)		
Maximum cranial length	–0.425	0.047
Basion-nasion distance	–0.467	–0.296
Maximum cranial breadth	–0.244	0.817
Minimum frontal breadth	–0.404	0.292
Basion-bregmatic height	–0.459	–0.395
Porion-bregmatic height	–0.410	–0.042
Facial skeleton (822 individuals without missing values)		
Bizygomatic breadth	0.450	–0.309
Upper facial height	0.431	0.308
Orbital breadth	0.328	–0.118
Orbital height	0.260	0.677
Nasal breadth	0.308	–0.340
Nasal height	0.441	0.275
Bigonial breadth	0.385	–0.383

In PC2 (assumed as the shape factor) several significant results are found: the Gepidic and Early Avar ages are the only subsequent periods that differ significantly ($z = –4.049$, $p < 0.001$). The other periods are nonsubsequent: transition period–Late Avar age ($z = –4.412$, $p < 0.001$); transition period–10th century ($z = –3.376$, $p = 0.012$); Gepidic epoch–Late Avar age ($z = –6.024$, $p < 0.001$); Gepidic epoch–10th century ($z = –5.003$, $p < 0.001$); Gepidic epoch–11th century ($z = –3.380$, $p = 0.012$); and Late Avar age–11th century ($z = 3.209$, $p = 0.021$). [A priori, the analysis appropriately considered the basion-nasion distance as related to the neurocranium; conversely, the set of measurements specifically describing the basicranium is missing here, where the tested dichotomy is neuro- vs. splanchnocranium (facial skeleton), not the basicranial hinge].

Facial Measurements. The first two principal components explain 62.3% of the total variance (PC1: 46.9%; PC2: 15.4%). Bizygomatic breadth, nasal height,

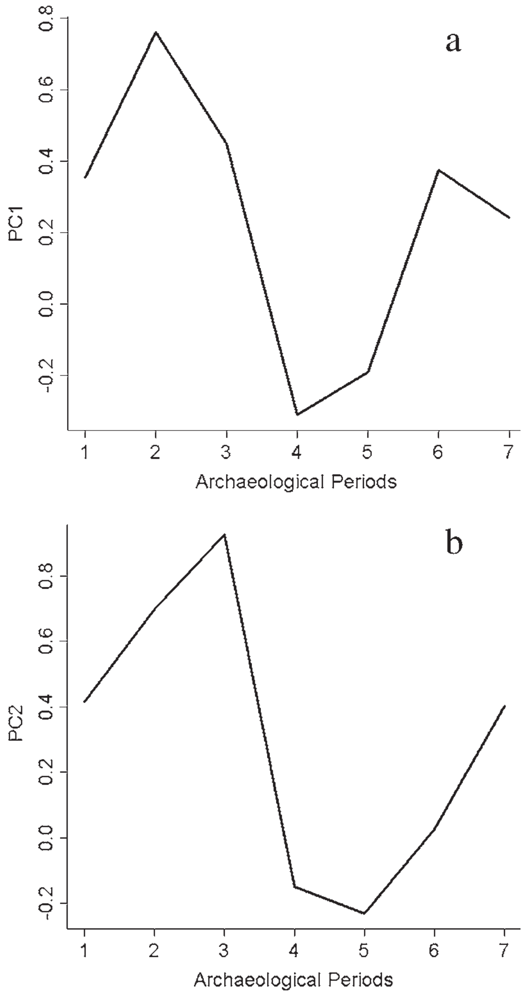

Figure 1. Means of neurocranial principal components: (a) PC1; (b) PC2. Numbers on the horizontal axis represent the seven archaeological periods. (1) Sarmatian period (1st–4th century; *n* = 57); (2) transition period (400–420; *n* = 53); (3) Gepidic epoch (420–567; *n* = 78); (4) Early Avar age (568–c. 670; *n* = 192); (5) Late Avar age (c. 670–895; *n* = 808); (6) Hungarian conquest and settlement (10th century; *n* = 192); (7) 11th century (*n* = 193).

and upper facial height are highly loaded on PC1, whereas the values for the other measurements form a diminishing series (see Table 5). On PC2 the major loading is that of orbital height. Nasal breadth and bigonial breadth have smaller but considerable loadings on PC2. A similar pattern of loadings of the neurocranial and facial measurements has also been demonstrated in previous research (Howells 1973; Peyre 1977, 1980).

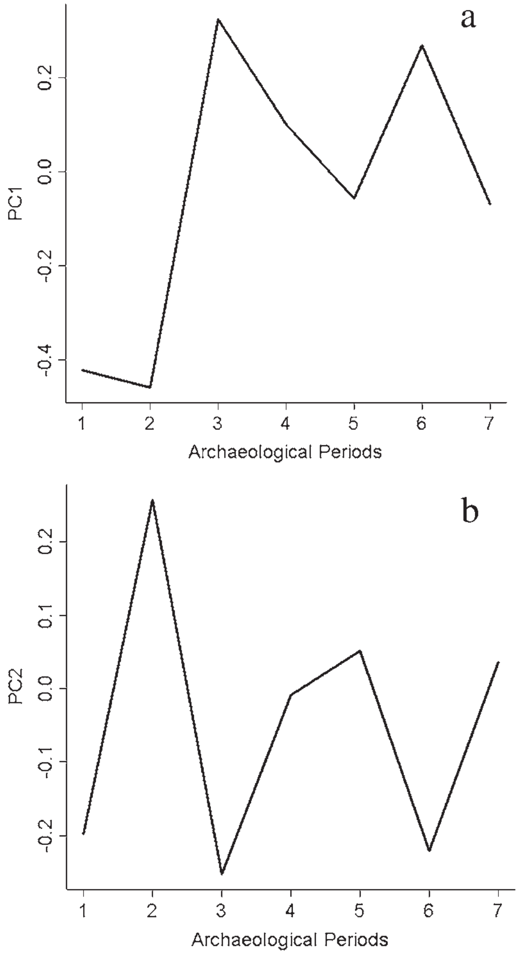

Figure 2. Means of facial principal components: (a) PC1; (b) PC2. Numbers on the horizontal axis represent the seven archaeological periods. (1) Sarmatian period (1st–4th century; $n = 20$); (2) transition period (400–420; $n = 27$); (3) Gepidic epoch (420–567; $n = 33$); (4) Early Avar age (568–c. 670; $n = 163$); (5) Late Avar age (c. 670–895; $n = 694$); (6) Hungarian conquest and settlement (10th century; $n = 152$); (7) 11th century ($n = 121$).

Analyses of variance (ANOVAs) of the LMMs show that archaeological period has no significant effect on any of the models (PC1: $\chi^2_6 = 7.753$, $p = 0.257$; PC2: $\chi^2_6 = 7.577$, $p = 0.271$).

Plots of the means of the principal components show some breaklike patterns in population continuity (Figure 2), but no trends can be detected.

Pairwise comparisons do not show any significant results either between subsequent or nonsubsequent populations.

To have a major control over the results, the analyses were repeated using only the 822 individuals who had no missing values (see Table 3).

Analysis of the Control Group. The results from the subsample with no missing data (control group of 822 crania) are similar to the already given results.

The first two neurocranial principal components account for 65.4% of the total variance (PC1: 48.2%; PC2: 17.2%). The same values for the facial principal components are 47.2% for PC1 and 15.5% for PC2; together they explain 62.6% of the variance. The eigenvalues and the variable loadings are presented in Tables 4 and 5.

ANOVAs of the LMMs indicate that the neurocranial principal components are significantly influenced by the archaeological period (PC1: $\chi^2_6 = 13.272$, $p = 0.0389$; PC2: $\chi^2_6 = 33.528$, $p < 0.001$) and that the effect on the facial principal components is not significant (PC1: $\chi^2_6 = 7.863$, $p = 0.248$; PC2: $\chi^2_6 = 5.463$, $p = 0.486$).

Figure 3, which represents the means of the neurocranial principal components of the control group, shows similar changes to the means indicated in Figure 1 (even if the graphs are inverted according to the positive-negative values of the y axis). Figure 4, which shows the means of the facial principal components of the control group, is almost identical with Figure 2.

The pairwise comparison tests produced six significant results for the neurocranium and no significant results for the facial skeleton. The following significant differences were obtained: for PC1 (of neurocranial measurements), Early Avar age–10th century ($z = 3.125$, $p = 0.026$); for PC2, transition period–Late Avar age ($z = 4.076$, $p < 0.001$), transition period–10th century ($z = 3.675$, $p = 0.004$), Gepidic epoch–Late Avar age ($z = 3.869$, $p = 0.002$), Gepidic epoch–10th century ($z = 3.554$, $p = 0.006$), and Late Avar age–11th century ($z = 3.003$, $p = 0.038$).

Comparing these results to those obtained from the analysis of the 1,573 skulls (i.e., the whole sample considered for the neurocranium), we note that it appears as though the analysis of the control group gives significant results for the same periods in five cases. In one case a different result is shown (PC1), and in two cases it is not possible to reveal the significant differences indicated by the analysis of the 1,573 individuals (Gepidic–Early Avar and Gepidic–11th century groups). Such a divergence in the results can be attributed to the lower number of cases in the control group.

Discussion and Conclusions

The results of our analyses suggest that the measurements of the neurocranium carry relevant information about the differentiation of diverse populations, whereas the facial skeleton does so to a minor extent.

A possible explanation of this difference between the two regions is that during ontogenesis, the neurocranium attains adult size and shape earlier than the

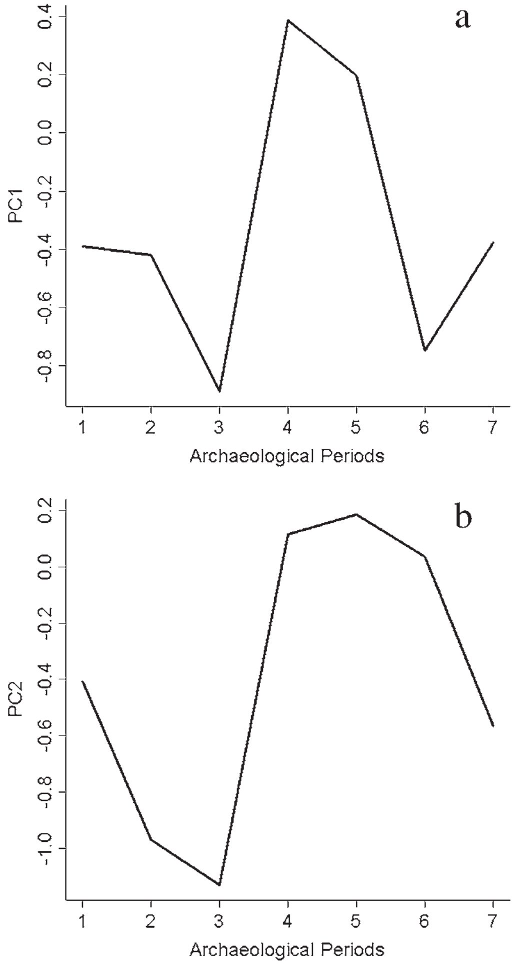

Figure 3. Means of neurocranial principal components of the 822 individuals without missing values: (a) PC1; (b) PC2. Numbers on the horizontal axis represent the seven archaeological periods. (1) Sarmatian period (1st–4th century; *n* = 19); (2) transition period (400–420; *n* = 18); (3) Gepidic epoch (420–567; *n* = 26); (4) Early Avar age (568–c. 670; *n* = 103); (5) Late Avar age (c. 670–895; *n* = 482); (6) Hungarian conquest and settlement (10th century; *n* = 86); (7) 11th century (*n* = 88).

facial skeleton does (Bastir et al. 2006, 2007; Bookstein et al. 2003; Sardi and Ramírez Rozzi 2005; Zollikofer and Ponce de León 2002). Consequently, the facial skeleton is exposed to environmental factors that are different from those acting on the neurocranium during its development, and for a longer time. Accordingly, the development of the face is expected to be more plastic compared to the development of the neurocranium (Bastir and Rosas 2004; Bastir et al. 2006;

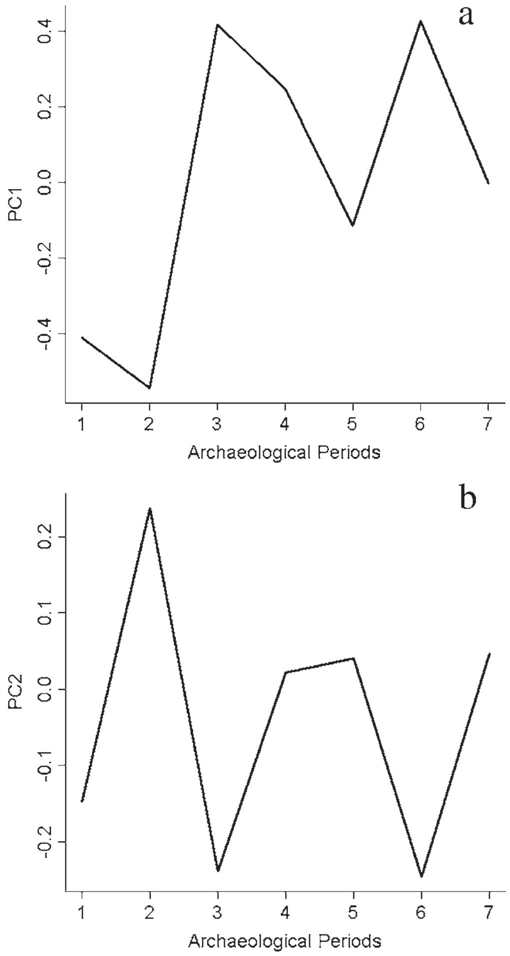

Figure 4. Means of facial principal components of the 822 individuals without missing values: (a) PC1; (b) PC2. Numbers on the horizontal axis represent the seven archaeological periods. (1) Sarmatian period (1st–4th century; *n* = 19); (2) transition period (400–420; *n* = 18); (3) Gepidic epoch (420–567; *n* = 26); (4) Early Avar age (568–c. 670; *n* = 103); (5) Late Avar age (c. 670–895; *n* = 482); (6) Hungarian conquest and settlement (10th century; *n* = 86); (7) 11th century (*n* = 88).

Kohn 1991; Strand Viðarsdóttir et al. 2002), and thus it can be expected that some genetically based population differences are better revealed by the neurocranium than by the face (Harvati and Weaver 2006).

In particular, our results are in close agreement with those obtained by Harvati and Weaver (2006). They compared genetic and three-dimensional geometric morphometric data of recent, globally distributed human populations and found that different cranial regions preserved population history differentially. Neutral genetic distances were associated with temporal bone, neurocranial shape, and total cranial shape distances, whereas facial shape distances did not show that kind of relationship. Harvati and Weaver (2006) also found an association of climatic variables to facial shape. However, the climatic influence on facial shape was mainly driven by the inclusion in the analysis of an arctic population (Inugsuks of Greenland). A similar influence of cold temperature was pointed out by Roseman (2004), who, using linear craniofacial measurements, attributed the large differences observed between the Siberian (Buryat) population and the rest of the world to a cold-mediated natural selection.

In an interesting study Martínez-Abadías et al. (2006) analyzed the morphological outcome on cranial dimensions of the gene flow caused by the Spanish-Amerindian contact. They examined the craniofacial shape of Spanish, Aztec, and admixed populations using a geometric morphometric method. They found that, in the admixed sample, some characteristics expressing global cranial morphology fell between those of the two ancestral groups but that some specific regions, mainly on the face, departed from the intermediate pattern (Martínez-Abadías et al. 2006). These findings also highlight the possibility that the facial skeleton does not reflect genetic distances in the same way that other regions of the skull do.

Nevertheless, different recent studies have emphasized that the facial skeleton is appropriate for reflecting genetic distances. For example, Perez et al. (2007) compared craniometric and genetic data of South American prehistoric populations and found that the facial data allowed them to infer population structure and history. Schillaci (2008) analyzed 10 linear craniometric traits, located mainly on the face, and successfully used them to investigate phylogenetic relationships of early modern humans. Betti et al. (2009) concluded that the best relationship between phenotypic diversity and geographic distance was reflected by a set of traits located on the facial skeleton (see Betti et al., Figure 3), whereas other facial and all neurocranial measurements were shown to be less informative. Smith (2009) recently investigated the relationship between molecular distances and different cranial regions. She pointed out that the morphology of the basicranium, temporal bone, upper face, and the entire cranium was highly correlated with molecular data, whereas the morphological characteristics of the mandible, upper jaw, and cranial vault were not significantly correlated with genetic distances. Smith focused on smaller cranial regions than the present study and showed that one facial region was genetically informative and that two other facial regions were noninformative. Therefore those results regarding the facial skeleton do not necessarily contradict the present findings. Conversely, the results concerning the cranial vault (Smith 2009) contradict our findings.

At least in part, the discrepancies recorded among different studies can be attributed to differences in sample size and composition and to different analytical methods. Nevertheless, our results cannot be completely attributed to the potential plasticity of the face (Betti et al. 2009; Perez et al. 2007; Schillaci 2008).

The marked difference between the neurocranium and the face presented by our results can also be assigned to as yet unexplored evolutionary mechanisms [see also Martínez-Abadías et al. (2006)].

We also deemed it useful to compare our results to heritability estimates of craniofacial measurements and regions presented in earlier publications. It should be noted that many of these analyses were conducted on recent or living populations. Notably, some studies were carried out on monozygotic and dizygotic twins, among siblings, and between parents and their offspring (e.g., Arya et al. 2002; Byard et al. 1984; Devor et al. 1986; Howells 1953, 1966; Nakata et al. 1974; Susanne 1975; Susanne et al. 1983).

Kohn (1991) compared the results of several anthropometric studies also from the point of view of heritability and concluded that there were no significant differences between heritabilities of neurocranial and facial dimensions. However, the problem arises of to what extent the results obtained from data on the skull covered by soft tissue correspond to data obtained from bony landmarks. Although the soft tissue thickness and cranial measurements have medium to high correlations (Simpson and Henneberg 2002), it is known that soft tissue thicknesses are under considerable environmental influence (Carson 2006), and therefore the results obtained through examination of living humans cannot fully overlap those derived from skeletal remains.

Heritability examinations performed on skeletons would be useful; however, they are rare because of a lack of pedigreed skeletal material. Sherwood et al. (2008) recently analyzed an extended pedigree of individuals (from the Fels Longitudinal Study). They used lateral radiographs to calculate narrow-sense heritability values (h^2, the proportion of phenotypic variance resulting from additive genetic effects). Although the study is likely to give more reliable heritability estimates than small samples from museum collections, we cannot compare our results to the h^2 values obtained by Sherwood and colleagues because they examined different cranial traits from those studied by our research group, with the basion-nasion length being the only exception (Sherwood et al. 2008).

However, a special skull series is suitable for heritability estimates: the decorated crania of Hallstatt, in Austria. This series was first analyzed by Sjøvold (1984) with the help of regression analysis. Sjøvold found that most of Howells's measurements were highly hereditable. Another analysis, using the maximum likelihood method and carried out by Carson (2006) on the same collection, established heritability values different from both those of Sjøvold (1984) and those from studies on living humans. Notably, Carson (2006) concluded that the average heritability value of neurocranial dimensions was higher than that of the facial measurements. However, by analyzing the same data set from Halstatt, Martínez-Abadías et al. (2009) pointed out that there was no significant difference among the heritabilities of facial and neurocranial dimensions. Martínez-Abadías et al. (2009) also concluded that the analyses carried out on the Halstatt crania could have such different results because of the relatively high standard errors resulting from the limited sample size and because of the slight differences in the exact sample composition, data treatment, and model definition. However, even though the two studies were performed on the same data set, the differences in heritability estimates are still striking. For example, Carson (2006) found that maximum cranial breadth, which has the major loading value on PC2 that is responsible for most of the significant results of the present paper, had a heritability value of 0.233 ± 0.115 (minimum $h^2 = 0.000 \pm 0.000$ and maximum $h^2 = 0.867 \pm 0.156$; Carson 2006, Table 3), and Martínez-Abadías et al. (2009) found a heritability value of 0.36 ± 0.14 (minimum $h^2 = 0.00 \pm 0.00$ and maximum $h^2 = 0.43 \pm 0.13$; Martínez-Abadías et al. 2009, Table 2). Although these heritability estimates are currently in use (Betti et al. 2009; Schillaci 2008), divergent results suggest caution in their use, especially when one attempts to examine evolvability (Hansen et al. 2003). It is also important to point out that all these estimations are limited to information on the heritability of single cranial measurements, because they mostly rely on univariate analyses. Therefore, as with univariate methods in general, they do not explain the degree of contribution of single measurements to the general pattern. However, because the human cranium is viewed as a morphologically integrated structure (Ackermann 2005; Bastir and Rosas 2004, 2005, 2006; Bookstein et al. 2003; Cheverud 1982; González-José et al. 2004; Lieberman et al. 2000), we can take these pieces of information into account to only a limited extent.

As a conclusion, we can state that our results support the idea that the neurocranium expresses dimensional differences between diverse populations more effectively than the facial skeleton does. Further research should focus on the comparison of different analytical methods applied to the same data set in order to yield more accurate information on the variation of the human cranium.

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Literature Cited

Ackermann, R. R. 2005. Ontogenetic integration of the hominoid face. *J. Hum. Evol.* 48:175–197.

Acsádi, Gy., and J. Nemeskéri. 1970. *History of Human Life Span and Mortality*. Budapest, Hungary: Akadémiai Kiadó.

Arya, R., R. Duggirala, A. G. Comuzzie et al. 2002. Heritability of anthropometric phenotypes in caste populations of Visakhapatnam, India. *Hum. Biol.* 74:325–344.

Bastir, M., P. O'Higgins, and A. Rosas. 2007. Facial ontogeny in Neanderthals and modern humans. *Proc. R. Soc. Lond. B* 274:1125–1132.

Bastir, M., and A. Rosas. 2004. Facial heights: Evolutionary relevance of postnatal ontogeny for facial orientation and skull morphology in humans and chimpanzees. *J. Hum. Evol.* 47:359–381.

Bastir, M., and A. Rosas. 2005. Hierarchical nature of morphological integration and modularity in the human posterior face. *Am. J. Phys. Anthropol.* 128:26–34.

Bastir, M., and A. Rosas. 2006. Correlated variation between the lateral basicranium and the face: A geometric morphometric study in different human groups. *Arch. Oral Biol.* 51:814–824.

Bastir, M., A. Rosas, and P. O'Higgins. 2006. Craniofacial levels and the morphological maturation of the human skull. *J. Anat.* 209:637–654.

Bates, D. 2007. *lme4: Linear Mixed-Effects Models Using S4 Classes—R Package Version 0.99875-9*. http://www.r-project.org/.

Betti, L, F. Balloux, W. Amos et al. 2009. Distance from Africa, not climate, explains within-population phenotypic diversity in humans. *Proc. R. Soc. Lond. B* 276:809–814.

Bookstein, F. L., P. Gunz, P. Mitteroecker et al. 2003. Cranial integration in *Homo*: Singular warps analysis of the midsagittal plane in ontogeny and evolution. *J. Hum. Evol.* 44:167–187.

Byard, P. J., K. Sharma, J. M. Russel et al. 1984. A family study of anthropometric traits in a Punjabi community. II. An investigation of familial transmission. *Am. J. Phys. Anthropol.* 64:97–104.

Carson, E. A. 2006. Maximum likelihood estimation of human craniometric heritabilities. *Am. J. Phys. Anthropol.* 131:169–180.

Cheverud, J. M. 1982. Phenotypic, genetic, and environmental integration in the cranium. *Evolution* 36:499–516.

Collard, M., and B. Wood. 2000. How reliable are human phylogenetic hypotheses? *Proc. Natl. Acad. Sci. USA* 97:5003–5006.

Devor, E. J., M. McGue, M. H. Crawford et al. 1986. Transmissible and nontransmissible components of anthropometric variation in the Alexanderwohl Mennonites. I. Description and familial correlations. *Am. J. Phys. Anthropol.* 69:71–82.

Enlow, D. H. 1990. *Facial Growth*. Philadelphia: Saunders.

González-José, R., F. V. Ramírez Rozzi, M. L. Sardi et al. 2005. Functional-cranial approach to the influence of economic strategy on skull morphology. *Am. J. Phys. Anthropol.* 128:757–771.

González-José, R., S. Van der Molen, E. González-Pérez et al. 2004. Patterns of phenotypic covariation and correlation in modern humans as viewed from morphological integration. *Am. J. Phys. Anthropol.* 123:69–77.

Gunz, P., F. L. Bookstein, P. Mitteroecker et al. 2009. Early modern human diversity suggests subdivided population structure and a complex out-of-Africa scenario. *Proc. Natl. Acad. Sci. USA* 106:6094–6098.

Hallgrímsson, B., D. E. Lieberman, W. Liu et al. 2007. Epigenetic interactions and the structure of phenotypic variation in the cranium. *Evol. Dev.* 9(1):76–91.

Hansen, T. F., C. Pelabon, W. S. Armbruster et al. 2003. Evolvability and genetic constraint in *Dalechampia* blossoms: Components of variance and measures of evolvability. *J. Evol. Biol.* 16:754–766.

Harvati, K., and T. D. Weaver. 2006. Human cranial anatomy and the differential preservation of population history and climate signatures. *Anat. Rec. A* 288A:1225–1233.

Hlusko, L. J. 2004. Integrating the genotype and phenotype in hominid paleontology. *Proc. Natl. Acad. Sci. USA* 101:2653–2657.

Holló, G., L. Szathmáry, A. Marcsik et al. 2008. History of the peoples of the Great Hungarian Plain in the first millennium: A craniometric point of view. *Hum. Biol.* 80:655–667.

Hothorn, T., F. Bretz, and P. Westfall, with contributions by R. M. Heiberger. 2008. *Multcomp: Simultaneous Inference in General Parametric Models—R Package Version 1.0-0*. http://www.r-project.org/.

Howells, W. W. 1953. Correlations of brothers in factor scores. *Am. J. Phys. Anthropol.* 11:121–140.

Howells, W. W. 1966. Variability in family lines vs. population variability. *Ann. NY Acad. Sci.* 134:624–631.

Howells, W. W. 1973. *Cranial Variation in Man: A Study by Multivariate Analysis of Patterns of Difference Among Recent Human Populations*. Papers of the Peabody Museum of Archaeology and Ethnology, v. 67. Cambridge, MA: Harvard University Press.

Hsu, J. C. 1996. *Multiple Comparisons*. London: Chapman & Hall.

Jakab, G., P. Majkut, I. Juhász et al. 2009. Paleoclimatic signals and anthropogenic disturbances from the peatbog at Nagybárkány (north Hungary). *Hydrobiologia* 631(1):87–106.

Johnston, F. E. 1961. Sequence of epiphyseal union in a prehistoric Kentucky population from Indian Knoll. *Hum. Biol.* 33:66–81.

Kohn, L. A. P. 1991. The role of genetics in craniofacial morphology and growth. *Annu. Rev. Anthropol.* 20:261–278.

Lieberman, D. E., B. M. McBratney, and G. Krovitz. 2002. The evolution and development of cranial form in *Homo sapiens*. *Proc. Natl. Acad. Sci. USA* 99:1134–1139.

Lieberman, D. E., K. M. Mowbray, and O. M. Pearson. 2000. Basicranial influences on overall cranial shape. *J. Hum. Evol.* 38:291–315.

Manica, A., W. Amos, F. Balloux et al. 2007. The effect of ancient population bottlenecks on human phenotypic variation. *Nature* 448:346–348.

Martin, R. 1928. *Lehrbuch der Anthropologie*, vols. I and II, 2nd ed. Jena, Germany: Fischer.

Martínez-Abadías, N., M. Esparza, T. Sjøvold et al. 2009. Heritability of human cranial dimensions: Comparing the evolvability of different cranial regions. *J. Anat.* 214:19–35.

Martínez-Abadías, N., R. González-José, A. González-Martín et al. 2006. Phenotypic evolution of human craniofacial morphology after admixture: A geometric morphometrics approach. *Am. J. Phys. Anthropol.* 129:387–398.

Nakata, M., P.-L. Yu, B. Davis et al. 1974. Genetic determinants of craniofacial morphology: A twin study. *Ann. Hum. Genet.* 37:431–443.

Nemeskéri, J., L. Harsányi, and Gy. Acsádi. 1960. Methoden zur Diagnose des Lebensarters von Skelettfunden. *Anthropol. Anz.* 24:70–95.

Perez, S. I., V. Bernal, and P. N. Gonzalez. 2007. Evolutionary relationships among prehistoric human populations: An evaluation of relatedness patterns based on facial morphometric data using molecular data. *Hum. Biol.* 79:25–50.

Peyre, E. 1977. *Etude anthropologique qualitative et quantitative de la population mérovingienne de la nécropole de Maule (France, Yvelines)*, 2 vols. Doctoral thesis, Université Pierre et Marie Curie, Paris, France.

Peyre, E. 1980. Analyse multivariée sur le calvarium des mérovingiens de Maule (France, Yvelines). *Bull. Mem. Soc. Anthropol. Paris.* 7(13):233–257.

R Development Core Team. 2008. *R Project for Statistical Computing: Version R-2.6.2 for Windows.* http://www.r-project.org/.

Rácz, L. 2001. *Magyarország éghajlattörténete az újkor idején* [History of the climate of Hungary in the modern age]. Szeged, Hungary: JGYF.

Reiczigel, E., A. Harnos, and N. Solymosi. 2007. *Biostatisztika* [Biostatistics]. Nagykovácsi, Hungary: Pars Kft.

Relethford, J. H. 2004. Boas and beyond: Migration and craniometric variation. *Am. J. Hum. Biol.* 16:379–386.

Roseman, C. C. 2004. Detecting interregionally diversifying natural selection on modern human cranial form by using matched molecular and morphometric data. *Proc. Natl. Acad. Sci. USA* 101:12,824–12,829.

Roseman, C. C., and T. D. Weaver. 2007. Molecules versus morphology? Not for the human cranium. *Bioessays* 29:1185–1188.

Sardi, M. L., and F. V. Ramírez Rozzi. 2005. A cross-sectional study of human craniofacial growth. *Ann. Hum. Biol.* 32:390–396.

Schillaci, M. A. 2008. Human cranial diversity and evidence for an ancient lineage of modern humans. *J. Hum. Evol.* 54:814–826.

Searle, S. R. 1971. *Linear Models*. New York: Wiley.

Sherwood, R. J., D. L. Duren, E. W. Demerath et al. 2008. Quantitative genetics of modern human cranial variation. *J. Hum. Evol.* 54:909–914.

Simpson, E., and M. Henneberg. 2002. Variation in soft-tissue thicknesses on the human face and their relation to craniometric dimensions. *Am. J. Phys. Anthropol.* 118:121–133.

Sjøvold, T. 1984. A report on the heritability of some cranial measurements and nonmetric traits. In *Multivariate Statistical Methods in Physical Anthropology*, G. N. van Vark and W. W. Howells, eds. Dordrecht, Netherlands: Reidel, 223–246.

Smith, H. F. 2009. Which cranial regions reflect molecular distances reliably in humans? Evidence from three-dimensional morphology. *Am. J. Hum. Biol.* 21:36–47.

Sparks, C. S., and R. L. Jantz. 2002. A reassessment of human cranial plasticity: Boas revisited. *Proc. Natl. Acad. Sci. USA* 99:14,636–14,639.

Strand Viðarsdóttir, U. S., P. O'Higgins, and C. B. Stringer. 2002. A geometric morphometric study of regional differences in the ontogeny of the modern human facial skeleton. *J. Anat.* 201:211–229.

Sümegi, P., G. Jakab, P. Majkut et al. 2009. Middle Age paleoecological and paleoclimatological reconstruction in the Carpathian Basin. *Időjárás Q. J. Hungarian Meteorol. Service* 113:265–298.

Susanne, C. 1975. Genetic and environmental influences on morphological characteristics. *Ann. Hum. Biol.* 2:279–287.

Susanne, C., E. Defrise-Gussenhoven, P. Van Wanseele et al. 1983. Genetic and environmental factors in head and face measurements in Belgian twins. *Acta Genet. Med. Gemellol.* 32:229–238.

Szathmáry, L., A. Marcsik, Zs. Lenkey et al. 2008. Az Alföld népességeinek továbbélése az 1. századtól a 13. századig [Survival of the populations of the Hungarian Great Plain from the 1st century to the 11th century]. In *Árpád előtt, Árpád után* [Before and after Árpád], L. Szathmáry, ed. Szeged, Hungary: JATE Press, 7–25.

Zollikofer, C. P. E., and M. S. Ponce de León. 2002. Visualizing patterns of craniofacial shape variation in *Homo sapiens*. *Proc. R. Soc. Lond. B* 269:801–807.