15. Earliest Upper Paleolithic crania from Mladeč, Czech Republic, and the question of Neanderthal-modern continuity: metrical evidence from the fronto-facial region

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Abstract

Direct AMS radiocarbon dates of around 31 ka BP (Wild et al., 2005) for several well preserved crania and other human specimens from Mladeč, Czech Republic, confirm their association with the Aurignacian. This material, which thus represents the earliest modern European remains with archaeological associations, has long featured in discussions of regional continuity or gene flow from Neanderthal into early Cro-Magnon populations. Here, the four most complete Mladeč crania are compared with Neanderthal fossils in metrical characters of the fronto-facial region. Both univariate and multivariate analyses show no evidence of Neanderthal affinities, and thus of Neanderthal-derived genes.

Introduction

In a commentary on the evidence from molecular biology, Gibbons (2001: 1052) stated that no-one can rule out the possibility that some of us have inherited nuclear DNA from Neanderthals, but detection of such archaic lineages is so difficult that many geneticists despair that they will ever be able to prove or disprove whether the genetic replacement of archaic people outside of Africa was complete. A population geneticist (Rosalind Harding) is cited in this article as saying, "we're going to have to let the fossil people

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answer this one." However, since the effects of genetic exchange are difficult to estimate with polygenic morphological features, this question is also a challenge for fossil experts. For example, there is continuing disagreement whether the presence of cranial features such as a bun-like morphology of the occiput or a supranuchal depression found in some early Cro-Magnons is the result of gene flow from Neanderthals. Also, the identification of a possible Neanderthal – Cro-Magnon hybrid from Lagar Velho (Zilhão and Trinkaus, 2002) is disputed and alternative explanations have been suggested (Tattersall and Schwartz, 1999; Stringer, 2002a; Bräuer, 2006).

Several different perspectives can currently be distinguished regarding the Neanderthal-modern transition in Europe (Bräuer, 2006): (1) an ancestor-descendant relationship as proposed by the classic Multiregional Evolution model, which sees a considerable Neanderthal ancestry for modern Europeans (Frayer et al., 1993; Wolpoff et al., 2001); (2) modern humans moved into Europe accompanied by significant assimilation of Neanderthals (Churchill and Smith, 2000; Trinkaus, 2005; Smith et al., 2005); (3) the Out-of-Africa replacement view, which allows for gene flow but sees little evidence for interbreeding in the fossil record (Bräuer and Stringer, 1997; Bräuer, 2001; Stringer, 2002b); and (4) the complete replacement view, which excludes any gene flow between Neanderthals and dispersing modern humans (e.g., Tattersall, 2003).

In order to reach further agreement on the extent of gene flow at the archaic-modern interface in Europe we feel that it is important to carefully examine all suggested indications of regional continuity (Bräuer and Stringer, 1997: 197). With this intention, the present paper examines aspects of fronto-facial morphology in the earliest anatomically modern cranial remains from the Czech Republic, and their affinities to Neanderthals. This material represents the best early modern sample from Central Europe, and if there was either regional continuity or significant Neanderthal-derived gene flow into such a population we should expect to see traces in the morphology of these specimens. Indeed, it has been claimed by Wolpoff et al. (2001) that such traces can be recognized and even quantified.

Material and Methods

The early modern sample from the Czech Republic examined here includes the four well-preserved crania Mladeč 1 (assumed ♀), 2 (assumed ♀), 5 (assumed ♂), 6 (assumed ♂), and the maxillary fragment Mladeč 8 (assumed ♂). Recent direct AMS dating of several Mladeč specimens including Mladeč 1 and 2, as well as Mladeč 8, yielded ages of about 31 ka BP (Wild et al., 2005) which are in agreement with the Aurignacian artifacts (Vlček, 1995) and previous AMS dates for associated calcite deposits (Svoboda et al., 2002). This confirms the Mladeč assemblage as the oldest directly dated substantial assemblage of modern human remains in Europe (Wild et al., 2005). In addition to this early sample, the three somewhat more recent Brno specimens 1 (assumed ♀), 2 (assumed ♂) and 3 (assumed ♀) have been examined. A direct AMS date for the Brno 2 skeleton, associated with the Moravian Gravettian, yielded a date of 23,680 ± 200 yrs BP (Pettitt and Trinkaus, 2000). The probable female calvaria from Zlatý Kůn, formerly thought to date to the Aurignacian or Szeletian (Jelínek, 1978) has now been redated by AMS to about 13 ka BP (Svoboda et al., 2002). This specimen was also included in our Upper Paleolithic comparative sample. With the exception of Mladeč 6 and Brno 3, of which only casts survive, the originals were measured by one of us (HB).

The comparative material (Table 1) includes Neanderthals, early modern humans from Africa and the Levant, additional Upper Paleolithic Europeans, and the terminal

Table 1. Comparative material used

Site	*abbr.*	*sex*	*Site*	*abbr.*	*sex*
			European Neanderthals		
European Upper Palaeolithic			La Chapelle	LACP	(♂)
Abri Pataud 1	ABRI	(♀)	La Ferrassie 1	LAF1	(♂)
Arène Candide 1	ARCA	(♂)	La Quina 5	LAQ5	(♀)
Barma Grande 5	BAG5	(♂)	Le Moustier	LEMR	(♂)
Bruniquel 24	BRUN	(♀)	Monte Circeo	MOCI	(♂)
Chancelade 1	CHAN	(♂)	Neandertal	NEAN	(♂)
Combe Capelle 1	COMB	(♂)	Spy 1	SPY1	(♀)
Cro-Magnon 1	CRO1	(♂)	*Near Eastern Neanderthals*		
Cro-Magnon 2	CRO2	(♀)	Amud 1	AMU1	(♀)
Dolní Věstonice 3	DOL3	(♀)	Shanidar 1	SHA1	(♂)
Duruthy (Sorde) 3	DUR3	(♀)	Shanidar 5	SHA5	(♂)
Grottes des Enfants 4	GRE4	(♂)	Tabun 1	TAB1	(♀)
Kostenki Markina Gora 2	KOS2	(♂)	*Early modern specimens (Near East)*		
Oberkassel 1	OKA1	(♂)	Qafzeh 6	QAF6	(♂)
Oberkassel 2	OKA2	(♀)	Qafzeh 9	QAF9	(♀)
Paderborn 1	PADB	(♂)	Skhul 4	SKH4	(♂)
Pavlov 1	PAV 1	(♂)	Skhul 5	SKH5	(♂)
Předmosti 3	PRD3	(♂)	Skhul 9	SKH9	(♂)
Předmosti 4	PRD4	(♀)	*Early modern specimens (Africa)*		
Předmosti 9	PRD9	(♂)	Border Cave 1	BOR1	(♂)
Předmosti 10	PR10	(♀)	Omo Kibish 1	OMO1	(♂)
St. Germain-La-Riviére 4	STG4	(♀)	Dar-es-Soltane 5	DAR5	(♂)
Urtiaga 1	URT1	(♂)	Nazlet Khater	NAZK	(♂)
			Wadi Kubanniya 1	WAKU	(♂)

In addition, 23 specimens from Afalou-bou-Rhummel and Taforalt including 4 ♀♀ (AFA3, AF29, TO8C, T171) were included.

Pleistocene Afalou/Taforalt series from northern Africa. The metrical data were derived from different published sources (Heim, 1976; Howells, 1975; Sergi, 1974; Suzuki and Takai, 1970; Trinkaus, 1983, 1987; Vandermeersch, 1981; Bräuer and Rimbach, 1990), from the present authors, and also kindly provided by D. Ferembach, D. Frayer, W. Henke, F. Smith, and F. Wendorf.

The metrical variables used to describe aspects of fronto-facial morphology follow Howells (1973) and Bräuer (1988). Both univariate and multivariate comparisons were conducted. For Principal Components Analysis (PCA) of Neanderthal and modern groups, individual size was eliminated by using log-shape data (cf., Darroch and Mosiman, 1985; Simmons et al., 1991).

Results

In spite of individual variation, a receding flat frontal squama is a typical plesiomorphous feature of the Neanderthals (e.g., Stringer and Trinkaus, 1981; Delson et al., 2000). The results with regard to the Frontal Angle (FRA) show clear differences between European and western Asian Neanderthals on the one hand, and the Czech sample (this study), other Upper Paleolithic Europeans, Skhul/Qafzeh and the Afalou/Taforalt series on the other (Figure 1). There is a slight overlap between the ranges of variation of Neanderthals and Afalou/Taforalt. Mladeč 1 and 5 show the greatest differences from Neanderthals among all the modern samples included. This is especially remarkable since Mladeč 1 is sexed as

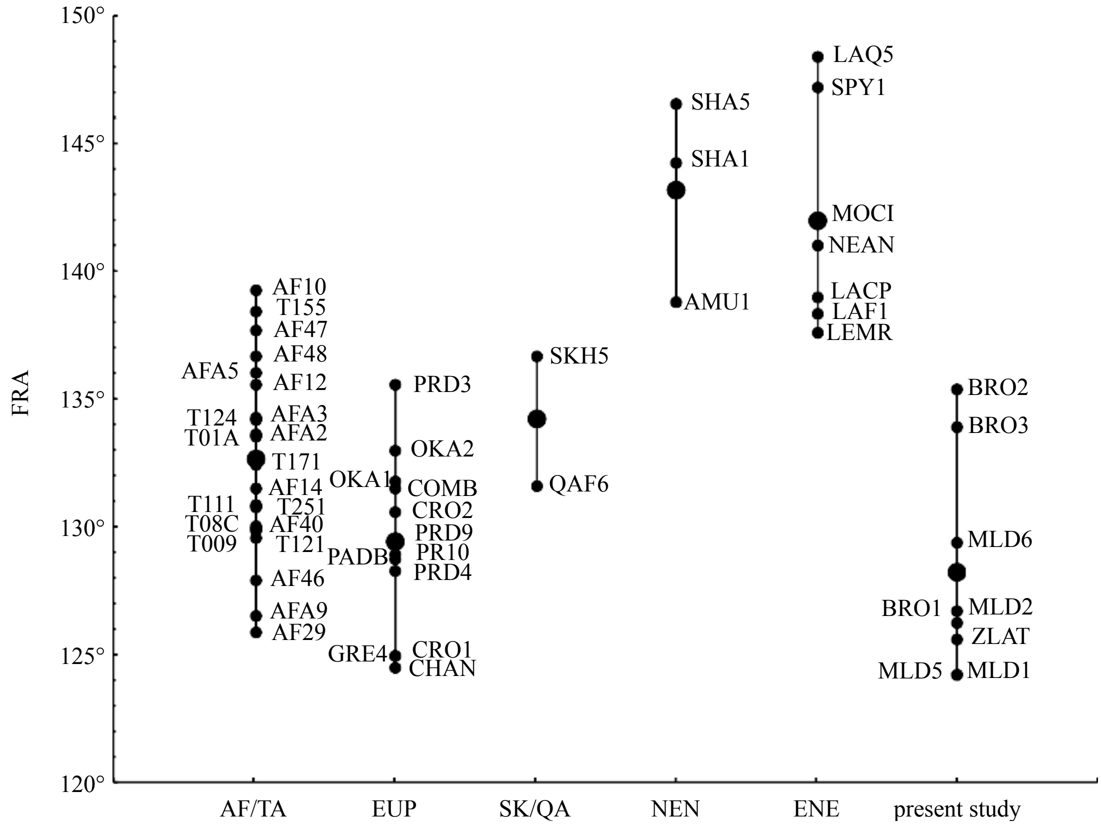

Figure 1. Frontal Angle (FRA). Comparison of early modern specimens from Czech Republic to European Neanderthals (ENE), Near Eastern Neanderthals (NEN), Skhul/Qafzeh (SK/QA), early Upper Palaeolithic Europeans (EUP) and the Afalou-Taforalt (AF/TA) sample (for abbr. see Table 1).

female and Mladeč 5 as male. Zlatý Kůn and Mladeč 2 also differ strongly from Neanderthals, as does Mladeč 6, which is close to several male and female specimens from Předmostí. The more recent Brno frontals show considerable variation even among the two females 1 and 3, but fall within the Upper Paleolithic as well as the Afalou/Taforalt ranges of variation.

Figure 2 presents the results of a PCA based on log-shape data of eight mid-sagittal frontal variables (see Table 2). Most variables, including the subtenses, have high loadings on PC1 (Table 2), which separates Neanderthals rather well from the diverse modern groups. Some Afalou/Taforalt specimens, as well as Skhul 5, show marginal affinities to the Neanderthal frontal curvature. The early modern Czech specimens again deviate most strongly from the Neanderthals, especially Mladeč 2 and 5, even approaching the very divergent Border Cave 1 specimen from South Africa. Mladeč 1 and 6, as well as Zlatý Kůn and Brno 1, also differ greatly from the Neanderthals. The robust specimen Brno 2 shows similarities to Předmostí 3 for FRA (see Figure 1), while Brno 3 exhibits a rather isolated position.

Projection of the midfacial region is one of the features in which Neanderthals have a clearly derived morphology (e.g., Stringer and Trinkaus, 1981; Stringer, 1989; Frayer, 1986, 1992). In the present study, facial morphology was analysed using the Nasio-Frontal Angle

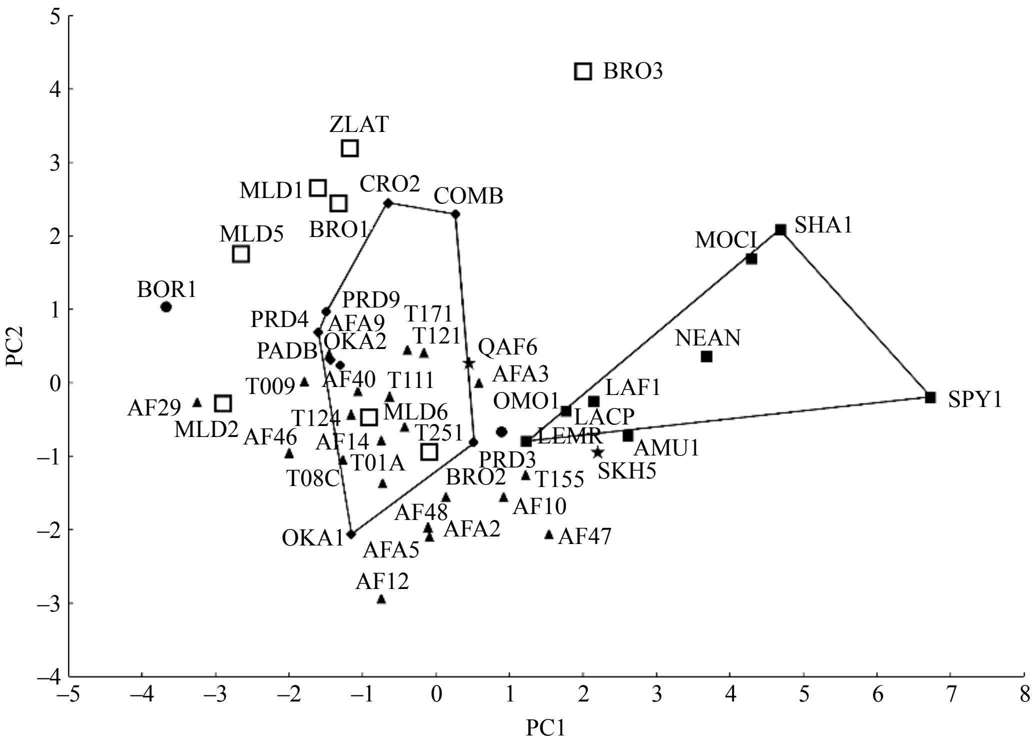

Figure 2. Principal Components Analysis based on eight frontal variables (log-shape data). PC1 accounts for 52,7% and PC2 for 28,2% of the total variance. Outlines indicate range of variation of the Neanderthal and European Upper Palaeolithic comparative samples.

Table 2. Principal Components Analysis based on log-shape data of eight mid-sagittal frontal variables.

Variable	*PC1*	*PC2*
Nasion-bregma arc (26)	0.51402	0.67050
Frontal subtense (FRS)	−0.88243	0.36641
Glabella-bregma chord (29d)	0.86574	0.38555
Glabella-subtense fraction (29f)	0.65579	−0.61420
Nasion-bregma chord (29)	0.73474	0.39576
Nasion-subtense fraction (FRF)	0.54410	−0.70677
Glabella-bregma arc (26a)	0.56439	0.65404
Glabella-bregma subtense (29e)	−0.91720	0.24823

Abbreviations after Howells (1973), numbers after Bräuer (1988).

(NFA), Subspinale (Zygomaxillary) Angle (SSA) and the major dimensions of the nasal aperture, as well as by PCA. The group means for NFA (Figure 3) show that, as expected, Neanderthals differ from the various modern samples by having smaller values, i.e., a more projecting nasion. The variation of the different groups shows some overlap between Neanderthals and the Upper Paleolithic (including Brno) and Afalou/Taforalt samples. However, the earliest Czech specimens are not only outside the Neanderthal range of variation but also show great deviations from them. Large differences between the Neanderthals and the Czech specimens Mladeč 1 and Brno 3 are also evident with regard to SSA (Figure 4) where there is no overlap between the Neanderthal and modern samples for this feature.

A large and broad nasal aperture is another plesiomorphous Neanderthal feature (e.g., Frayer, 1992; Stringer and Gamble, 1993; Delson et al., 2000) and was measured here by Nasal Breadth and Height. Only specimens for which both measurements were available were included. The Neanderthals are quite well separated from the modern groups

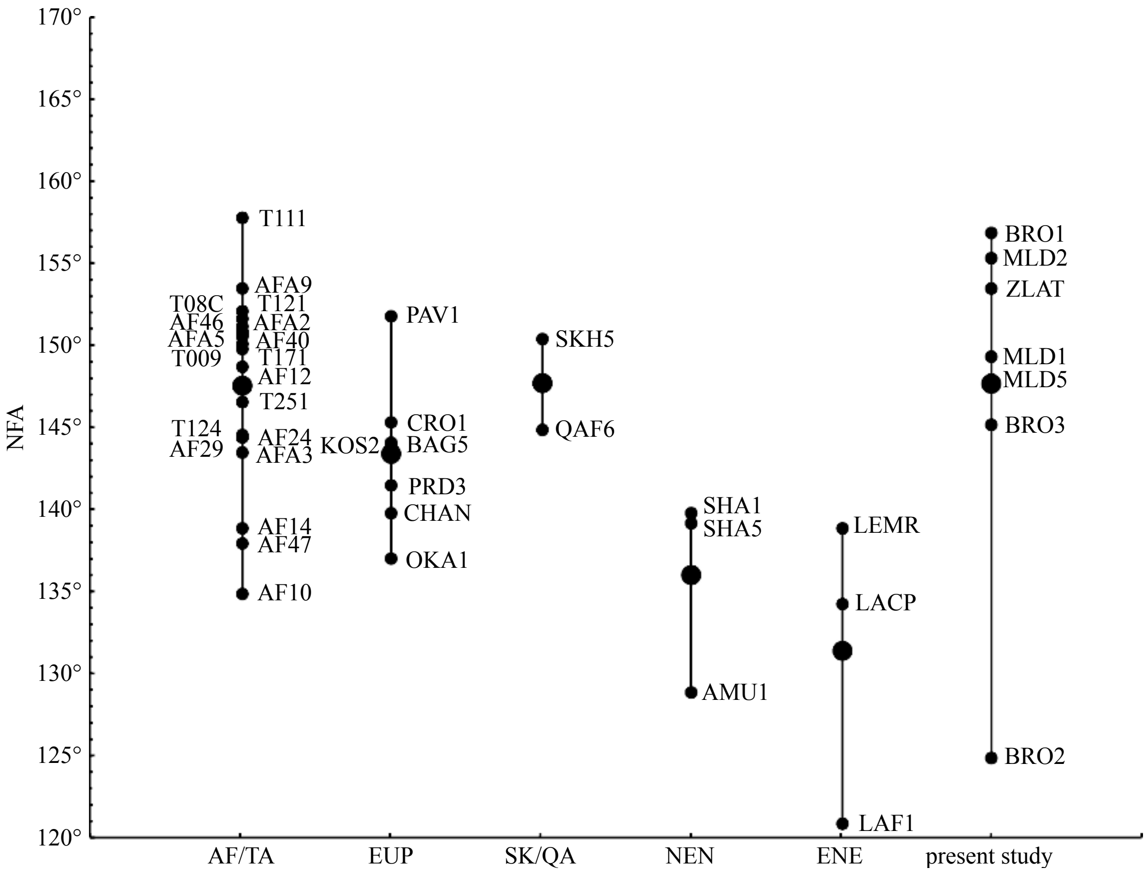

Figure 3. Nasio-frontal Angle (NFA). Comparison of early modern specimens from Czech Republic to European Neanderthals (ENE), Near Eastern Neanderthals (NEN), Skhul/Qafzeh (SK/QA), early Upper Palaeolithic Europeans (EUP) and Afalou-Taforalt (AF/TA).

(Figure 5) although some overlap is seen with regard to the western Asian Neanderthals and early moderns (Shanidar 1, Qafzeh 6). The earliest modern Czech specimens Mladeč 1 and 2 are quite distinct from Neanderthal dimensions, as is Brno 3. However, one of the Mladeč specimens (Mladeč 8), which only consists of a maxillary fragment and thus could not be included in this analysis, has a rather broad nasal aperture measuring c. 32 mm. Although this could be construed as a Neanderthal-like feature (cf., Frayer, 1992), it is also identical with the value of the early modern Qafzeh 6 (Figure 5).

Table 3. Principal Components Analysis based on log-shape data of nine facial variables

Variable	*PC1*	*PC2*
Upper facial height (48)	0.43648	0.84885
Basion-nasion length (5)	0.87654	0.19819
Basion-prosthion length (40)	0.79764	−0.31509
Bifrontal breadth (FMB)	0.90246	−0.28832
Bimaxillary breadth (ZMB)	0.69527	−0.49982
Bimaxillary subtense (SSS)	−0.83884	−0.06643
Nasio-frontal subtense (NAS)	−0.79401	0.04355
Nasal breadth (54)	0.41062	−0.38795
Nasal height (55)	0.62365	0.72629

Abbreviations after Howells (1973), numbers after Bräuer (1988)

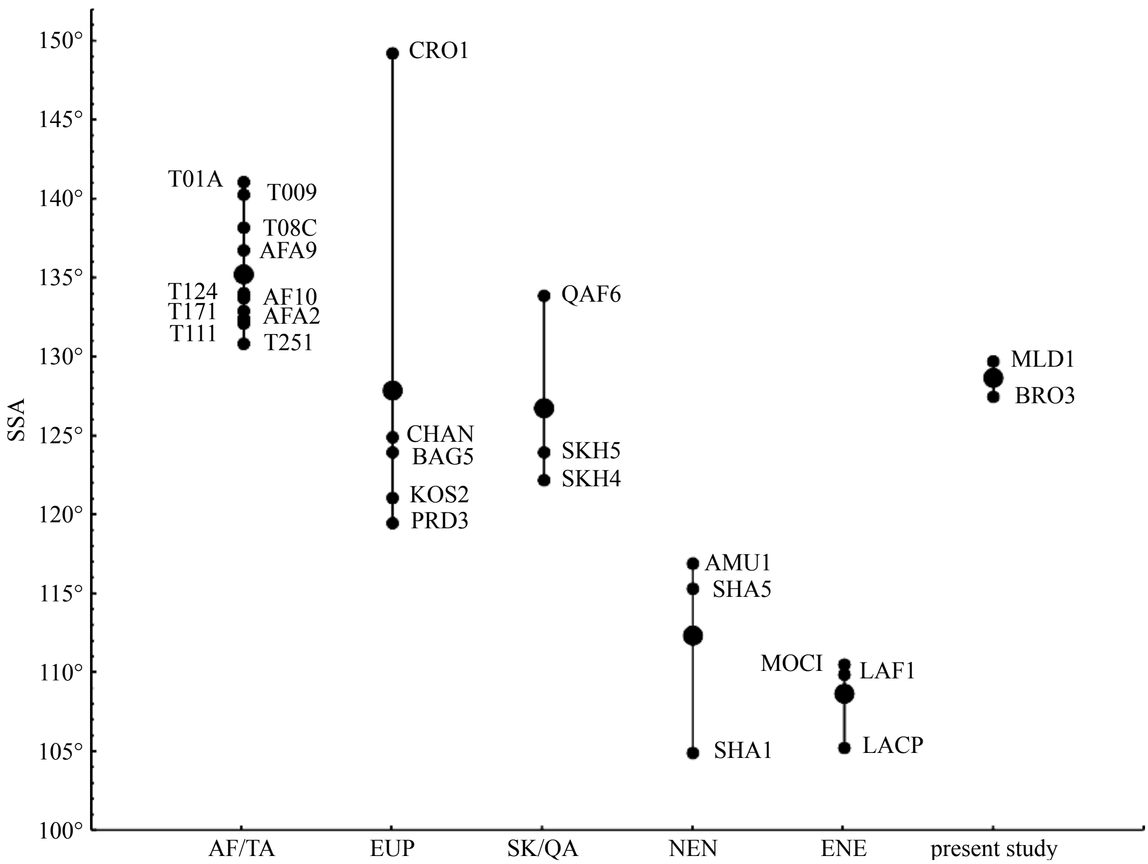

Figure 4. Zygomaxillary Angle (SSA). Comparison of early modern specimens from Czech Republic to different Neanderthal and anatomically modern samples (see Figure 3).

In a more complex approach, facial shape and projection were also analysed by PCA using log-shape data of nine variables (Table 3). These describe the dimensions of the mid-sagittal facial triangle and the nasal aperture, as well as upper facial and midfacial breadths and projections. Due to the lack of complete data sets, relatively few specimens could be included here (Figure 6). Nearly all variables have high loadings on PC1 (Table 3) and separate the three Neanderthals well from the modern specimens. Mladeč 1, the only early Czech cranium for which all variables were determinable, differs markedly from the Neanderthals, and Brno 3 also falls well within the modern group.

Conclusions

The analyses presented here suggest that the early moderns from the Czech Republic show no affinities to Neanderthals with regard to their frontal curvature. This statement holds true for the two robust (male) specimens Mladeč 5 and 6: Mladeč 5 exhibits the most strongly curved frontal measured, even showing close affinities to the probable early modern South African cranium Border Cave 1. With regard to facial morphology, no particular affinities to the Neanderthals could be found in facial projection (NFA and SSA) and the dimensions of the nasal aperture, although the maxillary fragment Mladeč 8 does exhibit

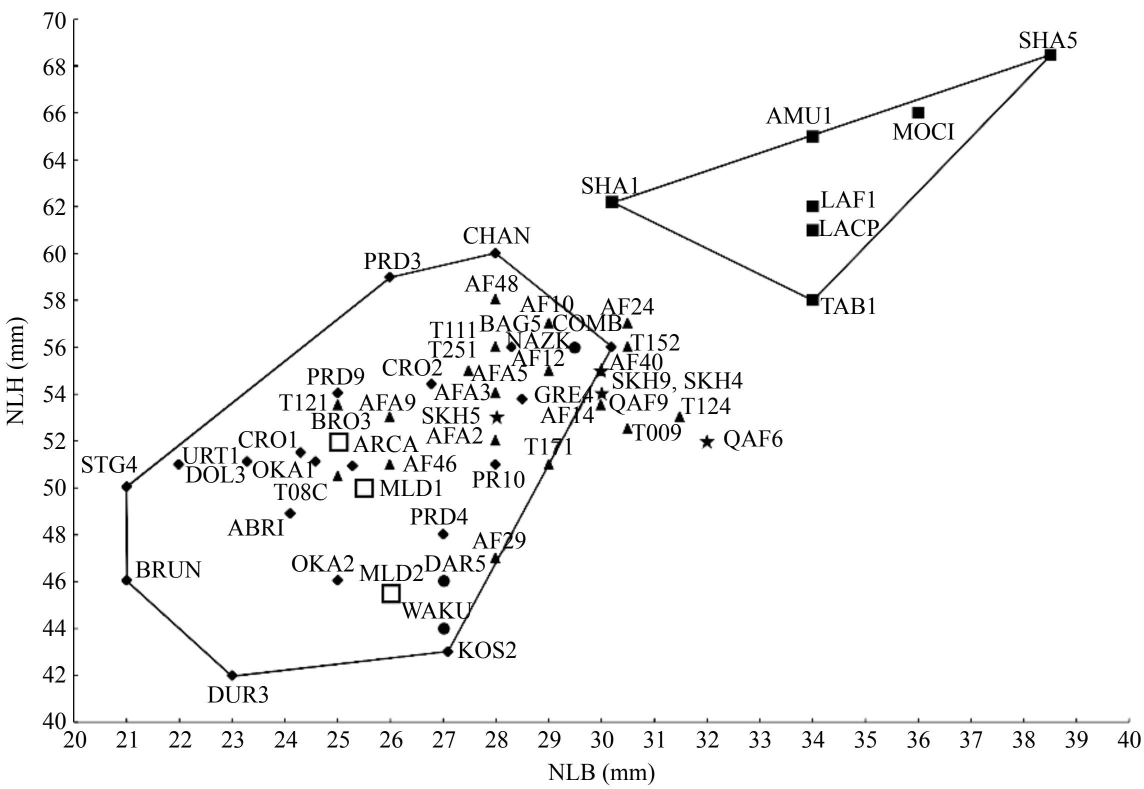

Figure 5. Bivariate scattergram for Nasal breadth and Nasal height. Comparison of early modern specimens from Czech Republic to Neanderthals and different anatomically modern samples (for abbr. see Table 1). Outlines indicate range of variation of the Neanderthal and European Upper Palaeolithic comparative samples.

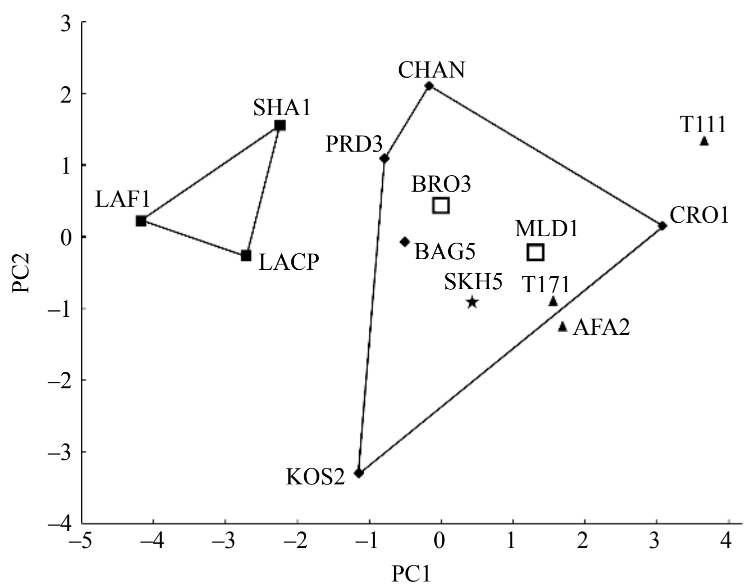

Figure 6. Principal Components Analysis based on nine variables (log-shape data) of facial shape and projection. PC1 accounts for 53.2% and PC2 for 20.9% of the total variance. Outlines indicate range of variation of the Neanderthal and European Upper Palaeolithic comparative samples.

a rather broad (Neanderthal-like or plesiomorphous?) aperture. Finally, the PCA of facial shape and projection reveals that there are no similarities between Mladeč 1 and the Neanderthals.

It can be concluded from the present study that major plesiomorphous and derived frontofacial aspects which generally distinguish Neanderthals from early moderns do not indicate any clear affinities between the oldest modern crania from the Czech Republic and the Neanderthals. This result supports a recent re-analysis of this early Czech material that examined possible Neanderthal or Neanderthal-reminiscent non-metrical features (Bräuer and Broeg, 1998). Of 10 relevant cranial traits examined in that study, not a single character indicative of Neanderthal ancestry was found in any of these Upper Paleolithic specimens. Moreover, it emerged that most of the proposed regional continuity features of the skull (e.g., Frayer, 1992) are either highly problematic or untenable (Bräuer and Broeg, 1998: 127). This result is inconsistent with claims that the Neanderthals could have been the ancestors of these early modern Europeans (e.g., Frayer, 1992). It also contradicts the recent findings of Neanderthal-derived features in the Mladeč crania made using Pairwise Difference Analysis (Wolpoff et al., 2001). Recent reviews of this latter study demonstrated that the claimed Neanderthal affinities of the two Mladeč specimens analysed (Mladeč 5 and 6) are largely based on inadequate assessment of features, the use of traits of dubious phylogenetic utility, the selectivity employed in excluding the most complete Mladeč crania from analysis, and the inappropriate method of pairwise difference analysis used (Collard and Franchino, 2002; Bräuer et al., 2004).

For example, there does not seem to be a generally accepted definition of the suprainiac fossa even among multiregionalists (see Frayer, 1986; Caspari, 1991). Other features used in Wolpoff et al.'s (2001) analysis of the Mladeč specimens are problematic: metric traits were divided into two alternative conditions without clear justification, e.g., long frontal (glabella-bregma length > 113 mm) or thick parietal at asterion (> 9 mm); "mastoid-supramastoid crests well separated" or "fronto-nasal suture arched" cannot be properly assessed without a clear scoring system and are of dubious phylogenetic relevance. Thus it is not surprising that the use of problematic data led to confusing results, as, for example, the minimum number of differences between Skhul 4 and Mladeč 5 and the maximum number of differences between Skhul 5 and Mladeč 5. As outlined in more detail elsewhere (Bräuer et al., 2004; Bräuer, 2006) we do not believe that Wolpoff et al. (2001) provided convincing evidence for a significant Neanderthal contribution to the early modern Europeans. Our conclusions are further supported by a recent metrical study of craniofacial and cranial variation (Harvati, 2003). This study in which specimens from Mladeč were also included did not provide evidence for close similarities between Neanderthals and Upper Paleolithic Europeans nor for a Neanderthal contribution to the evolution of modern Europeans.

Based on the present study as well as on other recent analyses (e.g. Bräuer, 2006), we conclude that there is little or no clear evidence for gene flow or continuity between these early modern Central Europeans and the Neanderthals. We do not wish to deny the possibility that further studies, using other characters or other fossils, such as the early modern Oase material from Romania (Trinkaus et al., 2003, 2006), might detect indications of gene flow from Neanderthals. However, no *significant* gene flow is indicated from the study of the Mladeč material or from the current evidence of other early modern European remains.

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