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A geometric approach to cranial sexual dimorphism in fossil skulls from Předmostí (Upper Palaeolithic, Czech Republic)

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Abstract. The recently rediscovered glass plate negatives of unique skeletal fossil material from Předmostí – their estimated ranges from 25–27 000 years but they were destroyed during World War II – were studied by means of geometric morphometrics. The aim of this study was to determine the sexual shape variability of the best preserved skulls of adult individuals, using the methods of statistical shape analysis. While the results roughly support Matiegka's sex estimation, skull 1 (Matiegka's female) is more similar to males. The differences between the skulls of the Předmostí specimens are "more striking" in the lateral, frontal and vertical views, whereas the inter-sexual differences affect the non-affine parts of changes in vertical, lateral and basal views in particular. The areas of the *metopion, glabella, auriculare, porion, asterion, gnathion* and *opisthocranion* landmarks present more striking variations, i.e. those with more discriminatory power. According to the computations made of the various skull distances, the male skulls are more similar to each other and the female skulls less similar. This suggests possible patrilocal behaviour on the part of the males.

■ **Geometric morphometrics, shape analysis, 2D landmarks, thin-plate splines, 3D order penalty, partial warps, sexual dimorphism, Upper Palaeolithic**

INTRODUCTION

The Middle and Upper Palaeolithic site of Předmostí is located at the southern entrance of the Moravian Gate, an important Central European pass. This site, one of the richest and most spectacular Palaeolithic sites anywhere in Central Europe, is traditionally cited as a more or less tragic case. Archaeological excavations started early in the 19th century but covered only limited areas, and were sometimes undertaken in the unfavourable atmosphere of industrial limestone and loess exploitation and personal competition between the archaeologists concerned. The site yielded the largest assemblage of Early Modern skeletons known hitherto. At the end of World War II, however, most of the accumulated material, including the human fossils, was damaged by a fire (Svoboda 2000).

An important part of the biological variability of one skeletal sample or a species is determined by gender. Sexual dimorphism is a common and sometimes prominent feature of the living world. Males and females differ in this way in a variety of traits. The magnitude of sexual dimorphism is used in phylogenetic analysis, as well as to infer the social structure of extinct species and their reproductive behaviour. In human populations, a reduction in the degree of dimorphism is also indicative of stress and relatively poor living conditions. In palaeoanthropology, a difference in the pattern and degree of sexual dimorphism may provide a means for discriminating between populations and explaining a component of intra-specific variation (Frayer et Wolpoff 1985). The ability to ascertain sex in skeletal and fossil remains is, however, critical for the reconstruction of the reproductive behaviour and biology.

An inevitable result of biological processes such as growth, development and evolution represents a change in the form of the object under study. The form of an object consists of both its size and shape. Most biological forms contain identifiable loci, which are referred to as biological landmarks. To be of analytical use, these must be present on all of the specimens under consideration. Landmark data are the co-ordinates of these biological loci (Lele et Richtsmeier 1992).

Given that the cranium is a complex, three-dimensional structure, and that the growth of the cranium involves the co-ordinated growth of many skeletal and soft-tissue elements, the "new morphometry" of geometric shape analysis should provide a more comprehensive, detailed understanding of sexual dimorphism (Hens 2002).

In recent years there has been an increasing interest in the use of geometric morphometric methods as opposed to the traditional multivariate analysis of selected distance measurements, angles, and ratios in studying variation in shape (Rohlf 2003). Traditionally, morphometric studies have relied on the statistical analysis of distances, angles or ratios to investigate morphometric variation among taxa. Recently, geometric techniques have been developed for the direct analysis of landmark data. Shape co-ordinates, thin-plate splines and relative warp analyses are the essence of these kinds of newer geometric techniques (Lynch et al. 1996, Dryden et Mardia 1999, Ross et al. 1999, Hennessy et Stringer 2002, Katina 2002).

Geometric morphometric methods usually begin with the digitised co-ordinates of numbers of landmark locations. The effects of variation in location, orientation, and scale of the specimens are eliminated and the differences that remain represent shape variation, expressed with respect to a suite of shape variables. Statistically, the advantage of this approach is that with sufficient sample sizes one may expect a much higher statistical power to detect shape differences, because landmark co-ordinates capture more information about shape than can be obtained from traditional morphometric measurements. Another advantage is that these methods usually provide better visualisations of the results (Bookstein 1991, O'Higgins 2000, Rohlf 2003, Katina 2003). Perhaps the greatest advantage of geometric morphometrics, however, is that it provides a means of quantifying the shape differences, and therefore differences in character states, of variable traits that cannot be directly linearly measured (Harvati 2003, Kováč et Katina 2003).

More than 100 years after its discovery, the Předmostí hominid samples remain the best documentation available for knowledge of individual variation among European Upper Palaeolithic hominids (Brůžek, Tillier 1996). They are still among the most extensive samples from the Upper Palaeolithic, and moreover are very homogeneous, and thus are quite rightly considered a representative sample of the whole population

The aim of the following study was to evaluate the sex assessments and consider the sexual differences among the best preserved skulls of adult individuals from the Předmostí collection through geometric morphometrics, with the aid of other kinds of penalty calculation. The classic sex determination proposed by Matiegka was based on the 20th century paradigm in which emphasis was placed on cranium morphology. Today it is known that this approach may be loaded by an error of as much as 20 % in a sufficiently large data file (Masset 1987). The study presented here is a continuation of the first analysis of the sexual dimorphism of the Předmostí skulls by the way of geometric morphometrics (Šefčáková et al 2003).

MATERIALS

The discovery of Matiegka's original, contemporary photodocumentation on glass plates in the Department of Anthropology and Human Genetics of the Faculty of Sciences at Charles University in Prague (Velemínská et al. 2003a, 2003b) has made it possible to achieve new insights into the skeletal sample of 27 subjects of different ages and sexes. Photographs from these negatives were used to illustrate the results of the anthropological investigation, which were published in two monographs by Prof. Jindřich Matiegka himself (Matiegka 1934, 1938). The estimated age of the skeletons is estimated at 25–27,000 years (Svoboda 2001).

The material used in this study consists of the professionally digitised glass plate negatives of fossil skulls (Předmostí 1 – P1, Předmostí 3 – P3, Předmostí 4 – P4, Předmostí 9 – P9, Předmostí 10 – P10) in the accessible norms: frontal, lateral sin., occipital, basal and vertical views. The skulls in question are those determined by Matiegka to have been females (P1, P4, P10) and males (P3, P9).

METHODS

a) Assessment of the morphologically characteristic and defined landmarks (craniometric points) by direct marking on the scans of negatives. In all, 40 landmarks were employed in five views (Appendix 1). In the frontal view (Fig. 1a): 35 landmarks, 13 of them in pairs. In left lateral view (Fig. 1b): 22 landmarks. In the occipital view, 7 landmarks, of which 3 in pairs. In the basal view: 11 landmarks, of which 5 paired. In vertical view – 7 landmarks, of which 2 in pairs.
b) Assessment of the baseline (reference line) – in the frontal, occipital and basal views the euryon-euryon distance, in the lateral and vertical views the glabella-opisthocranion distance. All were used for the standardisation of skull comparisons using Bookstein's co-ordinates.
c) Shape analysis was implemented using the S-PLUS 4.5 statistical package, employing specially constructed program routines by S. Katina (Katina 2002, Katina 2003) and I. L. Dryden's routines (Dryden et Mardia 1999).

Using these program routines each skull was compared to the others in a particular view (for example, P1 with P3, P1 with P4, P1 with P9, P1 with P10, etc.); a matrix of Bookstein penalties was then constructed for each view, as were global penalties for all the views together. Global penalties were counted as order-means of penalty-values for particular views. Next, the skull-set was divided into two groups (male and female) on the basis of penalty-similarities, and here group shape differences were analysed using Bookstein's mean

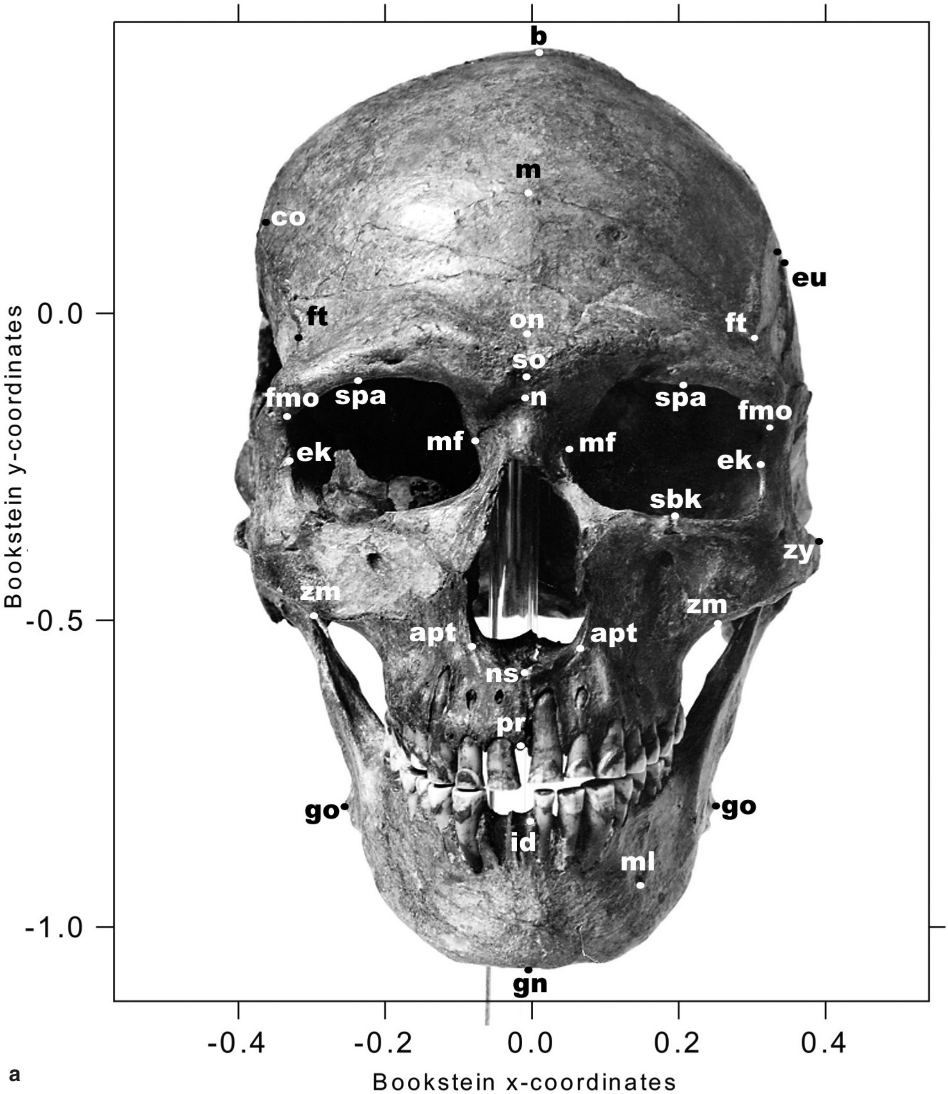
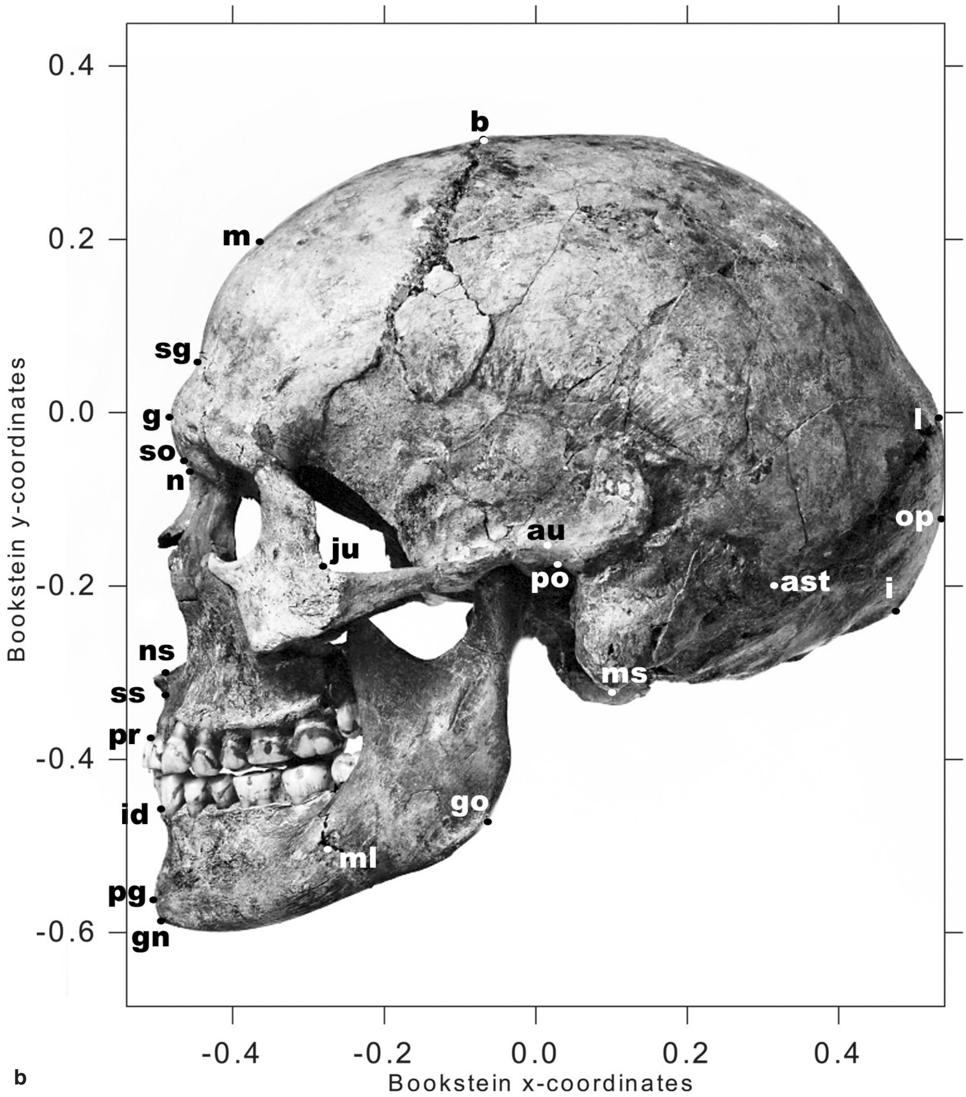


Fig. 1a. Frontal and lateral view sin.: Předmostí Cranium 3 with landmarks in Bookstein co-ordinates, Frontal view.

shapes. The same approach was used in the analysis of male and female differences as for global penalties. The inter-sexual order-means were counted on the basis of the order of penalty-differences from the reference object (P1) in particular views. Another criterion used for inter-sexual singularities is the percentage of affine and non-affine changes.

Not only the correctness of Matiegka's sex determinations were assessed, but also the power (measure) of the skull differences.

The algorithm of order-means counting may be understood as a specific approach to



b

Fig. 1b. Frontal and lateral view sin.: Předmostí Cranium 9 with landmarks in Bookstein co-ordinates, Lateral view sin.

shape analysis, where the researcher has only 2D and digital photographs from particular views (frontal, lateral, occipital, vertical and basal) available, but not the 3D material, as is the case with the skeletal material from Předmostí, which is now preserved only in the form of glass negatives. This paper uses an unweighted algorithm, but in general, particular views may be weighted by their anthropological significance. Other algorithms relating to the 2D/3D problem and their applications can be found in Šefčáková et al.(2003), Katina (2004) and Katina et al (submitted).

Table 1. Penalty table for skull P1 (in brackets – Bookstein penalty, order; global penalty – order-mean of particular views).

	Order 1	Order 2	Order 3	Order 4
lateral view	P9 (0.0111, 3)	P3 (0.0111, 2)	P10 (0.0074, 1)	P4 (0.0126, 4)
frontal view	P9 (0.0077, 1)	P3 (0.0090, 2)	P10 (0.0109, 3)	P4 (0.0242, 4)
vertical view	P9 (0.0023, 1)	P3 (0.0026, 2)	P10 (0.0095, 4)	P4 (0.0062, 3)
basal view	P9 (0.0042, 4)	P3 (0.0018, 2)	P10 (0.0012, 1)	P4 (0.0019, 3)
occipital view	P9 (0.0331, 2)	P3 (0.0374, 4)	P10 (0.0354, 3)	P4 (0.0239, 1)
GLOBAL	P9 (2.2)	P3 (2.4)	P10 (2.4)	P4 (3)

Table 2. Penalty table for skull P3 (in brackets – Bookstein penalty, order; global penalty – order-mean of particular views).

	Order 1	Order 2	Order 3
lateral view	P9 (0.0093, 1)	P10 (0.0114, 3)	P4 (0.0107, 2)
frontal view	P9 (0.0090, 1)	P10 (0.0091, 2)	P4 (0.0116, 3)
vertical view	P9 (0.0028, 1)	P10 (0.0104, 3)	P4 (0.0064, 2)
basal view	P9 (0.0126, 3)	P10 (0.0012, 1)	P4 (0.0024, 2)
occipital view	P9 (0.0187, 1)	P10 (0.0220, 2)	P4 (0.0688, 3)
GLOBAL	P9 (1.4)	P10 (2.2)	P4 (2.4)

Table 3. Penalty table for skull P4 (in brackets – Bookstein penalty, order; global penalty – order-mean of particular views).

	Order 1	Order 2
lateral view	P10 (0.0146, 2)	P9 (0.0103, 1)
frontal view	P10 (0.0544, 1)	P9 (0.0592, 2)
vertical view	P10 (0.0017, 1)	P9 (0.0024, 2)
basal view	P10 (0.0014, 1)	P9 (0.0093, 2)
occipital view	P10 (0.0122, 2)	P9 (0.0071, 1)
GLOBAL	P10 (1.4)	P9 (1.6)

Table 4. Percentage /100 of AP and PW deformation between mean (P3, P9) and mean (P4, P10) (AP (ZOW) – affine part (zero order warp), in brackets the x co-ordinate and y co-ordinate changes, PW – partial warp, GLOBAL – mean percentage/100).

	AP (ZOW)	PW
lateral view	0.1290 (0.1109; 0.0181)	0.8710
frontal view	0.4553 (0.0159; 0.4393)	0.5447
vertical view	0.0208 (0.0008; 0.0199)	0.9792
basal view	0.1522 (0.0407; 0.1115)	0.8478
occipital view	0.4101 (0.0153; 0.3948)	0.5899
GLOBAL	0.2335 (0.0367; 0.1967)	0.7665

RESULTS AND DISCUSSION

1) In general Matiegka's sex estimation may be supported. Only skull 1 (according to Matiegka a female) seems more similar to skulls 3 and 9 as well (Tab. 1), both of the latter being considered male. Is skull 1 also male? Such a conclusion might be supported by the similarities to male skulls P3 and P9 (Tab. 2). Finally, skull P4 is more similar to skull P10 (female) (Tab. 3).
2) Sex group assignments (excluding P1) enabled the determination of sex differences between the average male (shape average of skulls P3 and P9) and average female (the

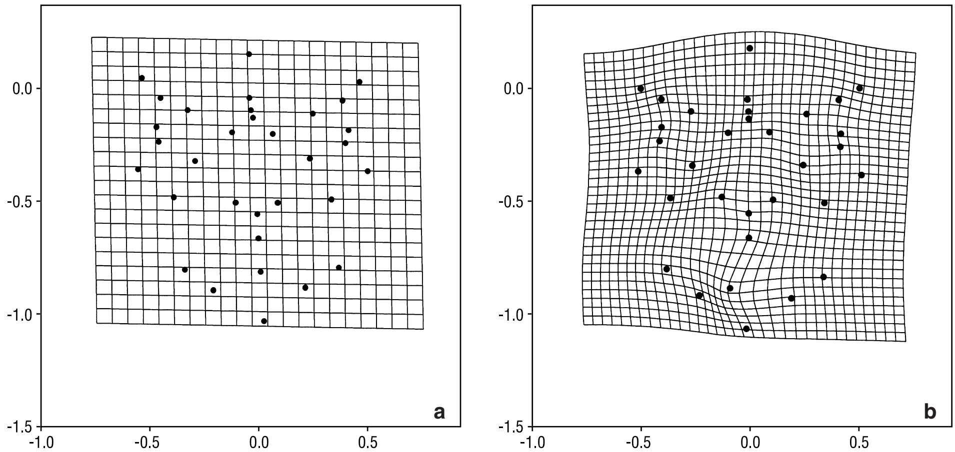


Fig. 2. Affine and TPS grids of the deformation of the average male skull (P3, P9) compared to the average female skull (P4, P10), frontal view sin.: a) AP component of PW grids, b) TPS grid

shape average of skulls P4 and P10). These could then be used to determine the landmarks with the highest variability and to depict the overall variability in TPS nets.

3) Inter-skull differences: Judging from the global penalties (allocation to orders), the skulls differ mostly in the lateral, frontal and vertical views – but adding the other views (occipital and basal) resulted in no changes to the ordering.
4) Inter-sexual differences: Skulls differ mostly in the non-affine part of changes in the vertical, lateral and basal views (Tab. 4). The frontal and occipital views have approximately the same percentages of affine and non-affine parts of changes.
5) Globally (Tab. 4) the affine (stretchable) component of the deformation of the average male skull to the average female skull presented 23.4 % variability, of which the variability on the x-axis orientation was 3.7 % and the variability on the y-axis orientation 19.7 %. Partial warps (PWs) of the non-affine (deformational) component presented 76.6 % variability.
6) In the frontal view (Fig. 2), the affine component part (AP) of PWs, by the deformation of the average male skull to the average female skull, presented a variability of 45.53 %, 43.93 % of which is attributed to the y-axis orientation, while the variability on the x-axis orientation is 1.59 %. Furthermore, the non-affine component part of PWs, by the deformation of the average male skull to the average female skull, presents a variability of 54.47 %.

The sex differences analysed in the frontal view revolve around the irregular movement in height (softly compression) with a mild inclination to the right side for the affine component of PWs as well as the movement in the forehead, nasal and jawline areas for non-affine parts of PWs. The areas of the bregma, euryon, coronale, frontotemporale, prosthion, infradentale, gnathion, mentale and gonion are the most variable (with the greater discriminatory power).

7) In the lateral view, which is particularly important (Tab. 4, Fig. 3), the affine component of PWs, by the deformation of the average male skull to the average female skull, presented a variability of 12.9 %, of which 11.0 % is attributable to the x-axis orienta-

Table 5. Differences between male and female groups on the base of differences in Bookstein penalties (P1 – reference object), in brackets – order; global difference – order-mean of particular views.

	distance (P3, P9)	distance (P4, P10)
lateral view	0.0000 (1)	0.0052 (2)
frontal view	0.0013 (1)	0.0134 (2)
vertical view	0.0003 (1)	0.0033 (2)
basal view	0.0024 (2)	0.0007 (1)
occipital view	0.0043 (1)	0.0115 (2)
GLOBAL	1.2	1.8

tion while the variability in the y-axis orientation is 1.8 %. Furthermore, the non-affine component of PWs, by the deformation of the average male skull to the average female skull, presents a variability of 87.1 %.

The sex differences analysed in the lateral view revolve around movement in the forehead and occipital areas for the affine component of PWs as well as the movement in the forehead, jawline, ear and occipital areas for non-affine parts of PWs. The metopion, glabella, auriculare, porion, asterion, gnathion and opisthocranion areas are the most variable (with greater discriminatory power).

8) According to the computation of various skull distances (Tab. 5), male skulls are more homogeneous than female skulls, which are less mutually similar. It follows that females were probably more heterogeneous and their morphological characteristics were impacted by a higher gene pool, more specifically by the patrilocal behaviour of males.

A priori these results accord with those of the authors' first study (Šefčáková et al. 2003), and with the studies by Ahlström (1996), and Rosas et Bastir (2002). According to these, sexual dimorphism is clearly expressed in the mandible, and the chin is more prominent in males. The occipital bone is strongly affected by the sex factor. Likewise the mastoids and the inion project more downward in males. Furthermore, most of the non-uniform shape changes are located in the posterior part of neurocranium.

In palaeoanthropological studies, the variability patterns of a fossil population are mostly unknown, making it difficult to determine to what extent sexual dimorphism is responsible for the variation detected in fossil samples. An important component of this uncertainty is the effect of size and sex on shape (Rosas et Bastir 2002).

The applications of geometrical morphometrics have been extended over the last few years (e.g. Bruner et al. 2003, Detroit 2000, O'Higgins 2000, Yaroch 1996, Zollikofer et Ponce de León 2001) with the aim of better describing morphological differences in the size and shape of fossil hominids in the genus Homo, and more pertinently to document the differences in particular taxa or chronospecies.

In palaeoanthropology, inter-population variability is hard to determine and intra-population variability is another, even more difficult problem. From the Upper Palaeolithic only isolated finds or burials with few individuals (e.g. Dolní Věstonice) are available. From this point of view, the Předmostí assemblage is unique. Only after understanding the variability of recent populations through geometrical morphometry, relevant information can be found.

Studies of inter-population variability and the sexual dimorphism of the craniofacial area in recent populations using geometrical morphology are not plentiful (Ahlström,1996, Rosas and Bastir 2002, Ross et al. 1999, Lynch et al. 1996). The outcomes of these studies are often inconsistent, e.g. the "finding of no sexual dimorphism in Romano-British crania and therein no clear confirmation" (Hennessy et Stringer, 2002). According to Rosas et Ba-

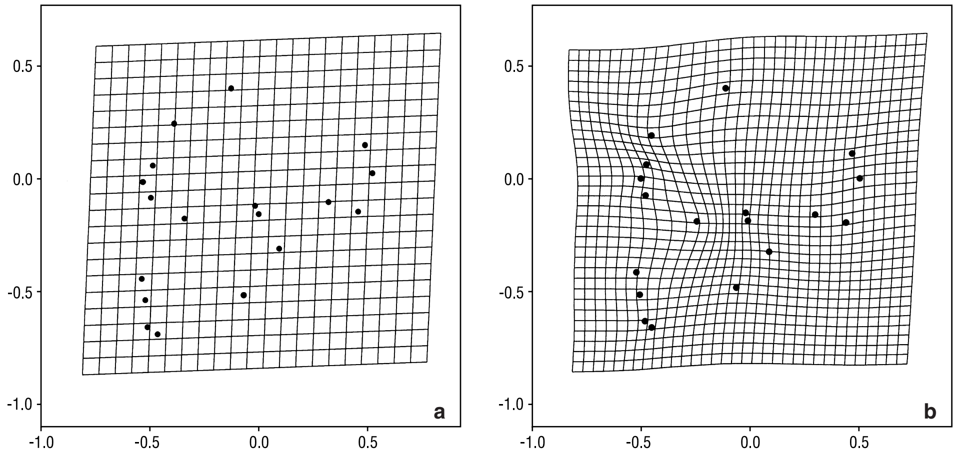


Fig. 3. Affine and TPS grids of the deformation of the average male skull (P3, P9) compared to the average female skull (P4, P10), lateral view sin.: a) AP component of PW grids, b) TPS grid

stir (2002), "no difference in the influence of size on shape was detected in females and males and that both size (explained 54 %) and sex (explained 37 % of the total variance) had significant influence on shape". It is possible to allow that in the range of one population there exists shape affinity of individuals with the same sex.

Because of Matiegka's classic sex determination, it could be admitted that – from the results of this study – Předmostí 1 is a male cranium.

In conclusion it must be said that the aim of this study was achieved by providing the first analysis of adult skulls representing all of the Předmostí fossils. This study is seen as a preliminary work, while further investigations will require the collection of a larger comparative sample of recent and fossil specimens, as made, for example, by Rosas et Bastir (2002).

CONCLUSIONS

The unweighted order-mean approach for the global penalty and finding differences between male and female groups on the basis of differences from a reference object lead to the same results as the using of a special form of Euclidean norm in Šefčáková et. al. (2003).

The Předmostí 1 skull is more similar to the skulls in the male group. The skulls analysed differ mostly in the lateral, frontal and vertical views. The inter-sexual differences between the skulls are mostly in the non-affine part of changes in the vertical, lateral and basal views. This deformational component represents 76.6 % of the total. As expected, the influence of centroid size on shape (allometry) revealed a shift in the proportions of the neurocranium and the viscerocranium, with marked allometric variation of the lower face.

Overall, in the frontal view the affine component presents the same changing part as the non-affine component part (cca 50 %) of PWs. In the lateral view the non-affine (deformation) component of PWs represents a variability of 87.1 %.

According to the computation of the various skull distances, females were probably more heterogeneous and males more homogeneous.

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APPENDIX 1.

List of the landmarks in five different views, after Martin (Bräuer 1988, Malinowski et Božilow 1997).

Landmarks	lateral	frontal	occipital	basal	vertical
apt – apertion		Y *			
ast – asterion	Y		Y *	Y *	
au – auriculare	Y				
b – bregma	Y	Y			Y
ba – basion				Y	
co – coronale		Y *			Y *
ek – ektokonchion		Y *			
enm – endomolare				Y *	
eu – euryon		Y *	Y *	Y *	Y *
fmo – frontomalare orbitale		Y *			
ft – frontotemporale		Y *			
g – glabella	Y				Y
gn – gnathion	Y	Y			
go – gonion	Y	Y *			
i – inion	Y		Y	Y	
id – infradentale	Y	Y			
ju – jugale	Y				
l – lambda	Y		Y		Y
m – metopion	Y	Y			
mf – maxillofrontale		Y *			
ml – mentale	Y	Y *			
ms – mastoidale	Y		Y *		
n – nasion	Y	Y			

* pairs landmarks

Landmarks	lateral	frontal	occipital	basal	vertical
ns – nasospinale	Y	Y			
o – opistion			Y	Y	
ob – obelion			Y		Y
ol – orale				Y	
on – ophryon		Y			
op – opistocranion	Y			Y	Y
pg – pogonion	Y				
po – porion	Y				
pr – prostion	Y	Y			
sbk – subkonchion		Y *			
sg – supraglabellare	Y				
so – supraorbitale	Y	Y			
spa – suprakonchion		Y *			
ss – subspinale	Y				
sta – staphylion				Y	
zm – zygomaxillare inferior		Y *		Y *	
zy – zygion		Y *		Y *	

* pairs landmarks