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Variability of the Upper Palaeolithic skulls from Předmostí near Přerov (Czech Republic): Craniometric comparison with recent human standards

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Abstract

One of the largest skeletal series of the Upper Palaeolithic period from Předmostí was destroyed during the Second World War, but the study of this material continues up to the present. The discovery of Matiegka's original photographic documentation on glass plates [Velemínská et al., 2004. The use of recently re-discovered glass plate photo-documentation of those human fossil finds from Předmostí u Přerova destroyed during World War II. J. Nat. Mus. Nat. Hist. Ser. 173, 129–132] gives an opportunity to perform a new and detailed craniometric analysis of five adult skulls in their lateral projection.

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The craniometric data were analysed using specialised Craniometrics software, and the analysis included morphological and dimensional comparisons with current Central European norms. The aim of the study was not only to monitor the skull shape as a whole, but predominantly, to evaluate the size and shape of various parts of the splanchnocranium.

The Upper Palaeolithic skulls are significantly longer, and male skulls are also higher than the current norms. The crania of anatomically modern humans are characterised by two general structural features: mid-lower facial retraction and neurocranial globularity. The height of the face of the Palaeolithic skulls corresponds to that of the current Central European population. The face has a markedly longer mandibular body (3–4 SD), while female mandibular rami are shorter. The skulls are further characterised by a smaller gonial angle, the increased steepness of the mandibular ramus, and the greater angle of the chin. These changes in the size and shape associated with anterior rotation of the face produce a strong protrusion of both jaws, but the sagittal inter-maxillary relationships remain unchanged. The observed facial morphology is similar to the Czech Upper Palaeolithic skulls from Dolní Věstonice.

This study confirms the main diachronic changes between skulls of Upper Palaeolithic and present-day human populations.

Introduction

The fossil bone remains of almost 30 skeletons from Předmostí near Přerov are among the most important finds of anatomically modern humans in the world (Ferrie, 1997; Smith, 1997). Some of the fossils were discovered by Jindřich Wankel, Karel J. Maška, Jan Knies and Martin Kříž as early as the second-half of the 19th century, and the others were found by Karel Absolon and J. Skutil (Vlček, 1996) in the first-half of the 20th century. Their estimated age is 25,000–27,000 years (Svoboda, 2001).

The sample from Předmostí has drawn much attention since its discovery because, due to certain morphological characteristics, it was regarded as belonging to a less advanced type of modern human than the Cro-Magnon. It was generally held by scholars that members of this population bridged the gap between Neandertals and recent Europeans (Smith, 1997). The reasons for the morphological similarities or the archaic nature of certain characteristics of the Central European Gravettian fossils serve as an argument for the multi-regional model of evolution (Wolpoff, 1999) and, are also discussed as "evidence that supports some degree of prior admixture with regional Neandertal populations" (Trinkaus and Svoboda, 2006).

Following the destruction of most of the fossils as a result of a fire at the Mikulov Castle at the end of the Second World War in 1945, the only sources of information on the human fossil finds at Předmostí are the two-part monograph by Matiegka (1934, 1938) and several casts (Jelínek and Orvanová, 1999). The recent discovery of the photographic documentation on glass negatives of a series of skeletal remains from Předmostí (Velemínská et al., 2004) at least partially compensates for the loss of the original skeletons.

Morphometric data on the Upper Palaeolithic series from Předmostí are still used as comparative material in palaeoantropology; for example, they are used for assessing facial proportions and their changes between the Neanderthals and anatomically modern human (Trinkaus, 2003), and for studying cranial shape development in the European population (Brace et al., 2006). In some studies, where cranial morphology of the Neanderthals is compared with those of other groups, up to a half of the material from the European Upper Palaeolithic (EUP) period comes from Předmostí (e.g. Harvati et al., 2004; Thackeray et al., 2005).

It is generally acknowledged that cranial size and shape are strongly controlled by genetic mechanisms (Manfredi et al., 1997; Johannsdottir et al., 2005). Therefore, the study of cranial size and shape can yield information on intra-population variability and possible family connections within the group, as was indicated in the case of the individuals from Palaeolithic Dolní Věstonice (Alt et al., 1997).

The purpose of this study is to monitor diachronic variability in the size and shape of skulls within the territory of Central Europe since the Upper Palaeolithic until today. We have posed the question whether we can prove, using selected methods, that the most typical evolutionary changes of *Homo sapiens* are the development of neurocranial globularity and decreased facial convexity (Lieberman et al., 2002). Our argument is based on detailed craniometric analysis of the photographs of Předmostí adult skulls in the lateral projection, with special emphasis on facial morphology and a comparison with recent human standards.

Skulls from Předmostí are compared with the craniometric variability of recent males and females and with the variability of individuals from Dolní Věstonice (Vlček and Šmahel, 2002; Trinkaus and Svoboda, 2006). All samples used in this study derive from the same geographic area of Moravia. The fossil samples belong to the Pavlovian cultural group, the central European form of the Gravettian culture of Upper Palaeolithic Europe. The standard information acquired was supplemented by certain measurements and angles not commonly taken in the first-half of the last century (see e.g. Bernhard et al., 2002). Although lateral radiographs have only been used relatively recently in palaeoanthropology (Argyropoulos et al., 1989; Vlček and Šmahel, 2002; Kuroe et al., 2004; Cuozzo, 2005), this technique can offer important information; for example, for assessing changes in cranial shape in relation to the expansion of the brain during the course of evolution (e.g. Ross et al., 2004), and for assessing the facial morphology of an individual from the skull.

Materials

Craniometric photographs of five adult fossil skulls from Předmostí (male skulls P1, P3, P9, female skulls P4, P10) were evaluated. The sex of the fossils was previously estimated by several researchers (Matiegka, 1934; Šefčáková et al., 2003; Katina et al., 2004). Despite the existence of certain discrepancies between sex determination according to the skulls and the pelves of some individuals from

Předmostí (Brůžek et al., 2008), the sex of the skulls in this study remains the same as determined by Matiegka (1934).

Craniometric data of Předmostí were compared with norms based on lateral radiographs of 52 healthy males and 36 females from the archive of the Clinic of Plastic and Reconstructive Surgery, 3rd Faculty of Medicine, Charles University in Prague. All adults represented a randomly selected group of volunteers from among students and patients hospitalised with minor trauma at the Departments of surgery and plastic surgery of Charles University Faculty of Medicine. The first group included 52 men of average age 28 years and 10 months and their radiographs were taken in the mid-1970s. The second group included 36 women of average age 20 years and 4 months and was compiled from radiographs taken in the mid-1990s. Photographs and images only of healthy Czech individuals who had no obvious shape disharmony, had clinically acceptable occlusion and no prior orthodontic treatment have been used. Cases of congenital anomalies were excluded.

In order to expand the sample of Czech Upper Palaeolithic skulls, to the original group of five we added radiographs from Vlček and Šmahel (2002). As in the case of the previous group, we also based our work on the measurement of lateral radiographs. For comparison, we used metric data of male skulls from Dolní Věstonice (DV 13, 14, 16). The young adult, Dolní Věstonice 15, who suffered serious congenital developmental malformations (Trinkaus et al., 2001), was not included in the study. The DV3 skull has not been evaluated since it also showed traumatic damage to the right side of the face and there were no images of this skull.

Methods

The glass negatives of fossil skulls were digitised using special software (RGB 360 dpi at 30 cm, implementation by a Rollei scanning screen and SilverFast 6.0 software). Twenty x, y coordinates of key craniometric landmarks were obtained by using SigmaScan software, which created basic data entry for the special Craniometric software (Fig. 1). This technique is currently used in orthodontics, clinical anthropology, osteology and even palaeoanthropology for measuring lateral radiographs. As the photographs of fossils were taken in the 1930s, we could not ensure stable conditions during exposure. It is very important to preserve the insertion of mandibles into the TM joints and articulation of the teeth. The fact that the position of the mandibles was not always entirely correct (see Figs. 2 and 3) has been the reason why the dental relations were not evaluated. Testing the reliability of photograph measurements was the first prerequisite for the subsequent metric analysis. The coefficient of reliability was between 0.87 and 0.97, the systematic error was significant at the lowest level of significance ($\alpha = 0.05$) in only one dimension (Nasion-Mentale), and occurred randomly (Velemínská et al., 2003).

It is important to stress that our study is based on the comparison of dimensions acquired by different techniques – via measurements of photographs and radiographs. The application of both techniques is common in forensic anthropology in

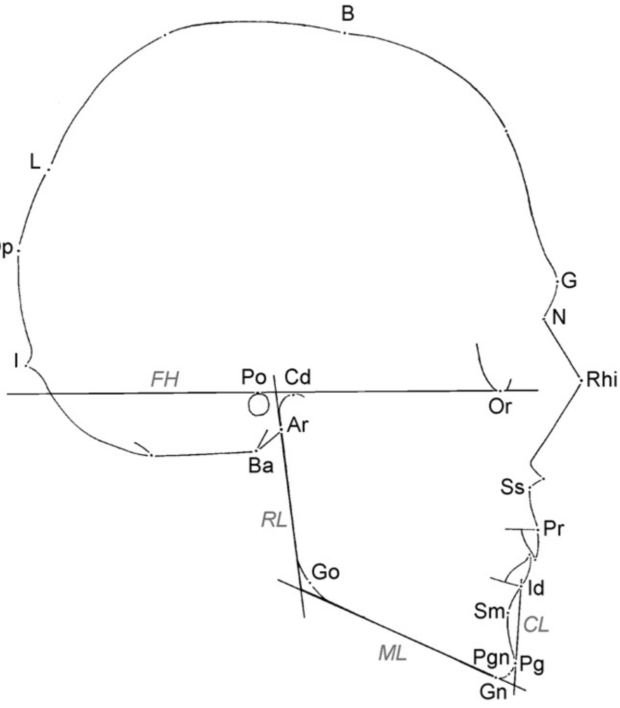

Fig. 1. Cephalometric points (landmarks) and reference lines used in this study: Ar (articulare) – intersection of inferior contour of the posterior cranial base and posterior contour of the ramus; B (bregma) – intersection of the coronal and sagittal sutures; Ba (basion) – most posteroinferior point on the clivus; Cd (condylion) – most superior point on the condylar head; G (glabella) – the most anterior point on the arcus superciliaris; Gn (gnathion) – the lowest point of the mandibular symphysis; Go (gonion) – point on the angle of the mandible determined by the axis of ML/RL angle; I (inion) – top of the protuberantia occipitalis externa; Id (infradentale) – point of the alveolar contact with the lower central incisor; L (lambda) – intersection of the sagittal and lambda sutures; N (nasion) – the most anterior point on the frontonasal suture; Op (opistocranion) – point on the surface of the cranial vault farthest from the glabella point; Or (orbitale) – the lowest point on the orbital margin; Pg (pogonion) – the most anterior point on the bony chin; Pgn (prognathion) – point on the mandibular symphysis farthest from Cd; Po (porion) – the most superior point on the porus acusticus externus; Pr (prosthion) – point of alveolar contact with the upper central incisor; Rhi (rhinion) – the most anteroinferior point on the nasal bone; Sm (supramentale) – the deepest point on the anterior contour of the mandibular symphysis; Ss (subspinale) – the deepest point of the subspinal concavity; CL – the line through Pg and Id; FH – the line through Or and Po points; ML – tangent to the mandibular body through Gn; RL – tangent to the mandibular ramus through Ar.

super-projection methods, or in research into historical personalities (Vlček and Šmahel, 1998). Metric evaluation of skull photographs is considered acceptable (Benson and Richmond, 1997), although errors of this method are likely to be

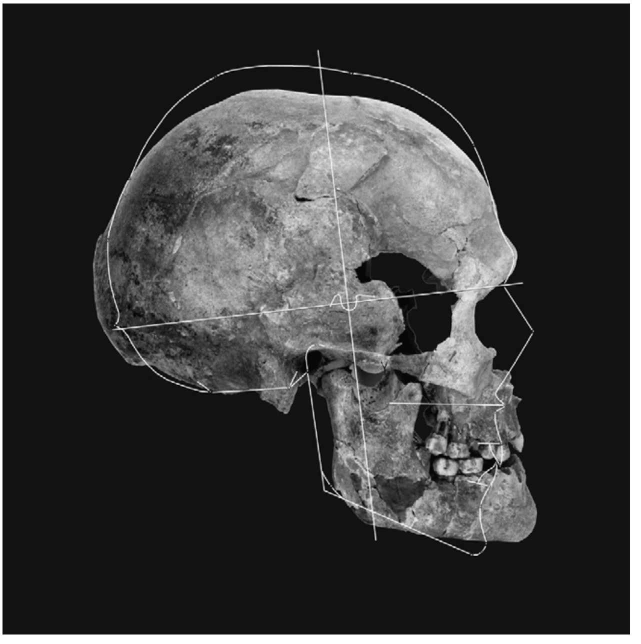

Fig. 2. Illustration of the size and shape differences between a fossil (photograph of skull P1) and a recent (male craniogram) skull.

greater than those due to digitisation of radiographs. Comparison of dimensions from photographs and radiographs of the same series of skulls (Hudcová, 2006) demonstrated that in five of six linear dimensions also analysed in this study (G–Op, G–L, B–L, N–B, N–Pr), the confidence coefficient of measurements was between 0.95 and 0.90. The lowest value of the confidence coefficient (0.84) was in the case of the N–Rhi dimension.

The use of photographs represents another difficulty of the method: the lack of information regarding the conditions under which photographs of the Předmostí skulls were taken (magnification, focal length, or type of camera). We resolved this difficulty by not relying on truly measured variables, but by using the *z*-score values. Thus, while there are some technical difficulties in combining and comparing data derived from radiographs and photographs, overall the procedure seems to be reliable (Benson and Richmond, 1997).

The Craniometrics software was used for detailed craniofacial metric analysis of lateral radiographs or photographs. The (N–B) value (Matiegka, 1934) was chosen as the scale for measuring skull photographs.

We evaluated 30 linear or angular (shape) variables. Size dimensions were marked as two points (G–Op), angular characteristics as three points (N–B–L) or two line intersections (ML/RL). B–NL is the perpendicular distance from bregma (B) to the connecting line NL. Nine characteristics were located on the neurocranium (G–Op, G–L, B–L, N–B, L–Ba, B–Ba, B–NL, N–B–L, N–I–L) and with exception of three of

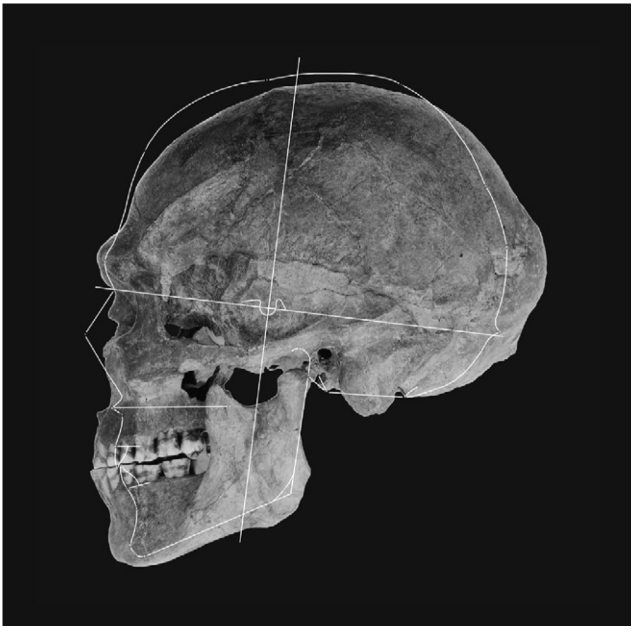

Fig. 3. Illustration of the size and shape differences between a fossil (photograph of skull P3) and a recent (male craniogram) skull.

these (B–NL, N–B–L, N–I–L), they were measured directly on the skulls by Matiegka (1934).

In the splanchnocranium, we analysed nine size variables (N–Rhi, N–Pr, N–Gn, Id–Gn, Pgn–Go, Cd–Go, Ss–Ar, Sm–Ar and Pgn–Ar) and 12 shape variables (Ss–N–Sm, Pr–N–Id, N–Ss–Pr, ML/RL, ML/FH, RL/FH, CL/ML, Ar–N–Ss, Ar–N–Sm, Ar–N–Pg, N–Ar/RL and N–Ar/ML). All characteristics were compared with the recent norm, and ten characteristics were chosen for comparison with similar craniometrics of Upper Palaeolithic skulls from Dolní Věstonice (Vlček and Šmahel, 2002).

The recent Czech osteological standards were created using recent radiographs (Macková, 2004). Attention was paid to the different preservation (completeness) of skulls and to the measurement availability on photographs. Shape characteristics were related to the nasion-articulare distance (N–Ar). Similar dimensions can be also expressed in relation to the Frankfurt horizontal line (FH). These two lines made it possible to measure shape variables on photographs where the sella, an important craniometric point, was missing. Some of these lateral radiographs (35 females and 36 males) were used for the construction of mean male and female craniograms (Šmahel et al., 1998). These were used for the comparison of modern Czechs reference samples with Předmostí 1, 3, 4, 9 and 10 (Figs. 2–6).

Average values and standard deviations (SD) of the dimensions of the recent population have been used to calculate the *z*-score. The *z*-score is the distance in SD

Fig. 4. Illustration of the size and shape differences between a fossil (photograph of skull P9) and a recent (male craniogram) skull.

of a measurement or an individual value of a Předmostí skull from the mean of the reference sample (standard). A fossil deviation of minimally two SDs from this mean is considered as significant. The calculations are accompanied by plots, where the zero axis represents the average of recent male and female skulls, the highlighted points represent the magnitude of the *z*-score.

Similarity (or dissimilarity) of the skull shape in Předmostí versus recent samples was evaluated using the multivariate method of cluster analysis. The mutually similar skulls were clustered on the basis of Euclidean distance. To determine the distance among objects in a cluster, three methods of joining the cluster tree were used: single linkage, complete linkage and Ward's method. The calculations and graphs were done using MS Excel 2003 and Statistica 6.0 statistical software packages.

Results

The lists of assessed linear and shape variables are presented in Tables 1–3, supplemented for each skull by the SD from the mean value in the sample of skulls from the recent population expressed as a magnitude of SD (*z*-score). In Tables 1

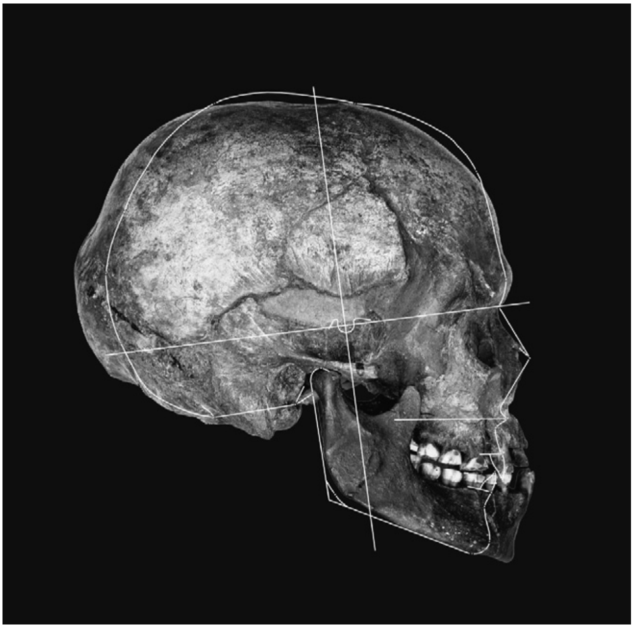

Fig. 5. Illustration of the size and shape differences between a fossil (photograph of skull P4) and a recent (female craniogram) skull.

Fig. 6. Illustration of the size and shape differences between a fossil (photograph of skull P10) and a recent (female craniogram) skull.

Table 1. Size and shape variables of male Upper Palaeolithic skulls from Předmostí, recent standard (mean, SD), and *z*-score (bold marked values over ±2 SD)

variable	Mean (recent)	SD (recent)	P1	*z*-score	P3	*z*-score	P9	*z*-score
G–Op	180.559	4.921	189.000	1.715	201.500	**4.256**	196.000	3.138
G–L	173.790	4.696	183.000	1.961	193.000	**4.091**	187.000	2.813
B–L	109.826	5.748	125.000	**2.640**	120.000	1.770	120.000	1.770
N–B	114.404	5.150	107.000	−1.438	120.000	1.087	115.000	0.116
L–Ba	115.308	4.872			116.000	0.142	116.000	0.142
B–Ba	140.312	4.935			133.000	−1.482	134.000	−1.279
B–NL	71.657	4.849	71.412	−0.051	73.022	0.281	74.895	0.668
N–B–L	100.387	3.633	103.000	0.719	105.160	1.313	102.253	0.513
N–I–L	77.252	3.810	87.801	**2.769**	80.852	0.945	83.680	1.687
N–Rhi	23.078	3.599					19.638	−0.956
N–Pr	69.855	3.991			78.757	**2.230**	68.673	−0.296
N–Gn	120.281	6.704			131.365	1.653	117.855	−0.362
Id–Gn	32.193	2.883	31.716	−0.166	43.133	**3.794**	31.638	−0.193
Ss–Ar	85.582	4.090			102.116	**4.042**	96.792	**2.741**
Sm–Ar	96.741	4.375			112.824	**3.676**	111.049	**3.270**
Pgn–Ar	111.041	4.782			125.166	**2.954**	124.888	**2.896**
Ar–N–Ss	62.933	3.432			71.770	**2.575**	74.816	**3.462**
Ar–N–Sm	60.644	3.354			66.752	1.821	71.704	**3.298**
Pgn–Go	73.311	3.802	83.172	**2.593**	90.180	**4.436**	87.808	**3.812**
Cd–Go	61.619	4.118	61.631	0.003	65.505	0.944	65.741	1.001
ML/RL	121.772	7.001	101.870	**−2.843**	105.430	**−2.334**	109.640	−1.733
CL/ML	70.943	5.926	68.350	−0.438	89.450	**3.123**	72.080	0.192
ML/FH	21.655	6.782	6.230	**−2.274**	18.330	−0.490	13.840	−1.152
RL/FH	79.894	4.318	84.400	1.044	92.990	**3.033**	84.170	0.990
N–Ar/ML	47.458	7.111			40.530	−0.970	34.760	−1.790
N–Ar/RL	105.707	4.612			115.460	**2.110**	105.260	−0.100
Ss–N–Sm	2.353	2.161			5.019	1.234	3.112	0.351
Pr–N–Id	2.741	1.408			1.200	−1.094	2.732	−0.007
N–Ss–Pg	178.587	5.006			168.138	**−2.087**	176.742	−0.369

and 2, bold letters indicate the *z*-score values of those dimensions whose magnitude is at least 2 SD. The 95% of the *z*-score values lie within the ±2 SD interval (normal, Gaussian distribution).

The size and shape differences of the fossil skulls with regard to recent standards are also illustrated in Figs. 7–9.

The individual evaluation of fossil skulls is presented as compared to the recent population (modern standard) represented by a recent Czech reference sample, then, the generalised evaluation follows in subsequent paragraphs. The determined size and shape properties of the skulls from Předmostí are then compared to the fossil skulls from Dolní Věstonice.

Table 2. Size and shape variables of female Upper Palaeolithic skulls from Předmostí, recent standard (mean, SD), and *z*-score (bold marked values over ±2 SD)

variable	Mean (recent)	SD (recent)	P4	*z*-score	P10	*z*-score
G–Op	173.982	173.982	191.500	**2.129**	185.500	1.400
G–L	168.829	8.460	185.000	1.912	175.000	0.729
B–L	111.906	7.656	120.000	1.057	107.000	−0.641
N–B	108.685	4.825	114.000	1.102	112.000	0.687
L–Ba	112.357	6.285	121.000	1.375		
Ba–B	134.924	5.128	136.000	0.210		
B–NL	71.277	4.893	73.882	0.532	69.510	−0.361
N–B–L	99.201	4.194	101.308	0.502	103.689	1.070
N–I–L	81.253	3.537	85.780	1.280	82.705	0.411
N–Rhi	23.025	4.074	21.005	−0.496	16.371	−1.633
N–Pr	64.794	4.674	62.194	−0.556	62.867	−0.412
N–Gn	109.785	7.627	111.461	0.220	107.142	−0.346
Id–Gn	28.476	2.860	30.803	0.814	26.617	−0.650
Ss–Ar	80.554	80.554	86.588	1.628	90.514	**2.687**
Sm–Ar	89.988	89.988	102.445	**2.948**	100.879	**2.577**
Pgn–Ar	101.909	4.806	109.378	1.554	109.825	1.647
Ar–N–Ss	62.731	2.906	73.013	**3.538**	72.971	**3.524**
Ar–N–Sm	60.625	3.047	68.914	**2.720**	68.082	**2.447**
Pgn–Go	70.034	3.619	86.142	**4.451**	82.975	**3.576**
Cd–Go	55.240	4.787	47.010	−1.719	51.636	−0.753
ML/RL	120.134	6.938	115.690	−0.641	112.800	−1.057
CL/ML	71.238	6.479	83.930	1.959	76.490	0.811
ML/FH	21.484	6.921	21.560	0.011	14.900	−0.951
RL/FH	81.351	4.142	85.990	1.120	82.250	0.217
Ss–N–Sm	2.106	2.182	4.099	0.913	4.889	1.276
Pr–N–Id	3.426	1.745	2.243	−0.678	5.493	1.184
N–Ss–Pg	179.077	5.819	168.318	−1.849	171.275	−1.341

Předmostí skull 1 (P1)

The male skull, P1, is the least well preserved of all the five studied skulls. As a significant section of the skull base and the skeleton of the upper face are missing, we limited our evaluation to the section of the cranial vault and the lower jaw (Table 1, Figs. 7–9). The overall shape of the skull in the lateral view and its differences compared to the average of the recent population are depicted only in Fig. 2.

The cranium of P1 is longer by 1.7 SD than the average of the recent population. This difference is mostly due to the significantly longer B–L chord (2.6 SD), while the N–B chord is shorter compared to the recent population (−1.4 SD). Another chord, B–L concurrently influences the angle N–I–L, which is larger by 10° compared to the recent population (2.8 SD). On the basis of the photograph in Fig. 2, the cranium

Table 3. Shape and size variables of male Upper Palaeolithic skulls from Dolní Věstonice, recent standard (mean, SD), and *z*-score values

Variable	Mean (recent)	SD	DV13	*z*-score	DV14	*z*-score	DV16	*z*-score
G–Op	180.559	4.921	198.000	3.544	187.000	1.309	203.000	4.560
Ba–B	140.312	4.935	131.000	−1.887	134.000	−1.279	137.000	−0.671
Ar–N–Ss	62.933	3.466	79.500	4.780	64.500	0.452	72.500	2.760
Ar–N–Sm	60.644	3.386	71.000	3.058	62.500	0.548	69.000	2.468
Ar–N–Pg	62.314	3.488	72.000	2.777	63.000	0.197	71.000	2.490
ML/RL	121.772	7.069	113.500	−1.170	110.000	−1.665	113.000	−1.241
N–Ar/ML	47.458	7.111	41.000	−0.908	44.500	−0.416	37.000	−1.471
N–Ar/RL	105.707	4.612	108.000	0.497	115.000	2.015	104.000	−0.370
Ss–N–Sm	2.353	2.182	8.500	2.817	2.000	−0.162	3.500	0.526
N–Ss–Pg	178.587	5.055	163.500	−2.985	176.500	−0.413	176.000	−0.512

appears significantly lower. This information cannot be evaluated metrically in view of the absence of the skull base.

The mandible of P1 differs from the recent population with its markedly longer body, while the length of its ramus corresponds to the average of the reference population. The mandibular angle and the inclination of the body with respect to the Frankfurt horizontal are significantly smaller, which is documented not only by the graph but also by Fig. 2. The question remains, whether the markedly different position of the mandible with respect to the Frankfurt horizontal is not the consequence of maxillary reconstruction.

Předmostí skull 3 (P3)

The very well preserved male skull P3 enables the evaluation of all the studied variables, with the exception of the length of the nasal bones (N–Rhi) (Table 1, Figs. 3 and 7–9).

Compared to the recent population, the neurocranium of P3 is markedly longer (4.3 SD) and at the same time lower (−1.5 SD). The length of the skull is affected, to a great extent, by the vaulted section of the glabella and the length of the parietal bone (G–L), and less so by the frontal bone chords (N–B). The cranial angular dimensions show no significant shape differences, compared to the recent population.

The height dimensions of the splanchnocranium are greater than in the recent population. The smallest difference is noted for the total height of the face (1.7 SD), while more marked differences are noted in the partial height dimensions of the upper (3.8 SD) and lower (4.4 SD) face, which are affected by the strong protrusion of both jaws. The protrusion itself is best characterised by the great differences expressed with the aid of the linear dimensions Ss–Ar, Sm–Ar and the angles

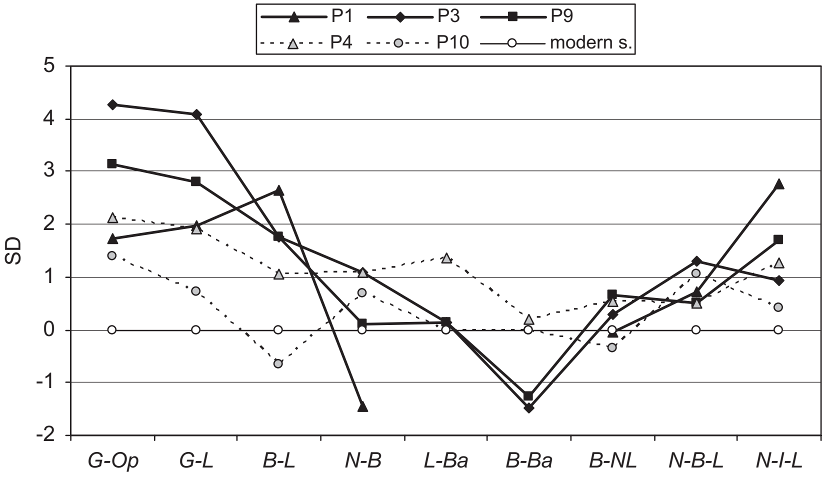

Fig. 7. Plot of the size and shape differences of the neurocranium in the Předmostí fossil skulls sample in relation to the recent reference sample using z-score.

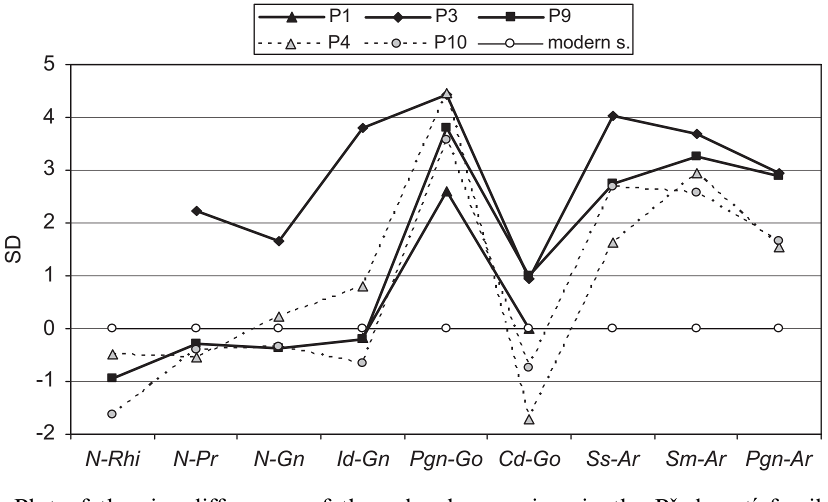

Fig. 8. Plot of the size differences of the splanchnocranium in the Předmostí fossil skulls sample in relation to the recent reference sample using z-score.

Ar–N–Ss, Ar–N–Sm. The skull has a typically large convexity of the face, N–Ss–Pg (−2.1 SD)

The lower jaw of P3 significantly differs in the length of its body (4.4 SD), less so in the length of its rami (1.7 SD). The mandibular angle is sharper (−2.3 SD), while the gonial angle is markedly larger (3.1 SD). The position of the mandible with respect to the Frankfurt horizontal differs only in the area of the inclination of its rami. Although both jaws differ from the recent group in their protrusion, sagittal intermaxillary relations do not differ significantly.

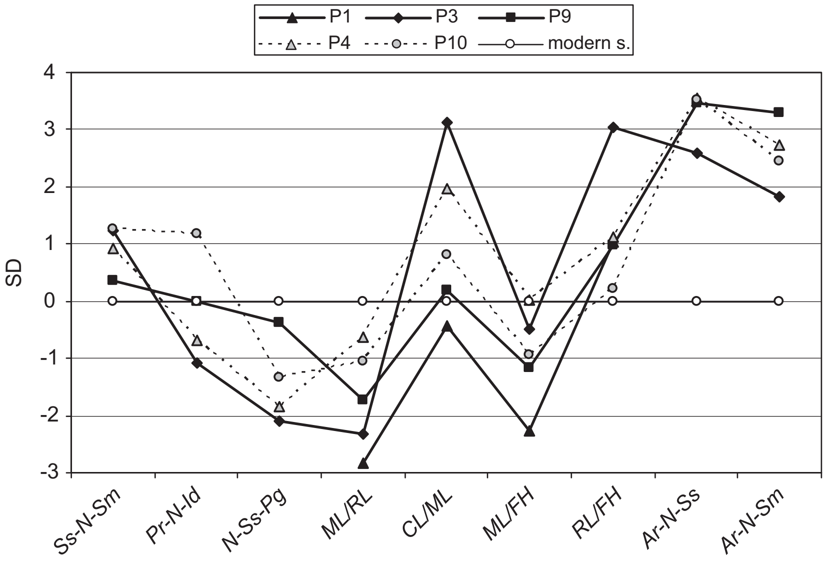

Fig. 9. Plot of the shape differences of the splanchnocranium in the Předmostí fossil skulls sample in relation to the recent reference sample using *z*-score.

Předmostí skull 9 (P9)

The state of preservation of the male skull P9 enables the evaluation of all the studied variables (Table 1, Figs. 4 and 7–9). Compared to the recent population, the cranium of the skull P9 is longer (3.1 SD) and lower (−1.3 SD). The markedly greater length of the cranium is least of all due to the area of the frontal bone N–B. The angular characteristics of the cranium show no marked differences in shape, compared to the recent population.

The height dimensions of the face correspond to the average of the recent population. The dimensions Ss–Ar (2.7 SD) and Ar–N–Ss (3.5 SD) characterise the greater protrusion of the upper jaw. Similarly, the protrusion of the mandible is characterised by the dimensions Sm–Ar (3.3 SD), Pgn–Ar (2.9 SD) and Ar–N–Sm (3.3 SD). The mandibular body is significantly longer (3.8 SD), but its ramus is longer by only 1 SD. The mandibular angle is sharper (−1.7 SD), but its position with respect to the Frankfurt horizontal does not differ when compared to the recent population. The sagittal inter-maxillary relations are comparable to those of the recent population.

Předmostí skull 4 (P4)

The preservation of the female skull P4 enables the evaluation of all the studied variables (Table 12, Figs. 5 and 7–9). The greatest length of the cranium is 2.1 SD longer than the average of the recent population, while the height of the skull does not differ. The G–L and L–Ba dimensions are longer in accordance with the greatest length of the cranium. The chords N–B and B–L do not differ significantly. The angular characteristics of the cranium also show no differences in shape, compared to the recent population.

The height dimensions of the face correspond to the average of the recent population. The dimensions Ar–N–Ss (3.5 SD) and N–Ss–Pg (1.8 SD) are in accordance with the greater protrusion of the upper jaw. As to the Ss–Ar dimension, the skull does not differ from the recent population. Both the studied dimensions, Sm–Ar (2.6 SD) and Ar–N–Sm (2.4 SD) correspond to the larger protrusion of the lower jaw. There is the greater convexity of the facial skeleton (−1.8 SD).

The lower jaw of P4 has a markedly longer body (4.5 SD) than the recent population, while the length of the mandibular ramus is shorter by 1.7 SD. The mandibular angle and its position with respect to the Frankfurt horizontal do not differ significantly. The gonial angle is greater by almost 2 SD than the average in the recent population. The sagittal inter-maxillary relations are comparable to the average of the recent (reference) population.

Předmostí skull 10 (P10)

The preservation of the female skull P10 enables the evaluation of all the studied variables, with the exception of the height of the cranium Ba–B and the dimension L–Ba (Table 2, Figs. 5 and 7–9). According to all the variables, the neurocranium does not significantly differ from the reference group. Even the length of the cranium corresponds to the values of the recent population (1.4 SD).

The height dimensions of the face do not differ from those of the recent population. In contrast, the dimensions Ss–Ar (2.7 SD), Ar–N–Ss (3.5 SD) as well as Sm–Ar (2.6 SD) and Ar–N–Sm (2.4 SD) express the marked protrusion of both jaws. The lower jaw of P10 has a significantly longer body (4.5 SD) and the mandibular ramus is actually shorter by 0.75 SD. The mandibular angle is smaller compared to the recent average (−1.1 SD). The gonial angle and the position of the mandible with respect to the Frankfurt horizontal are also identical with those of the recent population. The facial skeleton is slightly more convex (−1.3 SD), the values of the sagittal inter-maxillary relations still correspond to normal occlusion (Ss–N–Sm 4.9°, Pr–N–Id 5.5°).

Metric characteristics of the neurocranium

Differences between the neurocrania of fossil and recent skulls are illustrated in Fig. 7. All fossil skulls are longer (G–Op, G–L), which is more evident in the Předmostí 3 and 9 males, and the height of the skulls is lower (B–Ba; 1.3–1.5 SD). In females, these changes are less pronounced. The modern skulls are shorter on average, but in the only Předmostí female with preserved measurements (P4), B–Ba is less than in the modern Czech sample. The anterior chord of the skull (N–B) is, with the exception of P1 (2.9 SD), not much different from the modern norms (maximal value 1.1 SD), while the posterior chord (B–L) is greater in fossil male skulls (1.8–2.9 SD). Skull P1 is characterised by the significantly shortest N–B dimension, which is actually shorter than the average in the recent population.

The overall shape of the neurocranium is also documented by the shape variable (N–B–L), but Figs. 2–6 are more illustrative, showing recent mean craniograms overlaying the fossil skulls of corresponding sex. These figures demonstrate a lower forehead especially in the Předmostí males, and in all specimens a larger brow and a longer, more angular occipital region.

Metric characteristics of the splanchnocranium

The *z*-scores of the linear dimensions are shown in Figs. 8 and 9. The height dimensions of the Upper Palaeolithic splanchnocrania correspond to the values of the recent population. The only exception is the skull P3, whose cranium is more robust overall, and its upper facial height of 79 mm differs from the rest of the fossil skulls by an average of 2 SD.

All the skulls have in common a marked protrusion of the upper and lower jaws, expressed either as the linear (Ss–Ar, Sm–Ar) or angular dimensions (Ar–N–Ss, Ar–N–Sm). This is associated with the most marked sign of the splanchnocrania of Upper Palaeolithic skulls, and that is with the markedly longer body of the lower jaw. The mandibular ramus is only insignificantly longer in the male skulls (around +1 SD). In addition, the female lower jaws in the Gravettian sample have a slightly shorter mandibular ramus (Cd–Go; by about 1 SD) than in the recent population. On average, the mandibular angle (ML/RL) is similar or smaller than that of the recent population; however, the chin angle (CL–ML) is mostly larger. In comparison to the control file, the inclination of the mandibular ramus with respect to the Frankfurt horizontal (RL/FH) is greater and the inclination of the mandibular corpus (ML/FH) is smaller than in the recent population. Other dimensions (Ar–N–Pg) also show the anterior rotation of the fossil skulls compared to the recent population.

Fossil skulls do not differ substantially in their inter-maxillary and inter-alveolar relations (Ss–N–Sm, Pr–N–Id) from those of the recent population. On average, their faces exhibit greater convexity (N–Ss–Pg).

Comparison of Předmostí and Dolní Věstonice

We also compared the two most complete males from Předmostí (P3 and P9) with three male adults from Dolní Věstonice (Table 3), using two linear dimensions (Matiegka, 1934; Sládek et al., 2000) and eight angular variables from Vlček and Šmahel (2002).

The graphic comparison using the *z*-score of selected morphological variables of the male fossil skulls with regard to the recent standard is plotted in Fig. 10. We established the following common morphological features in both Central European samples: longer and narrower neurocranium than that of the recent population, sharper mandibular angle, anterior rotation of the lower jaw, major face convexity, protrusion of the skeletal profile of both jaws (1–5 SD with the exception of DV 14).

Shape similarity between the Upper Palaeolithic and the recent period was evaluated using the aforementioned eight angular dimensions and the method of

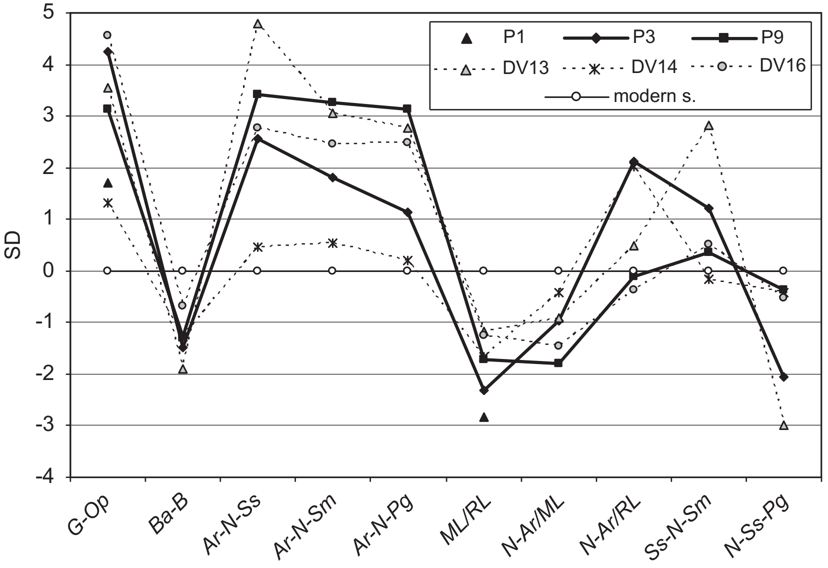

Fig. 10. The comparison of the male fossil skulls from Předmostí and Dolní Věstonice with the recent reference sample using *z*-score.

cluster analysis. Since the results of cluster tree methods – single linkage, complete linkage, the Ward's method – were very similar, only one dendrogram is shown for males (Fig. 11) and for females (Fig. 12). In both figures, it is evident that the Upper Palaeolithic skulls were clustered to one branch of the dendrogram. Also, these dendrograms illustrate that the Předmostí and Dolní Věstonice profile shapes are distant from the recent Czech skulls. Of the male Palaeolithic skulls, the most similar are skulls P9 and DV16; the least similar skull (in shape) compared to the others is skull P13. This mutual similarity of Palaeolithic skulls can also be seen in Fig. 10. The results of cluster analysis for both sexes confirm that the shape of the skeletal profile of Palaeolithic skulls differs from that of the overall variability in the analysed sample of the recent population.

Discussion and conclusion

Diachronic changes of the skulls of post-Pleistocene populations were studied in various parts of the Old World, such as Southeast Asia (Brown and Maeda, 2004), Sub-Saharan Africa (Henneberg and Steyn, 1993), Europe (Brace et al., 2006). With the exception of the confirmation of craniofacial similarity between the skulls of recent and Minoan populations (Argyropoulos et al., 1989) or the study of the brachycephalization of the populations living in the territory of former Czechoslovakia from the Neolithic Period until modern times (Hanáková and Stloukal, 1990),

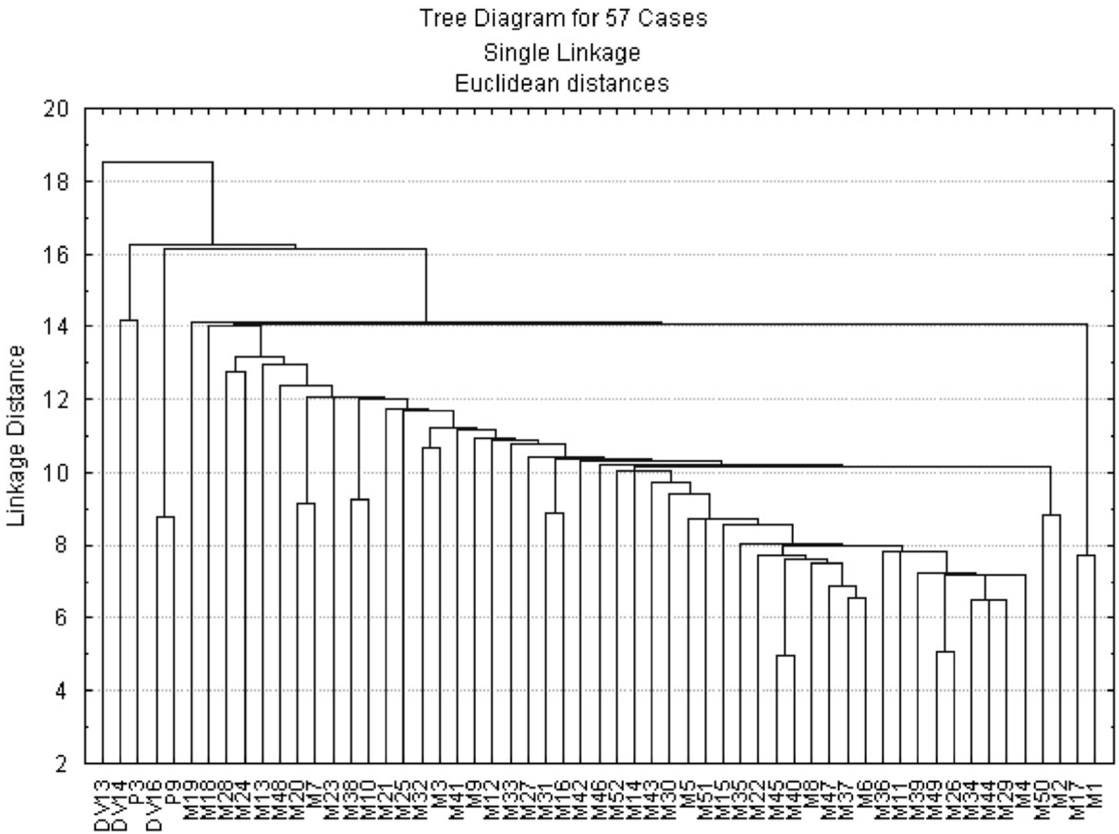

Fig. 11. The cluster analysis (single linkage, Euclidean distances) of recent ($n = 52$) and Upper Palaeolithic ($n = 5$) male skulls samples using the following variables: Ar–N–Ss, Ar–N–Sm, Ar–N–Pg, Ss–N–Sm, N–Ss–Pg, N–Ar/ML, N–Ar/RL, ML/RL.

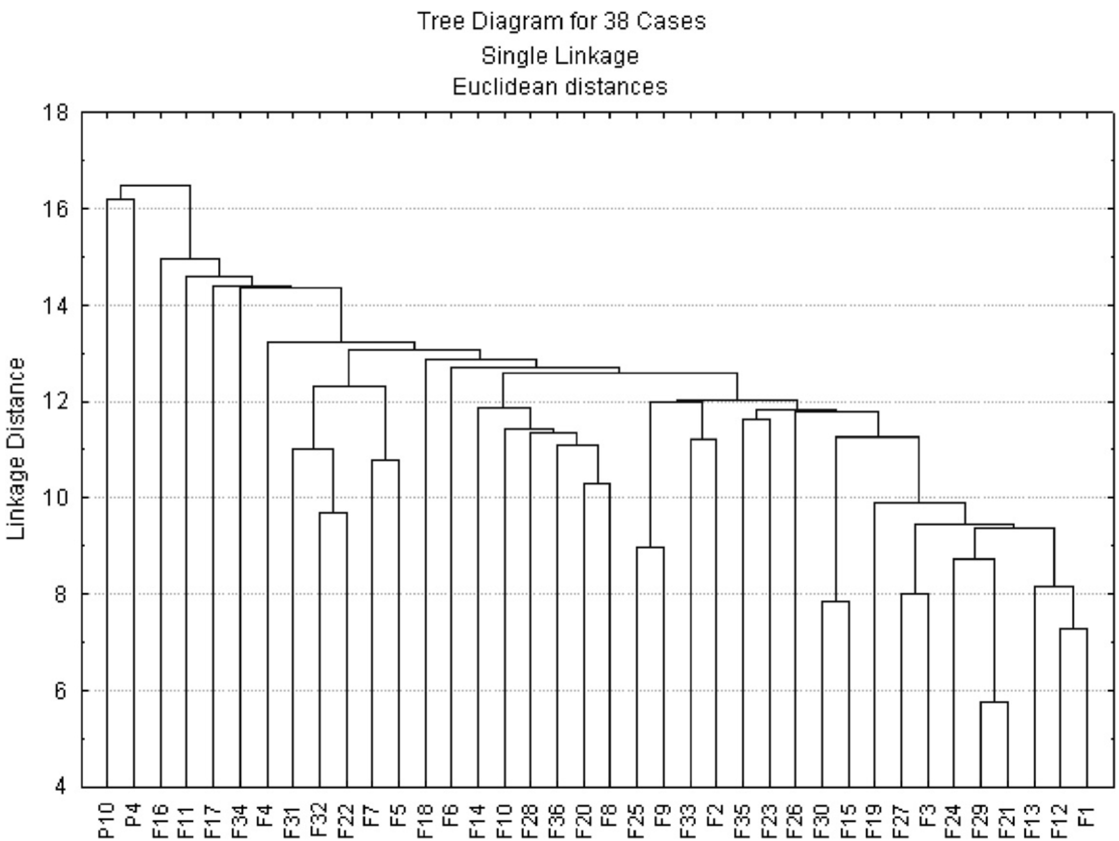

Fig. 12. The cluster analysis (single linkage, Euclidean distances) of recent ($n = 36$) and Upper Palaeolithic ($n = 2$) female skulls samples using the following variables: Ar–N–Ss, Ar–N–Sm, Ar–N–Pg, Ss–N–Sm, N–Ss–Pg, N–Ar/ML, N–Ar/RL, ML/RL.

little attention to date has been paid to the regional analysis of skull changes within small areas such as Central Europe. Study of diachronic trends is related to the issue of population affinity and resemblance. Genetic studies focus on the issue of prehistoric admixture and its traces in the genome of recent human populations (e.g. Semino et al., 2000; Dupanloup et al., 2004; Bauchet et al., 2007). The results of genetic and morphological studies, while both pursue the same goals, cannot be compared directly. The spread of haplo-groups of genetic markers is subordinate to different mechanisms than the genetics of multi-factorial traits such as skeleton dimensions. Evidence for admixture in these dimensions is only rarely studied in humans. It has been documented that major shape differences of the skull are restricted to inter-landmark distances measuring cranial vault length, occipital development, and facial flattening (e.g. Martínez-Abadías et al., 2006). The changes observed in Central European populations in our work support these conclusions. In view of the population movements in the Central European region over the past 30,000 years, we cannot speak about the affinity of the population nor of micro-evolutionary changes, but we retain the neutral term of diachronic change. The mere description of differences of skulls between the Gravettian and recent populations does not explain the observed changes. This is why we are turning both to data of archeogenetics as well as to published data regarding the craniometry of populations from the period between the Upper Palaeolithic and the Modern Age in the area of Czech Republic.

Analysis of hominid cranial morphology is of particular importance for research dealing with questions concerning both the phylogenetic and ontogenetic aspects of the *Homo* genus (Bernhard et al., 2002). The intention of this study was to describe the diachronic changes and variations from the Upper Palaeolithic to the recent period, and to determine to what extent the variation was caused by sexual dimorphism. We confirmed previous findings (Trinkaus and Svoboda, 2006) that Pavlovian samples show heterogeneity in size dimorphism, with homogeneity in overall shape. The same holds true for the Předmostí specimens, with the most robust male skull P3, for which several length (G–Op, B–L) and height dimensions (N–Pr, N–Gn, Id–Gn) differ from other Palaeolithic skulls by at least 1 SD. The supra-orbital projection is similar to that of the Pavlov male and more noticeable than in the Mladeč 5 male. However, distinct lambdoidal flattening is very similar to that in the Mladeč 5 male, as well as in Neandertal males (Frayer et al., 2006).

Despite these differences, if we focus on the dimensions characterising the eight specimens from Předmostí and Dolní Věstonice, the overall differences are not significant. Apart from the typically prolonged neurocranium, they have a markedly longer mandibular body in relation to the mandibular rami, strong protrusion of both jaws, and increased facial convexity with preserved normal sagittal inter-maxillary relations (Ss–N–Sm). The similar shape of the facial skeletal profile is described in many Central EUP fossils (Frayer et al., 2006).

Our comparison of the facial skeletal profile of the Upper Palaeolithic and recent populations revealed size and shape differences of the skulls in the lateral projection. This was caused by markedly longer mandibular bodies. However, female mandibular rami were actually slightly shorter. Both jaws were in strong protrusion in relation to the cranial base, the face thus developed more towards anterior rotation. Sagittal inter-maxillary relations remained unchanged in relation to recent values. These findings are in agreement with those of Vlček and Šmahel (2002). Besides these shape agreements with the Upper Palaeolithic sample from Dolní Věstonice, a smaller gonial angle and smaller steepness of the mandibular body was evident. The vertical dimensions up to the present have not changed very much. This supports the findings of Manfredi et al. (1997) that the vertical variables are under higher genetic control that the horizontal ones. According to them, heritability seems to have more influence on anterior-vertical dimensions than on posterior dimensions.

The conclusion from these observations is that the recent Central European skulls are significantly shorter in males, even in combination with the higher skull. According to Lieberman et al. (2002), the crania of anatomically modern *H. sapiens* are uniquely characterised by two general structural autapomorphies: facial retraction and neurocranial globularity. Less than 40% of the variation in neurocranial length and height was explained by cranial base breadth and endocranial volume. Similarly shaped features can also be observed in the Sunghir 1 skull from the Upper Palaeolithic period (Alexeeva and Bader, 2000). It is the major difference between the Upper Palaeolithic and recent skulls from the point of view of diachronic trends.

These results are in accordance with the statement (Brace et al., 2006) that craniofacial dimensions, with the exception of the tooth-bearing parts of the facial skeleton, are largely of neutral, adaptive significance. It means that an analysis of their variation can indicate genetic relationships between given populations. The results of the aforementioned study indicate that, in terms of their craniofacial shape, all modern European *H. sapiens* groups show that they are closely related to each other, and that the late Pleistocene skulls are more robust than those of the more recent human groups.

A difference from the present craniofacial shape is considered to be the contribution of the Neolithic population to the variability of the cranial dimensions of the recent European inhabitants (Brace et al., 2006). This is also evidence that the Neolithic people of Europe and their Bronze Age successors are not closely related to the modern inhabitants. It is possible that the variety and extent of the whole European continent does not permit monitoring and observation of diachronic trends that are apparent only in a small region such as the one we have just studied. It also cannot be ruled out that the morphological traits of skulls from the Neolithic until the present have changed significantly.

If we look at cranial length in Bohemia and Moravia (Central Europe) from the Upper Palaeolithic period until today (Neolithic, Eneolithic, Unetice culture, Middle Age) there is clear evidence of brachycephalization, with the lowest average cranial length value found in the recent population. Cranial height in the Neolithic, Eneolithic and the period of Unetice culture is, on average, comparable to that of the recent skulls, while Upper Palaeolithic and early medieval skulls are significantly lower (Černỳ, 1999; Černỳ and Velemínskỳ, 1998; Chochol, 1964; Velemínská et al., 2008). Comparison with medieval Czech skulls from the 9th century (Drozdová, 1997;

Velemínská et al., 2008) and another larger sample from the 16–19th century (Hanáková et al., 1984) have indicated a shorter Upper Palaeolithic height of the mandibular ramus and a longer mandibular body.

Current genetic studies show that there is a regional continuity among the inhabitants of the European continent and that the current genetic pool of European populations was affected by both Palaeolithic populations and Neolithic influence from the Near East (Semino et al., 2000; Belle et al., 2006). The estimated proportion of the admixture of European Neolithic populations is 20–50%. The results of the analysis of five individuals, dated between 13,000 and 3000 years BP, have shown the presence of haplotypes common in the current European population (Di Benedeto et al., 2000). Genetic studies of ancient mt-DNA of individuals from the early Neolithic in Central Europe have shown that only 25% of mt-DNA haplotypes of Neolithic farmers originate from the Near East (Haak et al., 2005). This corresponds to the results of recent work on molecular genetics, which shows that around 80% of the genetic make-up of the current population in the Czech territory has its roots in the Upper Palaeolithic (Kráčmarová et al., 2006; Luca et al., 2007). The continuity of settlement of Central Europe from the Upper Palaeolithic period until today was also presumed by Vlček (1991, 1996) on the basis of morphology, especially that of the cranial skeleton.

On the contrary, Van Vark et al. (2003) have argued that morphometric relationships between the crania of EUP inhabitants and modern populations may be a poor indicator for the determination of ancestral–descendant relationships. High variability among EUP crania (Van Vark, 1994) has been consistent with the evidence that only about 10% of modern European mt-DNA had derived from the Early Upper Palaeolithic, while 70% came from Late Upper Palaeolithic, with only 20% originating from the Mesolithic substrate from the Middle East (Sykes, 1999). Nevertheless, according to Jantz and Owsley (2003), Upper Palaeolithic crania are, for the most part, larger and represent more generalised versions of recent European crania. Howells (1995) has reached a similar conclusion with respect to European Mesolithic skulls.

Apparent sexual dimorphism of most size dimensions was detected in recent Central European norms (Šmahel et al., 1998; Macková, 2004) and also in Předmostí and Dolní Věstonice skulls. Franciscus and Vlček (2006) as well, described some level of sexual dimorphism in overall absolute facial height and breadth in the Pavlovian sample. Male crania are more robust with distinctive muscle markings, while females are more slender in many features. According to Wolpoff et al. (2006), Central European Early Upper Palaeolithic male skulls include a constellation of characteristics, beyond just size and muscularity, which represent the retention of Neandertal morphology.

Our results correspond to the micro-evolutionary secular changes described by Wescott and Jantz (2005). This process assumes increasingly stronger expression among the Upper Palaeolithic and recent reference samples, which were the object of our studies. The most typical evolutionary changes were the development of neurocranial globularity and decreased facial convexity. It is hard to define the ultimate causes of the abovementioned craniofacial alterations over time. We are of the opinion that, in addition to genetic changes and improved health and nutrition (Angel et al., 1987; Jantz and Meadows Jantz, 2000; Kouchi, 2000), biomechanical responses to a more processed diet (Carlson and Van Gerven, 1977; Larsen, 1997) could have had a crucial influence.

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