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Morphological affinities of the Šal'a 1 frontal bone

The human frontal bone from Šal'a, Slovak Republic, has previously entered into discussions of the morphological patterns of Central European Neandertals and the origins of early modern humans in that region. A morphological reassessment of its supraorbital region and a morphometric analysis of its overall proportions indicate that it falls well within expected ranges of variation of Late Pleistocene Neandertals and is separate from European earlier Upper Paleolithic early modern human crania. It is similar to the Qafzeh-Skhul sample in some metrical and supraorbital robusticity measures, but it contrasts with them in mid-sagittal curvature and supraorbital torus morphology. In the context of its probable oxygen isotope stage 5 age based on inferred biostratigraphic associations, it should not be employed directly for arguments relating to the emergence of modern humans in Central Europe.

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Introduction

In 1961 a human frontal bone was discovered by amateur archeologists in secondary deposits on a bank of a small island in Váh River near the town of Šal'a, Slovak Republic (Vlček, 1964, 1968, 1969; see also Smith, 1982). After extensive survey, faunal remains were found indicating a Late Pleistocene age. Šal'a 1 was initially described as a "progressive Neandertal" (Vlček, 1968) and has subsequently been seen as providing evidence of late archaic to early modern human continuity within

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central Europe (Jelínek, 1969; Smith, 1984; Wolpoff, 1999). Yet others (Bräuer, 1989; Stringer, 1989; Sládek, 1998) have questioned these interpretations of the frontal bone. In 1993 and 1995 in a similar context two isolated cranial vault bones of one individual (Šal'a 2), which have only been described preliminarily (Jakab, 1996), were discovered by amateur archeologists. In addition, extensive geological and vertebrate paleontological survey has been carried out in the region.

Given the additional work at the Šal'a localities and ongoing disagreements as to the morphological relationships of the Šal'a frontal bone and its implications, plus the evolved paleoanthropological framework for such an analysis since the original work of Vlček, we have undertaken a morphological and morphometric reassessment of the specimen. Specifically, we have addressed whether the Šal'a 1 fossil is distinct from contemporaneous Neandertal remains and shows indications of morphological affinity to early modern humans.

Previous interpretations of Šal'a 1

The first analyses of Šal'a 1 by Vlček (1968, 1969) described it as a member of the group of "progressive" Neandertals from Near East (e.g., Skhul 5 and Zuttiyeh 1), at a time when the Skhul sample was considered to be "Neandertal-like" and Zuttiyeh 1 was considered to be Late Pleistocene in age (e.g., Howell, 1958; Mann & Trinkaus, 1973). This interpretation was based on individual measurements, the angulation of frontal bone, the median sagittal contour and the morphology of supraorbital region. Šal'a 1 was also said to possess metric similarities with the late Middle Pleistocene Ehringsdorf 9 cranium. Vlček contrasted it with western European "classic" Neandertals and some of the Near Eastern individuals (e.g., Tabun 1). Subsequently, Jelínek (1969) used Vlček's metrical results to argue that Šal'a 1 belonged to his group of transitional central European Neandertals (e.g., Švédův stůl (Ochoz), Šipka) and that it provided evidence for continuous evolution from archaic (Neandertal) toward early modern humans in central Europe.

Subsequently, Smith (1982: 676) concluded that Šal'a 1 exhibits "some features which can be considered 'transitional' or 'progressive', [even though] its total morphological pattern is unquestionably Neandertal". He noted that in some of the metrical features Šal'a 1 contrasts with western European Neandertals and the Krapina sample and that the left supraorbital margin exhibits vertical reduction similar to that seen in the Vindija Neandertal remains, but that its projection was greater than the Vindija pattern and approached the earlier Krapina remains (Smith & Ranyard, 1980; Smith, 1984). Most recently, Wolpoff (1999: 628) has commented that "It is difficult to argue that the Šal'a 1 is more Neandertal-like than the Skhul 5 specimen." Yet, Bräuer (1989) and Stringer (1989) rejected the purported transitional pattern of Šal'a 1 and suggested that the morphology was affected by the sex or age of the specimen. In addition, one of us (Sládek, 1998) has previously argued, based on multivariate discriminant analyses, that Šal'a 1 is indistinguishable from the Neandertals and is separate from both the Qafzeh-Skhul sample and Middle Pleistocene humans.

History and location of the Šal'a 1 discovery

In his descriptions of the specimen, Vlček (1964, 1968, 1969) noted that it had been discovered by a local fisherman V. Čerňanský, who passed it to A. Czellarik of the Archeological Institute of the Slovak Academy of Sciences in Nitra. According to Čerňanský, Šal'a 1 was found on a bank of a small island in the Váh River near the town of Šal'a, approximately 600 m southeast of a road bridge (Figure 1). Vlček thought that the discovery of Šal'a 1 was connected with

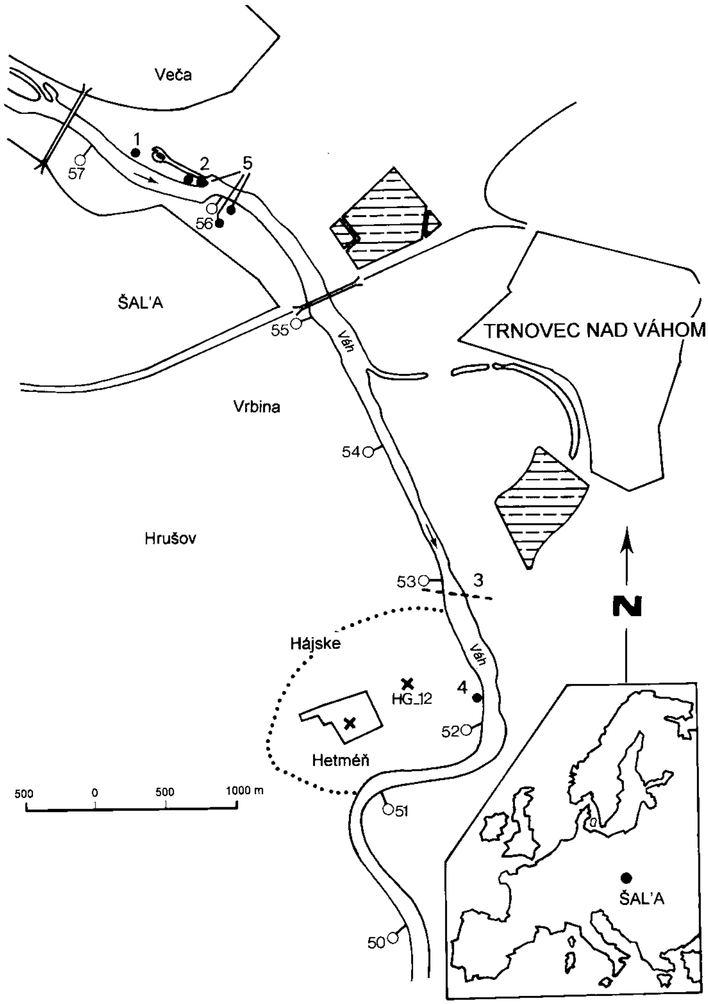

Figure 1. Map of the region of Šal'a and the purported findspots of the Šal'a 1 frontal bone. (1—Šal'a I site, interpretation of Vlček (1968); 2—Šal'a II site, Jakab (1996); 3—Oil pipe construction; 4—Šal'a I site, interpretation of Syrový; 5—Sites of fossil fauna remains; ×—bore-holes Hetméň and HG-12).

the dredging of Holocene and Pleistocene fluvial deposits from Váh River and that the frontal bone emerged from these transferred deposits after the flood of September 1961. These dredging deposits have been partly located near the Šal'a I site.

However, after recent discussions with local people as a result of the discovery of Šal'a 2 (by A. Šefčáková), J. Syrový mentioned that Šal'a 1 had been originally found by him and that V. Čerňanský had misidentified the location of the site. According to Syrový, the Šal'a 1 site is 5·2 to 5·3 km downstream from the previous one, approximately 3 km from the railway bridge on a gravel bar of the right side of the Váh River (Figure 1). Syrový's location of the Šal'a 1 site can be connected with oil pipe construction, which had taken place 700 m upstream from this location during 1961 with intensive destruction of the original Holocene and Pleistocene deposits. The accuracy of this sequence of events cannot be determined, since Syrový mentioned this new evidence 30 years after the discovery.

Additional arguments concerning the original location of Šal'a 1 come from the discovery of Šal'a 2 close to Vlček's original location for Šal'a 1, approximately 950 m southeast of the road bridge (Figure 1) (Jakab, 1996, 1998). Šal'a 2 preserves the left frontal and parietal bones separated by a fracture near the coronal suture, the frontal piece having been found in 1993 and the parietal one in 1995 (Jakab, 1996). All detailed structures of the bones are well preserved on Šal'a 2, and the color and degree of fossilization are similar to those of Šal'a 1 (Jakab, 1998). Jakab emphasized that both banks of the Váh River in the Šal'a 1 and 2 location have been raised ca. 2 m by dredging and that both individuals probably came from erosion of the surface of this relocated dredging deposit.

In light of the new evidence from the Šal'a 2 discovery, the original location of Šal'a 1 was probably closer to Vlček's interpretation that to Syrový's site. However, Syrový's interpretation has raised questions about the site of discovery, which unfortunately cannot be directly resolved. In either case, it is apparent from their excellent state of preservation that the specimens were not transported very far from their original stratigraphic locations.

Stratigraphy, paleoenvironmental context and geological age of the Šal'a 1 site

Seven layers of deposits were discovered in a profile on the island near the original location by J. Kukla in 1966 (Vlček, 1968). The stratigraphic analysis concluded that layers 1–3 from the bottom of the profile are of Pleistocene age. They are composed of sand and gravel with interstitial clay and evidence of cryoturbation (Vlček, 1969). A more precise age for layers 1–3 could not be determined from the stratigraphy, but Vlček proposed a younger Late Pleistocene age. The overlying layers 4–7 are Holocene in age, but since no pedocomplex could be identified within them, it was correlated with a younger phase of the Holocene.

Recent geological survey has confirmed the presence of the Late Pleistocene layers in the Váh River deposits (Czádar, 1998; Halouzka, 1995). Two bore-holes ("Hetméň" and HG-12) near Syrový's location provided a stratigraphy with Pliocene deposits at the base of a Pleistocene sequence. The Pleistocene sequence has only deposits of the younger stages of the Late Pleistocene from 4·2 m to 13·0 m in "Hetméň" bore-hole and from 4·8 m to 13·0 m in HG-12 bore hole. These Late Pleistocene layers have been identified as deriving from the Interpleniglacial (oxygen isotope stage (OIS) 3) and Pleniglacial B (OIS 2). The Pleistocene sequence is covered by Holocene deposits (ca. 4 m in "Hetméň" and 6 m in HG-12). The geological age of the Late Pleistocene layers in the bore-holes appears to be similar to those of the sites presented by Vlček and Syrový, associated with the younger phase of the Late Pleistocene (OIS 2 and 3).

The OIS 2 and 3 ages inferred for both Šal'a locations are in contrast with macrofaunal biostratigraphical implications indicating a probably Last (Eemian) Interglacial (OIS 5e) age (see below; Schmidt, 1962; Ďurišová, 1989, 1993, 1994); it is likely that both the fossil hominid fragments and the associated faunal remains were redeposited during the Late Pleistocene from their original sediments as a result of fluviatile activity. The original sediments containing the vertebrate remains are probably not preserved in the profiles of the Váh River in these sites, and the fossils apparently cannot be directly correlated with the layers documented in the geological survey and coring.

For example, in Vlček's Šal'a I site the remains of *Dicerorhinus hemitoechus*, *Megaceros giganteus hibernicus*, *Palaeoloxodon* and bone fragments of Bovidae were found

(Vlček, 1968). Later Ďurišová (1989, 1993, 1994) reported *D. hemitoechus*, *D. kirchbergensis*, *P. antiquus* and *M. primigenius* from the sites. A fluorine test between remains of *D. hemitoechus*, *Megaceros* and Šal'a 1 provided values of 3·14, 3·88 and 4·02 respectively (Vlček, 1968), supporting the association of these remains.

D. hemitoechus is rarely preserved in central Europe after the beginning of last glacial (OIS 5d) (Ďurišová, 1993; Vlček, 1968), thereby indicating a probable age of OIS 5e or perhaps older. In addition, the 1973 discovery of remains of *D. kirchbergensis* with fossilization and preservation similar to that of Šal'a 1 and morphological similarities to OIS 6 and 5e remains from Ehringsdorf (Germany) and OIS 5e remains from Gánovce (Slovak Republic) support this interpretation (Ďurišová, 1994). Similarly, remains of *P. antiquus* discovered in 1981 are similar to OIS 5e remains from the sites of Ehringsdorf, Taubach and Burgtonna (Ďurišová, 1989). In addition, even though *M. giganteus hibernicus* survived in part of Europe into the Holocene, in central Europe it disappeared at the beginning of the last glacial (Vlček, 1968). The *M. primigenius* remains, although indicating a last glacial age, contrast with the remains of the other faunal species and Šal'a 1 in preservation, in particular indicating significant fluviatile transport (Ďurišová, 1994).

The biostratigraphic information therefore suggests that the preserved Late Pleistocene deposits in both Vlček's and Syrový's locations of the Šal'a I site are younger than the fossils and that the original layer for the vertebrate remains is probably not preserved. Consequently, it is likely that the remains were redeposited during the Late Pleistocene (OIS 3 or 2), and all of the remains were further disturbed in 1961. Yet, combining the results of fluorine test, state of preservation, fossilization and color of the fossils, the best conclusion is that Šal'a 1 is correlated with warm adapted species of Last Interglacial (OIS 5e). If this biostratigraphic correlation between Šal'a 1 and the faunal remains is correct, and therefore that the OIS 5e age is accurate, Šal'a 1 should be close to the ages of the earlier Neandertals from sites such as Krapina and Gánovce.

Preservation

The Šal'a 1 frontal bone (Figure 2) is a virtually complete bone with squamal, orbital and nasal portions preserved; the bone is heavily mineralized to a dark brown color. There has been some minor loss of bone along the sutures, mainly in the nasal and orbital regions. The surface of the bone is well preserved with only small regions indicating minor polishing.

On the upper surface of the right supraorbital torus, in the middle of the right supraorbital trigonum, a small 12 by 10 mm ellipsoid depression is present (Figure 3). The pit is ca. 6 mm from the anterior boundary of supraorbital torus. Margins of the depression are rounded with the same amount of mineralization and color as the other parts of supraorbital bone. No residual marginal fracture line can be found. The pit is best interpreted as the product of a long since healed minor cranial trauma (see also Vlček, 1969, 1969; Smith, 1984), not unlike those found on other Neandertal specimens (Berger & Trinkaus, 1995). This injury has produced a marked asymmetry of the toral arches of Šal'a 1 (Figure 3). The left torus is continuous between the medial and middle portions, with a maximum height (11·5 mm) above the supraorbital notch and a minimum height (7·0 mm) near the lateral end of the middle section. On the right side, the maximum height is 11·0 mm and is also above the supraorbital notch, but the minimum height of 5·5 mm in the middle of the torus. Since this thinning of the right torus

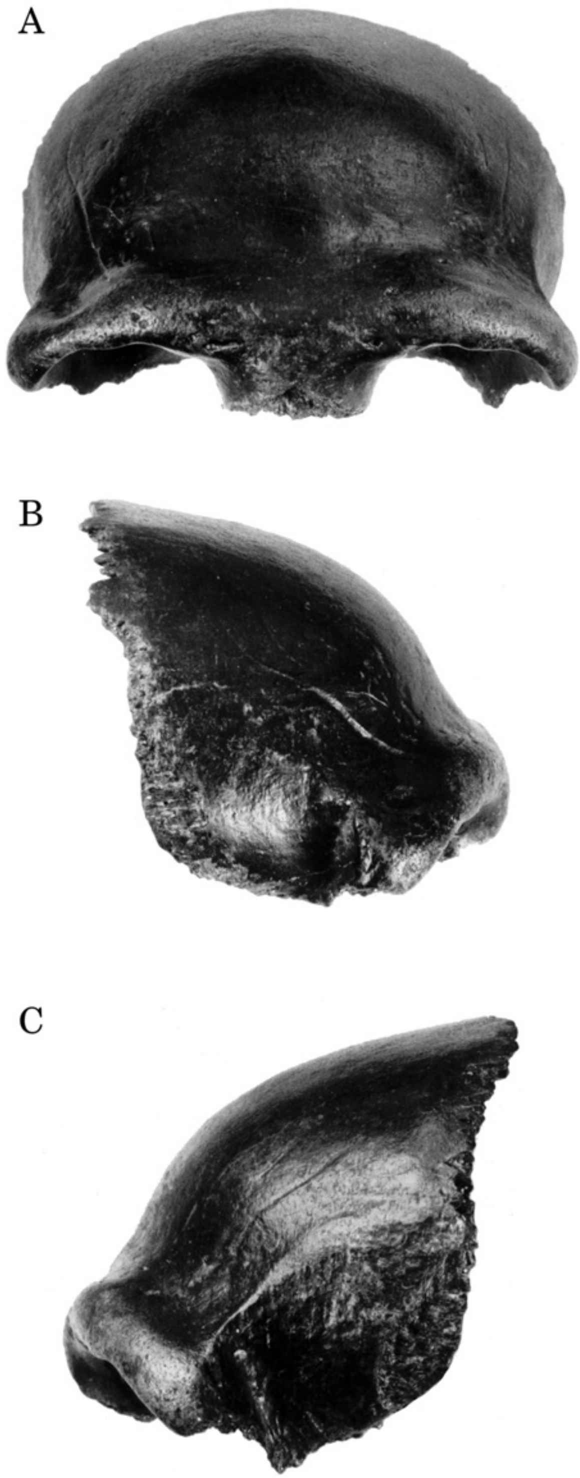

Figure 2. (a) anterior, (b) right lateral and (c) left lateral views of the Šal'a 1 frontal bone. For scale, the outer biorbital breadth is 115 mm, and the nasion–bregma chord is 110 mm. Lateral views are oriented approximately to the Frankfurt horizontal.

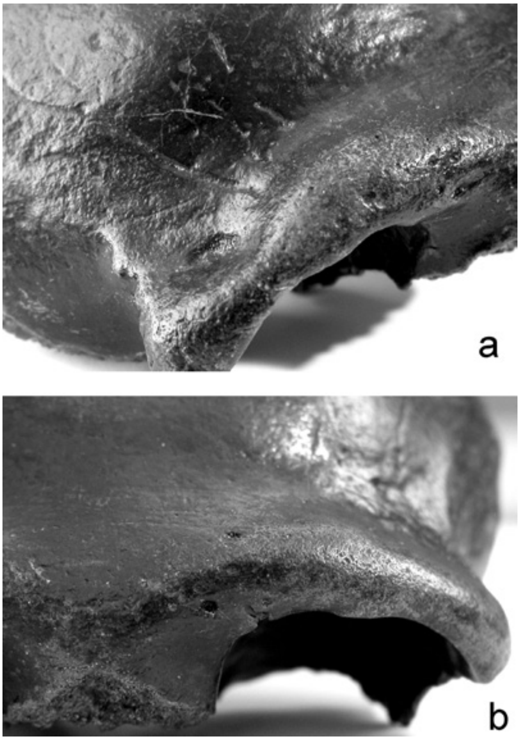

Figure 3. Details of the Šal'a 1 supraorbital torus. (a) supero-antero-lateral view of the traumatic lesions to the right suprorbital torus. (b) anterior view of the normal left supraorbital torus.

is secondary to an injury, the observations on supraorbital morphology below are based on the normal left side.

There are three forms of marks on the bone. First, there is a set of three large marks located on the anterior surface in lateral half of right supraorbital torus. The lengths range from 7·4 to 4·2 mm and they are deep, V-shaped, have sharp margins and contain small parallel marks. The color inside each large groove has a different shade than the surrounding surface, suggesting post mortem damage. Second, five linear shallow marks are located around the lateral part of the left supratoral sulcus and near the supraorbital foramen. The marks are shallow, visible under microscope magnification (10 ×), with lengths of 4 to 10 mm; the contained surface is the same as the adjacent bone. The third set is represented by shallow and relatively long linear marks in the supraglabellar region, continuing to the right side. Six of the grooves have maximum lengths of ca. 40 mm. Their color is the same as that of the surrounding surface. The second and third group of marks are probably scratches from gravel deposits early in deposition, whereas the first group is likely to have resulted from recent handling of the specimen. No pits or furrows indicating carnivore activity have been identified on the bone.

Sex and age

Vlček (1968, 1969) concluded that Šal'a 1 was female based on the overall size and perceived robusticity of the specimen. This is a reasonable interpretation, even if it is often difficult to assign sex to isolated Neandertal cranial remains (Smith, 1980; Trinkaus, 1980). The age-at-death of Šal'a 1 is difficult to determine, but the apparently completely open state of the coronal suture (scores 0 or 1 following Meindl & Lovejoy, 1985) indicates a prime age adult with a considerable range possible (Meindl & Lovejoy, 1985).

Materials and methods

Šal'a 1 is compared metrically to samples of Old World Middle Pleistocene archaic *Homo* (from Europe, the Near East and Africa), European and Near Eastern Late Pleistocene Neandertals, Middle Paleolithic early modern humans (Qafzeh and Skhul) and European and Near Eastern early Upper Paleolithic humans (Table 1). Since the Middle Pleistocene sample is heterogeneous in terms of chronology, geographical distribution, gender and morphological patterns, these groups should not be viewed as a coherent taxonomic unit but merely as representing the known range of variation

Table 1 **Comparative samples of fossil specimens used in the osteometric analyses**

Group/Specimen	Data
Middle Pleistocene humans (MPL)	
Atapuerca-SH 4*, 5*, 6	Arsuaga *et al.* (1997)
Broken Hill 1*	Personal measurement
Ehringsdorf 9*	Vlček (1993)
Florisbad 1*	Personal measurement
Irhoud 1*, 2*	Hublin (1991)
Petralona 1*	Stringer *et al.* (1979)
Zuttiyeh 1*	Personal measurement
Neandertals (Nea)	
Amud 1*	Personal measurement
La Chapelle-aux-Saints 1*	Personal measurement
Feldhofer 1*	Heim (1976)
La Ferrassie 1*	Personal measurement
Forbes' Quarry 1	Personal measurement
Guattari 1*	Sergi (1974)
Krapina 3, 4, 5	Smith (1976)
La Quina 5*	Personal measurement
Saccopastore 1	Condemi (1992)
Shanidar 1*, 5*	Trinkaus (1983)
Spy 1, 2	Personal measurement
Tabun 1*	Personal measurement
Mid. Paleol. early modern humans (QS)	
Qafzeh 6*, 9*	Personal measurement
Skhul 5*	McCown & Keith (1939)
Early Upper Paleolithic humans (EUP)	
Cro-Magnon 1*, 2*, 3*	Personal measurement
Dolní Věstonice 3*, 13*, 14*, 15*, 16*	Sládek *et al.* (2000)
Mladeč 1, 2*, 5*	Personal measurement
Nahal Ein Gev 1	Personal measurement
Pataud 1	Personal measurement
Pavlov 1*	Personal measurement
Předmostí 1*, 3*, 4*, 5, 7*, 9*, 10*	Matiegka (1934)
Zlatý Kůň-Koněprusy 1	Personal measurement
Recent humans (REC)	
Australian sample* (AUS)	Personal measurement
African sample* (AFR)	Personal measurement

*Individuals used in multivariate analysis.

during this time period. To this end, the individual specimens are labeled in the appropriate graphs.

Two samples of recent humans have been used, a craniofacially robust Australian one (n=17) and a craniofacially gracile African one (n=13). Both personal and published data are used. Because of different states of fossil preservation and the availability of comparative data for some specimens, different sets of individuals are used in each comparison.

Given difficulties in sex assignment to most fossil specimens, males and females are pooled in the analyses. Pooled-sex samples increase intragroup variability, but recent analyses have shown that Pleistocene and recent human pooled-sex samples exhibit patterns of morphological relationships similar to those of male or female samples (e.g., Turbón *et al.*, 1997; Van Vark *et al.*, 1992; Sládek, 2000).

Sixteen frontal measurements were taken on Šal'a 1 following Bräuer (1988) and Howells (1973) (see Table 3). Because of the limited data available for comparative specimens, only 13 measurements of Šal'a 1 are subsequently compared. In the univariate analysis, both neurocranial and facial raw variables are compared. The multivariate analysis is focused on the neurocranial measurements.

Because a goal of the paper is to assess the morphological relationships between Šal'a 1 and Middle and Late Pleistocene groups, univariate analysis, principal component, discriminant analysis, and comparisons of typical and posterior probabilities have been done using *Statistica 5.1* (StatSoft, 1984–1996), *Statgraphics Plus 5.0* (Statistical Graphics Corp., 1994–2000) and *StatXact 4.0* (Mehta & Patel, 1999). Additional portions of the analysis have been computed using personal software following published procedures; computation details not included in the software packages are explained below.

The univariate comparisons of Šal'a 1 are based on a modified *t*-test and using *z*-scores for Šal'a 1 relative to the means and standard deviations of the comparative samples, following Sokal & Rohlf (1995). The differences between the comparative samples were assessed using post-hoc ANOVA, based on the LSD-test in Statistica.

To evaluate size and shape between Šal'a 1 and the comparative samples, a multivariate allometric approach with principal components was followed (Klingenberg, 1996). Because of the expected influence of allometry between comparative groups, the data were transformed using $\ln_e$ in all multivariate analysis. Since only principal components extracted from the covariance matrix can be interpreted in a multivariate allometry framework (Johnson & Wichern, 1992; Klingenberg, 1996), the computation of the principal component coefficients and their eigenvalues are based on the covariance matrices computed either in Statgraphics or with the software of Phillips (1998).

Principal component analysis is designed principally for one group studies. However, Flury (1988) has proposed a hierarchical test of the multiple covariance matrices to find which model is the most appropriate one for the principal component analysis of multiple groups (Flury, 1988; Phillips, 1998). The hierarchical test has been computed using the software of Phillips (1998). Standard errors of eigenvalues and Anderson's test of isometry for PC 1 have been computed following Flury (1988).

To evaluate differences between the samples, several parameters of discriminant function analysis have been computed using $\ln_e$ transformed data and *Statistica*. The statistical significance between centroids of the selected groups was computed via *Statistica*. Only the cross-validation (jack-knife) procedure of posterior probability is employed (Dillon & Goldstein, 1984; Johnson & Wichern, 1992; Krzanowski, 1996). The Mahalanobis D^2 based on multivariate variables can be used to indicate where Šal'a 1 falls in relation to the variability of the studied groups. This probability has been described as "typical probability" (Albrecht, 1992), and it has been computed following Albrecht (1992) and Jantz & Owsley (2001).

In addition, the supraorbital torus is considered as a set of discrete features, with frequency distributions for the comparative samples scored as similar to, larger or more pronounced than, or smaller or less marked than Šal'a 1 (Table 2). The traits are considered individually, even though they are morphologically intercorrelated to some degree. Given the potential use of incomplete or

Table 2 Frequencies distributions of supraorbital discrete traits

		MPL (*n* total=9)	Nea (*n* total=18)	Q/Skh (*n* total=6)	EUP (*n* total=20)	*P*
(a) Relative size	*n*	9	17	5	19	<0·001*
	>	100·0	64·7	20·0	0·0	
	=	0·0	35·3	60·0	10·5	
	<	0·0	0·0	20·0	89·5	
(b) Sinusoid shape	*n*	9	14	3	16	<0·001*
	>	88·9	57·1	0·0	6·3	
	=	11·1	42·9	33·3	37·5	
	<	0·0	0·0	66·7	56·3	
(c) Depression between superciliary arches	*n*	8	10	2	18	0·017*
	>	87·5	70·0	0·0	38·9	
	=	12·5	30·0	100·0	22·2	
	<	0·0	0·0	0·0	38·9	
(d) Rounded shape of orbits	*n*	9	16	5	18	<0·001*
	>	44·4	68·8	0·0	0·0	
	=	33·3	25·0	0·0	5·6	
	<	22·2	6·3	100·0	94·4	
(e) Rounded connection torus-orbit	*n*	8	11	3	16	<0·001*
	>	50·0	81·8	0·0	0·0	
	=	37·5	18·2	0·0	12·5	
	<	12·5	0·0	100·0	87·5	
(f) Supraotral sulcus (glabella)	*n*	8	13	2	15	0·001*
	>	62·5	61·5	100·0	20·0	
	=	12·5	38·5	0·0	33·3	
	<	25·0	0·0	0·0	46·7	
(g) Supratoral sulcus (orbit)	*n*	9	18	6	19	<0·001*
	>	22·2	22·2	0·0	0·0	
	=	33·3	55·6	33·3	10·5	
	<	44·4	22·2	66·7	89·5	
(h) Anterior projection	*n*	9	18	6	20	<0·001*
	>	66·7	38·9	16·7	0·0	
	=	22·2	50·0	50·0	5·0	
	<	11·1	11·1	33·3	95·0	
(i) Rounded outline of glabella	*n*	6	9	2	17	0·671
	>	33·3	11·1	0·0	29·4	
	=	50·0	55·6	50·0	35·3	
	<	16·7	33·3	50·0	35·3	
(j) Sulcus in supraorbital area	*n*	8	18	5	20	<0·001*
	Present	50·0	11·1	100·0	100·0	
	Absent	50·0	88·9	0·0	0·0	
(k) Thinning	*n*	9	18	6	19	<0·001*
	>	0·0	0·0	33·3	68·4	
	=	11·1	44·4	33·3	31·6	
	<	88·9	55·6	33·3	0·0	

Traits are scored as larger or more marked than Šal'a 1 (>), equally developed (=), or smaller or less marked than Šal'a (<).

P-values for Kruskal–Wallis tests across the four samples; *P<0·05 after a sequentially rejective Bonferroni multiple comparison correction.

deformed specimens in this portion of the analysis, the sample sizes are generally larger than those available for the metrical analysis.

Description and comparisons

The Šal'a 1 supraorbital morphology

Supraorbital torus of Šal'a 1 consists of two arches slightly separated superiorly above glabella. The three primary elements (superciliary arch, middle orbital margin and lateral trigone) can be recognized: (1) the medial superciliary arch starts inferiorly near the lacrimal suture and superiorly just above nasion and continues laterally to near the supraorbital notch; (2) the middle portion extends from the supraorbital notch laterally approximately to the lateral third of the torus; and (3) the lateral trigone fills the lateral third of the torus.

The left supraorbital torus of Šal'a 1 provides in *norma frontalis* a rounded to rectangular superior orbital margin (Figure 3), and it is anteriorly projecting and well separated from the squamous portion by clear supratoral sulcus. The supratoral sulcus above glabella is shallow compared to the lateral portions of the sulcus. The supraorbital trigone is well marked and bounded by a robust temporal line. There is no evidence of segmentation of the superciliary arch in the middle portion of the torus (see discussion below). However, between middle of the torus and its most lateral portion, the torus thins slightly. The outline of glabella is rounded in *norma lateralis*.

In the following assessments, all of the differences across the comparative samples except for glabellar shape are significant at the $P<0{\cdot}05$ level (Table 2), indicating that at least in terms of the frequencies of the relative development of the features there are significant differences in most of these features between at least some of the Pleistocene reference samples.

Relative size of the supraorbital torus. In supraorbital torus size relative to the neurocranium, Šal'a 1 is smaller than all of the Middle Pleistocene individuals and the majority of the Neandertal ones, indicating some reduction in facial robusticity in Šal'a 1 and some Neandertals [Table 2(a)]. The Šal'a 1 torus is on average similar in relative size to those of the Middle Paleolithic early modern humans, being smaller than that of Skhul 5 but much larger than the supraorbital region of Qafzeh 9. There is a more dramatic shift to the earlier Upper Paleolithic sample, with the majority of the individuals having smaller tori and none of them having larger ones. The similarities between Šal'a 1 and some earlier Upper Paleolithic humans may be due sexual dimorphism, since all of the individuals scored as similar to Šal'a 1 are males with marked supraorbital regions (e.g., Mladeč 5 & Pavlov 1).

Overall shape of the supraorbital torus. The shape of the supraorbital torus has been scored using two features in *norma frontalis*, a sinusoidal shape of the supraorbital torus [Table 2(b)] and an inferiorly directed depression between the superciliary arches [Table 2(c)]. In the first of these features, there is a gradual shift from earlier to later archaic humans to earlier to later early modern humans. The Middle Pleistocene hominids, in comparison to Šal'a 1, mostly have a clear sinusoidal shape of the torus and a clear inferiorly directed midsagittal depression. In the first feature, Šal'a 1 resembles half of the Neandertals and about one-third of each of the early modern human samples. In the second feature, Šal'a 1 falls among the less marked of the Neandertal sample and in the middle of the two early modern human samples, but the Qafzeh-Skhul sample is represented only by Qafzeh 3 and 6 and the earlier Upper Paleolithic sample is influenced by the marked variability in superciliary arch development in that sample.

Shape of the superior margins of the orbits. Recent humans characteristically possess an overall rectangular shape of orbit, whereas Neandertals and Middle Pleistocene humans tend to have rounded orbits (Heim, 1976; Trinkaus, 1983). The shape of the superior orbital margin of Šal'a 1 has been evaluated by comparing the overall shape of superior margin [Table 2(d)] and the pattern of connection of the medial superior margin with medial orbital wall [Table 2(e)]. In both features, there is only modest overlap between the archaic and early modern human samples. Šal'a 1 is similar in these features to between one-fifth and two-fifths of the archaic samples, having less rounding of the orbital margins on average than the Neandertals. However, it contrasts with all but two of the early modern humans in at least one of these features.

Morphology of the supratoral sulcus. The supratoral sulcus is a complex character determined by the position of the face relative to the neurocranium, the size of the supraorbital torus and the forward expansion of the frontal squama (Aiello & Dean, 1990; Lieberman, 1995). To assess the sulcus of Šal'a 1, two interrelated features are employed, the depth of the supratoral sulcus above glabella [Table 2(f)] and its depth above the orbits [Table 2(g)]. Šal'a 1 possesses a relatively shallow supratoral sulcus above glabella in relation especially to the Neandertals and the Qafzeh-Skhul samples, but the earliest and latest samples are too variable in this feature to make meaningful comparisons. However, above the orbit, Šal'a 1 falls in the middles of the archaic human samples and among the early modern humans with the more pronounced sulci. None of the early modern humans has a supratoral sulcus larger than that of Šal'a 1.

Anterior projection of the supraorbital torus. There is a consistent trend in toral anterior projection [Table 2(h)] from the Middle Pleistocene sample to the earlier Upper Paleolithic one, with half of the Neandertals having a degree of projection similar to that of Šal'a 1. However, a third of each of the Middle Pleistocene and Qafzeh-Skhul samples show similar projection, and it is only among the earlier Upper Paleolithic sample that there is clear contrast with most (95%) of the specimens.

Shape of glabella. The shape of the glabellar region of Šal'a 1 is compared using the glabellar outline in *norma lateralis*. The frequency distributions [Table 2(i)] do not show a systematic pattern across the comparative samples, and Šal'a 1 falls in the middles of all of the distributions. Although similar to many Neandertals, it contrasts with the flat glabellar regions of Krapina 3 and 6.

Thinning of the supraorbital margin and segmentation. The supraorbital margin of recent humans is usually divided into the more medial superciliary arch and the more lateral supraorbital arch with a variably deep concavity or sulcus (the supraorbital groove) between them (Schwalbe, 1901). This segmentation (or the presence of a supraorbital groove) has been proposed to be a distinctive characteristic of modern human morphology, which is also found in Paleolithic early modern humans (Vandermeersch, 1981; Stringer *et al.*, 1984); it should therefore be absent from archaic *Homo*.

In addition, the separation of the superciliary and supraorbital arches has been suggested (e.g., Smith & Ranyard, 1980; Frayer *et al.*, 1993) to be associated with a distinctive superoinferior thinning of the midlateral supraorbital torus, such as is seen in Saint Césaire 1 and especially the Vindija tori. However, the relationship between the segmentation and the superoinferior thinning is unclear, and they appear to be reflecting two distinct, if possibly related, aspects of supraorbital morphology. These features were therefore evaluated separately, in terms of the presence of segmentation [Table 2(j)] and the relative degree of lateral toral thinning [Table 2(k)].

The Šal'a 1 torus has a smooth, nonconcave transition from the superciliary arch medially to the supraorbital arch more laterally. It therefore lacks toral segmentation, and in this it is similar to most of the Neandertals, half of the Middle Pleistocene humans, and none of the early modern humans.

Although none of the archaic humans is listed as having more lateral thinning than Šal'a 1, given the general nature of the tripartite categories employed, the superior margin of the Šal'a 1 lateral torus, where the thinning occurs, is in fact largely straight (Figure 3) rather than superiorly concave as it is in some Neandertal specimens and most early modern humans. Although none of the earlier Upper Paleolithic specimens has less thinning (or are thicker) than Šal'a 1, the pattern seen in Šal'a 1 falls well within the ranges of variation of all of the comparative samples.

Summary. From these trait by trait comparisons, which are not fully independent, it is apparent that the supraorbital morphology of Šal'a 1 is ambiguous as to its morphological affinities in a number of these features. However, in features reflecting general size and projection of the torus it is closest to the Neandertal and Qafzeh-Skhul samples and in features relating to the orbital margin morphology and segmentation of features, it is mostly closely aligned with the Neandertals and Middle Pleistocene archaic humans. In none of the features is it aligned with the early modern humans to the exclusion of the archaic *Homo* samples.

Morphometric comparisons of the Šal'a 1 frontal bone

Basic metrical description and univariate comparison. The osteometrics of the Šal'a 1 frontal (Table 3) show that there are no significant differences between Šal'a 1 and the archaic *Homo* samples in these raw measurements. They indicate a similar overall shape, with most of the measurements falling within one standard deviation of the Middle Pleistocene and Neandertal means (Figure 4). In most of the measurements, Šal'a 1 falls slightly below the archaic *Homo* means. Significant differences exist across the reference samples for five of the measurements, with the earlier Upper Paleolithic sample having smaller values on average for the three that measure overall frontal dimensions and exhibiting greater mid-sagittal curvature.

Šal'a 1 is not significantly different from the earlier Upper Paleolithic sample except for two related measurements, both of which measure nasion–bregma mid-sagittal curvature and one of which is calculated in part from the other, nasion–bregma subtense and frontal angle ($P=0{\cdot}022$ and $0{\cdot}029$ respectively). Given the global highly significant differences between the reference samples for these measurements ($P<0{\cdot}0001$ for each), these differences should remain important. They indicate a generally lower nasion–bregma arc in Šal'a 1 in the context of a minimally shorter (on average) chord (Table 3). Four Qafzeh-Skhul specimens provide a frontal angle of $132{\cdot}3° \pm 1{\cdot}6°$; and the Šal'a 1 value of 138° is also significantly different from this small sample.

Bivariate comparison. Given the contrasts in frontal subtense and angle, and the more modest contrasts in frontal length and breadth (Table 3; Figure 4), these values have been plotted against each other (Figure 5). The resultant distribution largely separates the earlier Upper Paleolithic sample from the archaic samples, with minimal overlap between specimens such as Předmostí 3 and archaic ones such as Amud 1, Broken Hill 1 and Irhoud 1. The very high positions for Shanidar 1 and 5 reflect their unusually flat frontal arcs (Trinkaus, 1983). Qafzeh 6 and Skhul 5 fall in the overlap zone between the archaic and early modern human samples. Šal'a 1 is well within the archaic distribution and separate from both the earlier Upper

Table 3 Measurements of the Šal'a 1 frontal and comparative descriptive statistics (mean ± SD (N) for Middle Pleistocene humans, Neandertals and Early Upper Paleolithic humans[1]

	Šal'a 1	Middle Pleistocene humans	Neandertals	Early Upper Paleolithic	*P*
Minimum frontal breadth (M 9)	105	108·9 ± 7·8 (10)	106·6 ± 5·2 (15)	100 ± 3·9 (21)	<0·001*
Maximum frontal breadth (M 10, XFB)	127	122·39 ± 6·1 (9)	123·7 ± 6·2 (11)	122·3 ± 3·9 (18)	0·781
Frontal sagittal arc (M 26)	121	126·9 ± 9·7 (10)	125·8 ± 7·1 (10)	132·33 ± 7·6 (21)	0·068
Glabella–bregma arc (M 26a)[2]	114	—	—	—	—
Frontal sagittal chord (M 29, FRC)	110	112·0 ± 6·7 (10)	112·2 ± 6·9 (11)	114·6 ± 6·0 (21)	0·352
Glabella–bregma chord (M 29d)[2]	108	—	—	—	—
Nasion–bregma subtense (M 29b, FRS)	21	22·0 ± 2·2 (4)	20·2 ± 2·9 (5)	27·6 ± 2·6 (21)	<0·001*
Nasion–subtense fraction (M 29c, FRF)	51	59·7 ± 5·1 (4)	56·0 ± 3·3 (5)	51·9 ± 5·4 (21)	0·019
Frontal angle (M 32(5), FRA)	138°	138·9 ± 5·1 (10)	141·7 ± 4·0 (10)	128·1 ± 4·1 (21)	<0·001*
Frontal angle from glabella (M 32(e))[2]	141°	—	—	—	—
Outer biorbital breadth (M 43)	115	123·0 ± 10·4 (4)	119·7 ± 3·8 (8)	109·7 ± 4·6 (10)	<0·001*
Bifrontal breadth (M 43a, FMB)	108	114·7 ± 8·5 (6)	113·8 ± 4·3 (6)	102·5 ± 5·3 (10)	0·001*
Nasion–frontal subtense (M 43b, NAS)	21	22·0 ± 3·6 (6)	25·1 ± 2·9 (5)	17·9 ± 3·9 (8)	0·009
Nasio–frontal angle (M 77a, NFA)	137°	138·2 ± 4·5 (6)	132·4 ± 4·4 (5)	141·6 ± 6·6 (8)	0·032
Interorbital breadth (M 49a, DKB)	31	32·9 ± 3·6 (6)	28·5 ± 8·0 (4)	25·33 ± 3·98 (6)	0·067
Anterior interorbital breadth (M 50)	30	29·5 ± 2·2 (5)	24·2 ± 7·5 (5)	23·4 ± 2·9 (7)	0·093

P-values for ANOVA comparisons across the three reference sample, with those measurements which are significantly different at $\alpha = 0{\cdot}05$ after a sequentially rejective Bonferroni multiple comparison correction indicated by*.

[1]All measurements are in millimeters, Martin numbers (M##) (Bräuer,1988); Howells (1973) abbreviation provided when appropriate.

[2]The measurements not compared in the study.

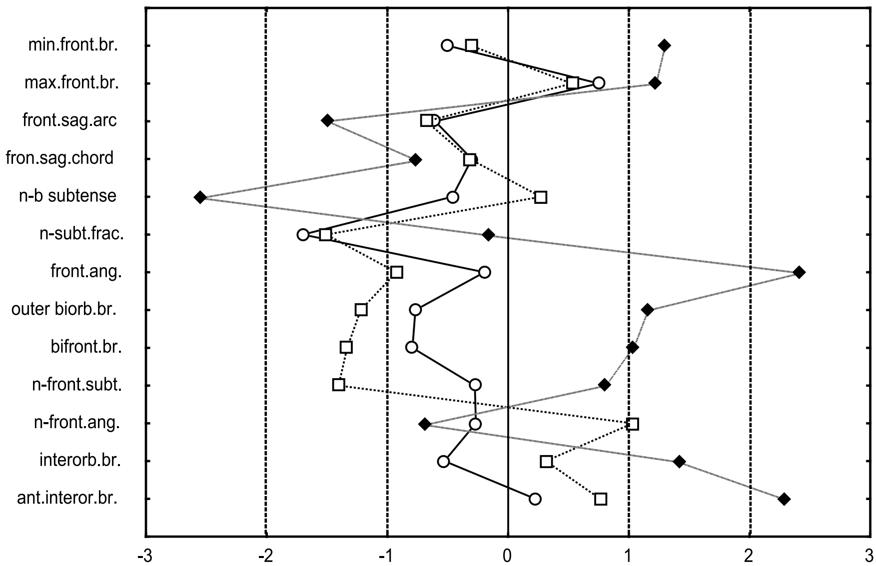

Figure 4. *Z*-score profile for Šal'a 1. Frontal measurements have been standardized to Middle Pleistocene (○), Neandertal (□), and early Upper Paleolithic (◆) sample means and standard deviations.

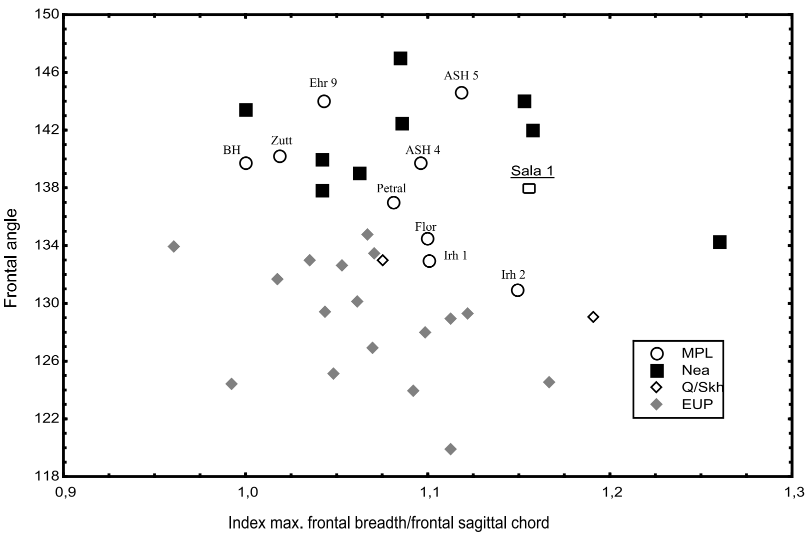

Figure 5. Scatter plot of frontal angle and the index of maximum frontal breadth to nasion–bregma chord.

Paleolithic sample and the two Qafzeh-Skhul specimens.

Principal component analysis. Principal component analysis has been carried out on Šal'a 1 and the group of Middle Pleistocene hominids (*n*=9, MPL), Neandertals (*n*=9, Nea), two Qafzeh/Skhul specimens, earlier Upper Paleolithic (*n*=17, EUP) and a sample of recent humans (*n*=27, REC). Given the limitations of preservation and available data, the number of measurements of the frontal bone has been reduced to ones measuring overall proportions so as to

Table 4 **Comparison of the first principal component of the separate covariance matrices among Pleistocene and recent human groups**

Eigenvector	PC 1-MPL	PC 1-Nea	PC 1-EUP	PC 1-REC
Minimum frontal breadth	0·636	0·280	0·108	0·332
Maximum frontal breadth	0·498	0·274	0·259	0·565
Frontal sagittal arc	0·493	0·592	0·709	0·571
Frontal sagittal chord	0·323	0·704	0·646	0·495
Eigenvalue[1]	87·8	78·6	66·3	76·3
Standard error[2]	41·4	37·0	22·7	20·8
Variance	0·676	0·66	0·709	0·706

Eigenvalue and standard error of eigenvalue are given as multiplied by 10^4.
[2]Standard errors for the estimate of the PC 1 eigenvalue follow the formula of Flury (1988: 26, 5·2) $[s(l_j)=(\sqrt{(2/n)})\ l_j\ ]$, where $s(l_j)$ is estimate of the standard error of the respective eigenvalue, n is sample size, and l_j is respective eigenvalue.

maximize sample size. The measurements are: minimum and maximum frontal breadth, frontal sagittal arc and frontal sagittal chord.

Covariance matrices were computed for each group, with Šal'a 1 and the two Qafzeh-Skhul specimens (Qafzeh 6 and Skhul 5) not included. The covariance matrices show similar ranges of variation between all groups, with the Middle Pleistocene and recent human samples having moderately more variability than the other two samples. However, the departure of homogeneity between all four covariance matrices is not statistically significant at $\alpha=0{\cdot}001$ based on Levene's univariate test and Sen and Purin's nonparametric multivariate test.

Principal components and their eigenvalue estimates have been computed for the four covariance matrices (Table 4). All groups show that their PC 1 components are size related. The highest eigenvalue of PC 1 is found in the Middle Pleistocene group (87·7); however proportionately PC 1 explains the largest amount of variation in the earlier Upper Paleolithic and recent groups (about 71%). The standard error estimates for the PC 1 eigenvalues are generally large for all samples; the largest error is in the Middle Pleistocene group ($SE=41{\cdot}4\times10^{-4}$). Such large standard errors can be explained by the small sample sizes, especially in the Middle Pleistocene and Neandertal groups, and the temporal and geographical heterogeneity of the former sample. This observation affects the principal component analysis of the four multiple group design.

The PC 1 coefficients indicate the largest departure from the isometry in the earlier Upper Paleolithic sample, but because of small sample sizes an objective test is needed. If isometry is present, then all values of the PC 1 coefficients will be equal to $p^{-0{\cdot}5}$ (isometric vector $p=[0{\cdot}5, 0{\cdot}5, 0{\cdot}5, 0{\cdot}5]'$) (Anderson, 1963; Flury, 1988; Klingenberg, 1996). The statistical significance of departure from isometry can be estimate by Anderson's test:

$$X^2=n\ (l_1\ \boldsymbol{\beta}_1^{0\prime}\mathbf{Cov}^{-1}\ \boldsymbol{\beta}_1^{0}+ l_1^{-1}\ \boldsymbol{\beta}_1^{0\prime}\mathbf{Cov}\ \boldsymbol{\beta}_1^{0})\quad (1)$$

where n is sample size, l_1 is the eigenvalue of a group, $\boldsymbol{\beta}_1^0$ is the hypothetical eigenvector (in our case it is the isometric eigenvector) and **Cov** is covariance matrix. The X^2 statistic has Chi-square distribution with $df=p-1$, where p is number of variables included in the model (Flury, 1988).

Using Anderson's test we cannot reject an H_o of overall isometry in the PC 1 of the Middle Pleistocene ($X^2=6{\cdot}55$, $P=0{\cdot}087$)

Table 5 **Comparison of covariance matrices among Pleistocene and recent human groups**

Model					
Higher	Lower	Chi-square	df	*P*-value	AIC[1]
Equality	Proportionality	2·687	3	0·442	36·9
Proportionality	CPC	11·679	9	0·232	40·3
CPC	CPC(2)	1·626	3	0·653	46·6
CPC(2)	CPC(1)	3·271	6	0·774	51·0
CPC(1)	Unrelated	17·731	9	0·038*	59·7
Unrelated	—	—	—	—	60·0

[1]AIC—Akaike information criterion, which indicates by minimal value the best solution for the model of principal component analysis among multiple groups (see details in Flury, 1988). In the case of the four Pleistocene and recent human samples, the best solution will be to expect the covariance matrix to be equal and the principal component model to be built according to the best pooled matrix.

and recent groups (X^2=4·42, P=0·22), but it can be rejected for the Neandertal (X^2=8·27, P=0·041) and especially the earlier Upper Paleolithic groups (X^2=14·94, P=0·002). The power of Anderson's test is related to sample size, and because of the small Middle Pleistocene sample an isometric pattern for the group can be questioned (when the sample size is increased to 11, isometry can be rejected at α=0·05). However, the sample of recent humans is large enough not to reject an H_o of overall isometry.

The above descriptions of the covariance matrix structure raise a question about the design of the principal component analysis for the comparison of Šal'a 1 with the multiple group pattern. Such a comparison can separate size-related variation in the multiple group analysis and can help to describe size and shape similarities of Šal'a 1 to the studied groups (Klingenberg, 1996). The problem for the multiple group design relates to the nature of the differences in parameters indicated above; are they just sampling errors due to small sample size or can these differences be seen as indications of important structural differences between the covariance matrices among the groups?

To determine the best model for the principal component analysis, the hierarchical test of multiple covariance matrices of Flury (1988) has been followed (see Phillips, 1998). Flury proposed a decompositon of the log-likelihood statistic for equality of multiple covariance matrices to test complex relationships between the multiple covariance matrices (Flury, 1988, Phillips & Arnold, 1999; Arnold & Phillips, 1999). Such a complex pattern can be seen when covariance matrices are proportional but not equal; covariance matrices of multiple groups can share similar principal component structures by similar principal components but be variable in their eigenvalues associated with these PCs. The Flury hierarchical test compares the statistical significance of each level in the hierarchy from unrelated to equality and tests the significance of each level against the next hierarchically lower level.

According to the hierarchial test of the multiple covariance matrices of our groups, there is only statistical significance between the hierarchical CPC(1) model and the unrelated matrix model, but no statistical significance between the models of equality or proportionality or higher models of common principal components (Table 5). This indicates that the matrices of the Middle Pleistocene, Neandertal, earlier Upper Paleolithic and recent samples are structurally similar at the highest hierarchical level of equality. Akaike (1973) has proposed criterion for model selection, which are related to maximum likelihood estimates and take into account the number of parameters included in the model. As Flury (1988) emphasized, the purpose of the Akaike's information criterion (AIC) is to find a "best fitting" model which is not necessarily the "true" model. The lowest AIC value is in the level of equality and proportionality (Table 5). However, even if the AIC cannot be seen as an objective hypothesis test, it fits well with our conclusion from the Flury hierarchical test and indicates that the best model for the principal component analysis among the four groups is based on the equality of the covariance matrices and therefore designed via the best pooled covariance matrix. Such a conclusion fits well with our previous comparison of Levene's univariate test and Sen and Purin's nonparametric multivariate test of equality between the studied covariance matrices.

Four PCs have been extracted from the best pooled covariance matrices (Table 6). The 65·9% percent of the variablity explained by the PC 1 is clearly size-related.

Table 6 Comparison of the principal components of the best pooled covariance matrix of the Pleistocene and recent human groups

Eigenvector	PC 1	PC 2	PC 3
Minimum frontal breadth	0·321	− 0·808	0·482
Maximum frontal breadth	0·454	− 0·325	− 0·812
Frontal sagittal arc	0·620	0·367	0·057
Frontal sagittal chord	0·553	0·325	0·323
Eigenvalue[1]	71·8	25·1	8·6
Standard error	12·9	4·5	1·5
Variance	0·66	0·23	0·08

[1]Eigenvalue and standard error of eigenvalue are given as multiplied by 10^4.

The eigenvalue is similar to the individual eigenvalue estimates for the four groups, but the standard error has been greatly reduced (12·9). The H_o of overall isometry in the PC 1 coefficients of the best pooled covariance matrix cannot be rejected by Anderson's test (X^2=5·53, df=3, *P*=0·14). Because of the isometry of the PC 1 coefficient, individuals in the analysis with similar values of shape PC's (PC 2–4 in our case) can be interpreted to be geometrically similar and not exhibit allometric changes in shape (Klingenberg, 1996).

The PC 2 has negative values for breadth variables and positive values for length variables, indicating a contrast between breadth and length; it explains 23·4% of the variation. PC 3 emphasizes shape differences between maximum frontal breadth and the other three variables, but it explains only 8·6% of the variation. PC 4 explains only 3·1% of the variance and is not discussed.

Based on PC coeficients of the best pooled covariance matrix, individual PC scores were computed, including Šal'a 1, Qafzeh 6 and Skhul 5, using the expression (Klingenberg, 1996):

$$Y_j = \mathbf{B}\mathbf{X}_j \tag{2}$$

where $\mathbf{Y}_j$ is a vector of the scores of the j-th individual, $\mathbf{B}$ is the matrix of the extracted PC coefficients, and $\mathbf{X}_j$ is the vector of the original values for the j-th individual (Figure 6).

The scores on PC 1 axis distinguish the Pleistocene samples from the recent humans. (Figure 6). The shape PC 2 axis partly separates the recent and earlier Upper Paleolithic samples from the both archaic groups, with the recent sample having generaly higher values than the EUP sample. There is clear overlap between both archaic samples and partly between the archaic samples and the earlier Upper Paleolithic group. Qafzeh 6 and Skhul 5 are generally close to the archaic samples, especially

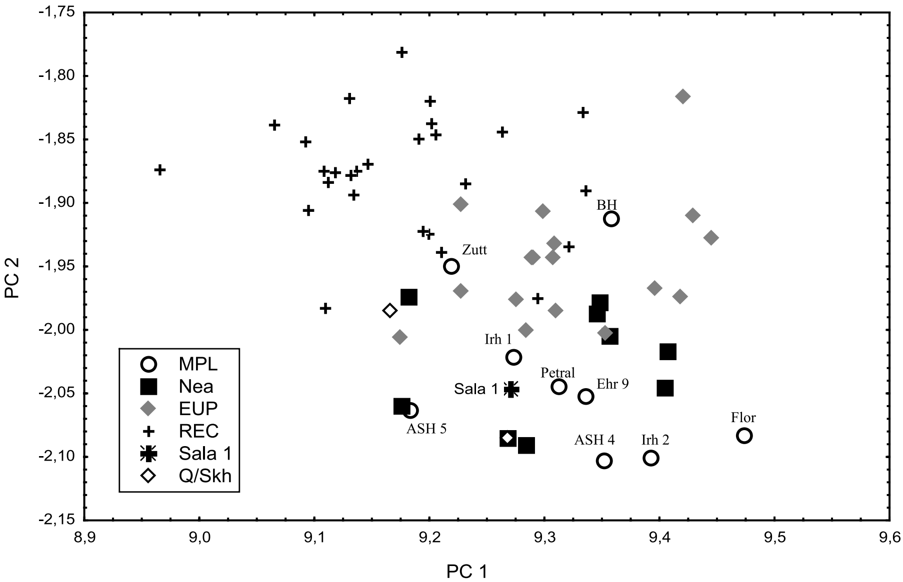

Figure 6. Scatterplot of PC 1 and PC 2 of the best pooled covariance matrix.

Qafzeh 6 which is close to the values of La Chapelle-aux-Saints 1 and Shanidar 1; Skhul 5 is close to the values of La Quina 5 and Mladeč 2. These data therefore place the Qafzeh-Skhul sample within the archaic samples with the same degree of overlap with the EUP sample. In the PC 1/PC 2 distribution, Šal'a 1 is included in the archaic samples, and it is separate from the earlier Upper Paleolithic sample. It does fall, nonetheless, between Qafzeh 6 and Skhul 5.

The PC 2 and PC 3 scores provide more of an indication of shape differences independent of size (Figure 7). There is little separation of the samples on PC 3, with two Neandertals, La Quina 5 and Tabun 1, providing high and low values respectively. The archaic and early Upper Paleolithic samples overlap only partially (mostly due to PC 2), and the two Qafzeh-Skhul specimens span much of the range of the archaic samples. In this, Šal'a 1 is closely aligned with the archaic and Qafzeh-Skhul specimens and separate from the earlier Upper Paleolithic remains.

Discriminant function analysis: overall pattern of separation. To further assess the morphological affinities of Šal'a 1, 62 individuals from four samples have been selected for discriminant function analysis. The best pooled covariance matrix has been used, with the same four *a priori* defined groups. Šal'a 1 and the Qafzeh/Skhul remains are not included in the design.

The overall pattern of metric variation between the four groups shows statistically significant separation at $P<0{\cdot}01$ (F-value= 10·70, df=12, 145). The separation is mostly based on the minimum and maximum frontal breadths and the frontal sagittal arc. However, the unique contribution to Wilk's lambda of the variables shows lower separation (lower Partial Wilk's lambda estimate) compared to our model of four variables. Despite the overall good separation based on Mahalanobis D^2 distances, the structure of the posterior probability differences among the individuals (see below) and the principal component analysis shows that the *a priori* groups

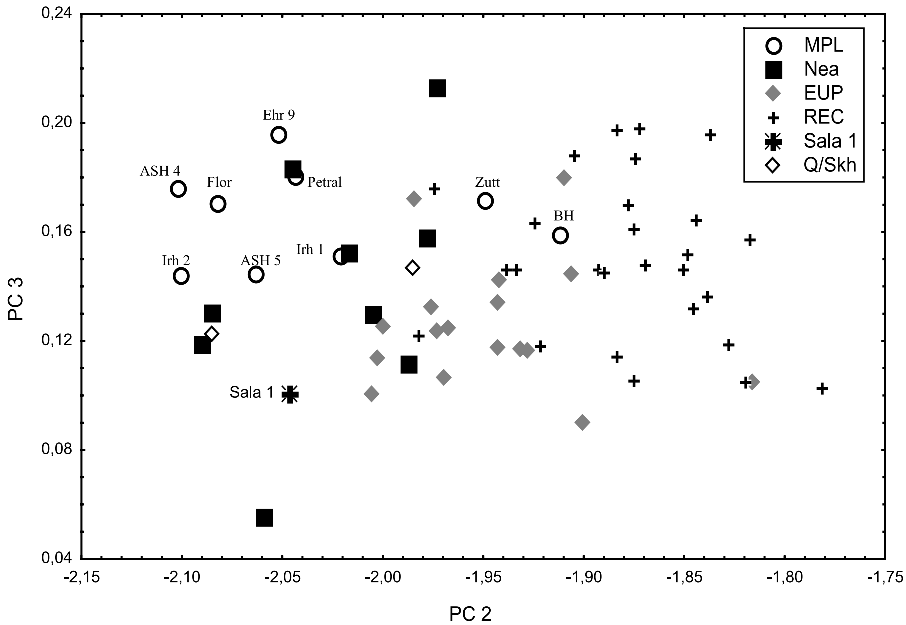

Figure 7. Scatterplot of PC 2 and PC 3 of the best pooled covariance matrix.

are not separated equally, but the Middle Pleistocene humans and the Neandertals partly overlap. The Wilk's lambda value therefore is due mostly to the separation of the recent and earlier Upper Paleolithic groups.

Mahalanobis D^2 distances between centroids. The Mahalanobis D^2 distances have been computed between the centroids using the best pooled covariance matrix already studied in the principal component analysis (Table 7). The Mahalanobis D^2 is computed from expression (3), where the vector of the compared individuals is changed by the vector of the group centroid (Dillon & Goldstein, 1984). Statistical significances have been established by an F-distribution with df=4, 55.

The largest D^2 distances can be found between the recent sample and the rest of the groups, and the smallest distance is between the Middle Pleistocene and Neandertal groups. Only the distance between the archaic groups does not show a significant difference.

Table 7 Squared Mahalanobis distances between Pleistocene and recent human groups (four variables design)

	MPL	Nea	EUP
Nea	1·8		
UP	6·9*	5·2*	
REC	21·5*	21·6*	14·7*

Marked values are statistically significant at $P<0·001$.

Classification based on the typical probability of Mahalanobis D^2 distances. Mahalanobis D^2 distances between individuals and group centroids can indicate the amount of differences in relation to the variability of the analyzed groups, using the "typical probability" of Albrecht (1992). In comparison to posterior probability, the typical probability does not expect the individuals to belong *a priori* to any of the reference samples (Jantz & Owsley, 2001).

Mahalanobis D^2 between individuals and group centroids are calculated by:

$$D^2 = (\mathbf{X}_{centr} - \mathbf{X}_j)' \, \mathbf{Cov}^{-1} \, (\mathbf{X}_{centr} - \mathbf{X}_j) \quad (3)$$

where $\mathbf{X}_{centr}$ is the vector of a group centroid, $\mathbf{X}_j$ is the vector of individual measurements, and **Cov** is the best pooled covariance matrix (Dillon & Goldstein, 1984). D^2 is referred to the Chi-square distribution with df=p, where p is a number of variables used in the model (Albrecht, 1992). The D^2 values between the four sample centroids and the individual specimens were computed using the cross-validation procedure. The probability values of individual specimens are in Table 8. Values smaller than 0·05 are considered to be statistically significant.

The pattern of typical probability classification among the Middle Pleistocene hominids shows a general classification into the archaic cluster. One Middle Pleistocene individual (Florisbad 1) has a significant distance from the Neandertal centroid (also approached by Petralona 1), and one individual is significantly different from expected group (Atapuerca-SH 5, also approached by Broken Hill 1). The largest difference is between the Middle Pleistocene and recent samples and to a lesser extent from the earlier Upper Paleolithic group. The Neandertals show a pattern similar to the Middle Pleistocene humans, but in this case three individuals are different from the Middle Pleistocene sample (Tabun 1, Shanidar 1 & 5) and two individuals from the Neandertal sample (Tabun 1 & La Quina 5). The earlier Upper Paleolithic individuals exhibit generally no statistical significance of the typical probability to any group and ambiguity of the typical probability classification. However, two individuals (Cro-Magnon 3 & Mladeč 5) are statistically significantly different from all of the *a priori* groups. The overall pattern of the typical probability classification for the recent sample is similar with the pattern of the distribution in the principal component analysis; only one individual from the recent sample exhibits a difference from the expected group, and there is clear statistical difference from the archaic samples.

Šal'a 1 is statistically significantly different at the $P<0{\cdot}05$ level only from the recent group. However, values of typical probability from the Middle Pleistocene archaic and earlier Upper Paleolithic groups are close to statistical significance ($P=0{\cdot}07$). Therefore, Šal'a 1 can be assigned to the Neandertal group with a small probability of being included in the Middle Pleistocene or earlier Upper Paleolithic samples.

Classification based on posterior probabilities of the discriminant function analysis. The cross-validation procedure has been used to compute posterior probabilities from $\ln_e$ raw data and the best pooled covariance matrix (Table 9). The Neandertals exhibit the lowest percentage of correct classification into expected group (44%) followed by the Middle Pleistocene sample (56%). The earlier Upper Paleolithic and recent samples provide higher percentages of correct classification. Overall, 72% of the archaic specimens are correctly classified as such, whereas 91% of the "modern" specimens are assigned to a "modern" sample. We can therefore expect that the recent and earlier Upper Paleolithic specimens will be appropriately classified according to their *a priori* defined groups and can be better recognized as such among the unknown specimens, but that the classification of the archaic specimens will be less reliable.

Comparison of individual posterior probabilities shows a more complex pattern (Table 10). In the Middle Pleistocene group only two individuals (Florisbad 1 and Petralona 1) have larger posterior probabilities than 0·80, which is here accepted for correct classification. Other individuals have smaller values. Atapuerca-SH 5 is

Table 8 **Typical probability classification of individual specimens (four variables design, based on cross-validation analysis)**

Specimen	Assigned group	Typical probability of membership in group Group			
		MPL	NEA	EUP	REC
Šal'a 1	—	0·07	0·59	0·07	<0·01*
Atapuerca-SH 4	MPL	0·31	0·36	<0·01*	<0·01*
Atapuerca-SH 5	MPL	0·03*	0·37	0·01*	<0·01*
Broken Hill 1	MPL	0·06	0·10	0·75	0·25
Ehringsdorf 9	MPL	0·67	0·38	0·03*	<0·01*
Florisbad 1	MPL	0·28	0·03*	0·01*	<0·01*
Irhoud 1	MPL	0·68	0·37	0·40	0·05*
Irhoud 2	MPL	0·38	0·24	0·03*	<0·01*
Petralona 1	MPL	0·50	0·08	0·06	<0·01*
Zuttiyeh 1	MPL	0·17	0·26	0·38	0·40
Amud 1	Nea	0·55	0·27	0·03*	<0·01*
La Chapelle 1	Nea	0·51	0·69	0·07	<0·01*
Le Ferrassie 1	Nea	0·70	0·72	0·31	<0·01*
Feldhofer 1	Nea	0·81	0·64	0·77	0·06
Guattari 1	Nea	0·53	0·94	0·58	0·01*
La Quina 5	Nea	0·12	0·02*	0·02*	0·08
Shanidar 1	Nea	0·02*	0·14	<0·01*	<0·01*
Shanidar 5	Nea	0·04*	0·33	0·16	<0·01*
Tabun 1	Nea	<0·01*	<0·01*	<0·01*	<0·01*
Qafzeh 6	—	0·23	0·12	0·05*	<0·01*
Skhul 5	—	0·26	0·46	0·29	0·18
Cro-Magnon 1	EUP	0·05*	0·08	0·65	0·01*
Cro-Magnon 2	EUP	0·08	0·47	0·59	0·07
Cro-Magnon 3	EUP	<0·01*	<0·01*	0·02*	0·01*
Dolní Věstonice 3	EUP	<0·01*	0·01*	0·33	0·31
Dolní Věstonice 13	EUP	0·39	0·43	0·98	0·35
Dolní Věstonice 14	EUP	0·89	0·63	0·46	0·08
Dolní Věstonice 15	EUP	0·31	0·50	0·99	0·35
Dolní Věstonice 16	EUP	0·12	0·15	0·87	0·58
Mladeč 2	EUP	0·04*	0·06	0·10	0·04*
Mladeč 5	EUP	<0·01*	<0·01*	<0·01*	<0·01*
Pavlov 1	EUP	0·06	0·04*	0·10	0·01*
Předmostí 1	EUP	0·10	0·19	0·63	0·21
Předmostí 3	EUP	0·31	0·58	0·82	0·02*
Předmostí 4	EUP	0·12	0·19	0·98	0·30
Předmostí 7	EUP	0·40	0·87	0·68	0·08
Předmostí 9	EUP	0·44	0·79	0·75	0·01*
Předmostí 10	EUP	0·54	0·96	0·67	0·04*

Marked values are statistically significant at $P<0·05$.

classified as Neandertal with a 0·95 posterior probability, which is the largest posterior probability value among the Middle Pleistocene humans. Only Shanidar 1 is classified into the expected group of Neandertals with posterior probability higher than 0·80, but Tabun 1 has a value of 0·88 for the earlier Upper Paleolithic sample. The earlier Upper Paleolithic humans exhibit a consistent pattern of classification, with only Dolní Věstonice 14 assigned to the Middle Pleistocene sample and Předmostí 10 to the Neandertal group. However, only two individuals from the earlier Upper Paleolithic group have posterior probabilities larger than 0·80. The

Table 9 **Posterior probability classification between the Pleistocene and recent groups and between archaic and modern clusters (four variables design, based on cross-validation analysis)**

	Correct	MPL	Nea	EUP	REC	Archaic	%	Modern	%
MPL	56%	5	2	1	1	7	78%	2	22%
Nea	44%	2	4	2	1	6	67%	3	33%
EUP	82%	1	1	14	1	2	12%	15	88%
REC	89%	1	1	1	24	2	7%	25	93%
Total	77%	8	9	18	27	13/4	72%	40/5	91%

differences between contrasting classifications are low for some individuals; for example Předmostí 7 is classified with similar values as Upper Paleolithic or Neandertal. Individuals from the recent group exhibit generally the highest values of posterior probabilities to be correctly classified. In this, Qafzeh 6 is largely aligned with the archaic samples (combined $P=0{\cdot}85$), but Skhul 5 has probabilities distributed evenly across all but the Middle Pleistocene sample

In the context of this, Šal'a 1 is clearly classified into the Neandertal group, with a value of 0·87. The value is only slightly smaller than that of Shanidar 1. Posterior probabilities for the other samples are all low. Therefore, despite the poor separation of the two archaic samples and the overlap with early modern humans, it should be reasonable to use these results to assign Šal'a 1 to the Neandertal sample.

Even though it reduces sample sizes, the same calculations were performed including frontal angle into the analysis (Tables 11 and 12). The correct classification rates are improved for the individual archaic samples and especially for the pooled archaic versus early modern human samples. Only Zuttiyeh 1 is assigned to an early modern human sample and only Předmostí 3 is aligned with an archaic sample, but their posterior probabilities for those samples (0·44 and 0·54) remain low and ambiguous. As with previous assessments, the two Qafzeh-Skhul specimens span most of the range of the reference samples. The posterior probability for Šal'a 1 is 0·91 for the Neandertal sample, further emphasizing its similarity to that sample.

One limitation of such posterior probability classifications is the theoretical condition that individuals must be allocated into the *a priori* defined groups (Dillon & Goldstein, 1984), and the posterior probability will not indicate any departure from the *a priori* defined allocation space. It is possible that the large value for Šal'a 1 is not a reflection of real morphological relationship but is a result the *a priori* design. However, the use of typical probabilities addresses this issue in part, and it shows that although Šal'a 1 can be classified at least into one of the three groups, its affinities are much closer to the Neandertal sample than to the other ones.

Classification of the posterior probability based on the cross-validation procedure, although conceptually highly desirable given the small samples sizes available, usually decreases the probability values. With respect to this, when Šal'a 1 is included *a priori* in the Neandertal sample its posterior probability is 0·90, putting Šal'a 1 in the Middle Pleistocene sample gives it a Neandertal probability of 0·78, in the earlier Upper Paleolithic group a probability of 0·77, and in the recent group a probability of 0·78. Therefore, different approaches provide a consistent pattern of allocation of Šal'a 1 into the Neandertal group.

Table 10 Posterior probability classification of individual specimen (four variables design, based on cross-validation analysis)

Specimen	Assigned group	Discriminant assigned group	Posterior probability of membership in group Group			
			MPL	Nea	EUP	REC
Šal'a 1	—	Nea	0·05	0·87†	0·08	<0·01
Ataouerca-SH 4	MPL	Nea*	0·42	0·57†	<0·01	<0·01
Atapuerca-SH 5	MPL	Nea*	0·03	0·95†	0·01	<0·01
Broken Hill 1	MPL	EUP*	0·01	0·02	0·76†	0·21
Ehringsdorf 9	MPL	MPL	0·68†	0·30	0·02	<0·01
Florisbad 1	MPL	MPL	0·91†	0·07	0·02	<0·01
Irhoud 1	MPL	MPL	0·41†	0·18	0·37	0·04
Irhoud 2	MPL	MPL	0·60†	0·36	0·05	<0·01
Petralona 1	MPL	MPL	0·82†	0·08	0·10	0·01
Zuttiyeh 1	MPL	REC*	0·05	0·10	0·32	0·54†
Amud 1	Nea	MPL*	0·74†	0·23	0·03	<0·01
La Chaplle 1	Nea	Nea	0·38	0·57†	0·05	<0·01
Le Ferrassie 1	Nea	Nea	0·41	0·38†	0·21	<0·01
Feldhofer 1	Nea	EUP*	0·30	0·17	0·51†	0·02
Guattari 1	Nea	Nea	0·16	0·48†	0·36	<0·01
La Quina 5	Nea	REC*	0·34	0·04	0·05	0·56†
Shanidar 1	Nea	Nea	0·10	0·89†	0·01	<0·01
Shanidar 5	Nea	Nea	0·04	0·54†	0·41	<0·01
Tabun 1	Nea	EUP*	0·03	0·08	0·88†	0·01
Qafzeh 6	—	MPL	0·60†	0·25	0·15	<0·01
Skhul 5	—	Nea	0·14	0·31†	0·30	0·25
Cro-Magnon 1	EUP	EUP	0·01	0·02	0·95†	0·01
Cro-Magnon 2	EUP	EUP	0·02	0·26	0·66†	0·06
Cro-Magnon 3	EUP	EUP	<0·01	<0·01	0·63†	0·37
Dolní Věstonice 3	EUP	REC*	<0·01	<0·01	0·39	0·60†
Dolní Věstonice 13	EUP	EUP	0·06	0·07	0·71†	0·16
Dolní Věstonice 14	EUP	MPL*	0·48†	0·23	0·25	0·04
Dolní Věstonice 15	EUP	EUP	0·04	0·09	0·71†	0·15
Dolní Věstonice 16	EUP	EUP	0·02	0·02	0·55†	0·42
Mladeč 2	EUP	EUP	0·08	0·14	0·51†	0·27
Mladeč 5	EUP	EUP	0·21	<0·01	0·72†	0·07
Pavlov 1	EUP	EUP	0·19	0·11	0·62†	0·08
Predmostí 1	EUP	EUP	0·03	0·07	0·69†	0·22
Předmostí 3	EUP	EUP	0·08	0·21	0·71†	0·01
Předmostí 4	EUP	EUP	0·01	0·03	0·81†	0·15
Předmostí 7	EUP	EUP	0·10	0·42	0·44†	0·04
Předmostí 9	EUP	EUP	0·12	0·34	0·54†	<0·01
Předmostí 10	EUP	Nea*	0·14	0·49†	0·36	0·01

*Incorrect classification according to *a priori* defined sample.
†Highest values of the posterior probability classification.

Discussion

The morphological assessment of the Šal'a 1 supraorbital torus and the morphometric analysis of its overall frontal proportions clearly indicate that the specimen is distinct from the earlier Upper Paleolithic humans of Europe and from a diverse recent human sample. This is evident in the several aspects of its supraorbital morphology and in the morphometric comparisons of its overall proportions. The bone is not clearly separated from the Qafzeh-Skhul sample

Table 11 **Posterior probability classification between the Pleistocene and the recent samples and between archaic and modern human clusters (frontal angle included, based on cross-validation analysis)**

	Correct	MPL	Nea	EUP	REC	Archaic	%	Modern	%
MPL	67%	6	2	0	1	8	89%	1	11%
Nea	67%	3	6	0	0	9	100%	0	0%
EUP	82%	0	1	14	2	1	6%	16	94%
REC	89%	1	0	2	24	1	4%	26	96%
Total	81%	10	9	16	27	17/2	94%	42/1	95%

metrically, but the morphological comparisons of its supraorbital regions, particularly the degree of rounding of the orbital margins and the presence/absence of segmentation, serve to separate it from those Middle Paleolithic early modern humans. Šal'a 1 and the Qafzeh-Skhul sample certainly share a general level of upper facial robusticity and associated aspects of anterior neurocranial proportions.

It is more difficult to determine whether Šal'a 1 could reasonably belong to the temporally and geographically heterogeneous sample of available Middle Pleistocene fossils. However, morphometrically it is as consistently separated from those earlier human remains as it is from the earlier Upper Paleolithic sample. Moreover, even though the form of its supraorbital torus overlaps the range of variation of the Middle Pleistocene sample, the general robusticity of its supraorbital torus is consistently less than those of the Middle Pleistocene frontal bones.

In all of these comparisons, the Šal'a 1 frontal bone falls well within, and frequently toward the middle of, the range of variation of the last interglacial and early last glacial Neandertal sample from Europe and the Near East. Morphometrically, its values are consistently close to the Neandertal central tendency, and the discriminant functional analyses consistently assign it overwhelmingly to the Neandertal sample with low probabilities of belonging to the other samples. In its supraorbital region, almost all of the morphological features have at least a third of the Neandertal specimens showing the same pattern as Šal'a 1 and in several of them the majority of the Neandertals have the same degree of development as Šal'a 1. Assuming that Šal'a 1 must derive from one of these samples, it is clearly to the Neandertal sample that it is most appropriately assigned.

Nonetheless, the Šal'a 1 frontal bone does show less development of some of the morphological features that appear to be relatively diagnostic of the Neandertal sample. In particular, the majority of the Neandertal supraorbital tori (69% and 82%) have more rounding of the orbital margins than Šal'a 1. Yet, all of the early modern humans exhibit less rounding of these margins than Šal'a 1. In addition, 56% of the Neandertals have less thinning of the lateral supraorbital torus and 44% of them are categorized as having a similar degree of such thinning [including specimens such as Saint Césaire 1 and the Vindija frontal bones, which have been interpreted as exhibiting toral reduction in the direction of early modern humans (Smith & Ranyard, 1980; Wolpoff *et al.*, 1981)], and in this Šal'a 1 is similar to a third of each of the early modern human samples. Yet, Šal'a 1 lacks a clear concavity of the left lateral supraorbital torus superior margin, and it shows a lack of toral segmentation, as do 89% of the Neandertals, half of the Middle Pleistocene

Table 12 Posterior probability classification of individual specimens (frontal angle included, based on cross-validation analysis)

Specimen	Assigned group	Discriminant assigned group	Posterior probability of membership in group Group			
			MPL	NEA	EUP	REC
Šal'a 1	—	Nea	0·06	0·91†	0·03	<0·01
Atapuerca-SH 4	MPL	MPL	0·82†	0·17	<0·01	<0·01
Atapuerca-SH 5	MPL	Nea*	0·08	0·92†	<0·01	<0·01
Broken Hill 1	MPL	Nea*	0·06	0·70†	0·24	<0·01
Ehringsdorf 9	MPL	MPL	0·77†	0·23	<0·01	<0·01
Florisbad 1	MPL	MPL	0·88†	0·11	<0·01	<0·01
Irhoud 1	MPL	MPL	0·56†	0·10	0·33	0·01
Irhoud 2	MPL	MPL	0·82†	0·12	0·06	<0·01
Petralona 1	MPL	MPL	0·92†	0·07	0·01	<0·01
Zuttiyeh 1	MPL	UP*	0·16	0·24	0·44†	0·16
Amud 1	Nea	MPL*	0·93†	0·01	0·06	<0·01
La Chapelle 1	Nea	Nea	0·25	0·75†	<0·01	<0·01
Le Ferrassie 1	Nea	MPL*	0·51†	0·46	0·03	<0·01
Feldhofer 1	Nea	Nea	0·38	0·58†	0·04	<0·01
Guattari 1	Nea	Nea	0·07	0·93†	<0·01	<0·01
La Quina 5	Nea	MPL*	0·95†	<0·01	0·01	0·04
Shanidar 1	Nea	Nea	0·07	0·93†	<0·01	<0·01
Shanidar 5	Nea	Nea	0·01	0·99†	<0·01	<0·01
Tabun 1	Nea	Nea	0·08	0·79†	0·13	<0·01
Qafzeh 6	—	MPL	0·68†	0·32	0·01	<0·01
Skhul 5	—	REC	0·01	0·002	0·41	0·58†
Cro-Magnon 1	EUP	UP	<0·01	<0·01	0·99†	0·01
Cro-Magnon 2	EUP	UP	<0·01	<0·01	0·85†	0·15
Cro-Magnon 3	EUP	UP	<0·01	<0·01	0·81†	0·19
Dolní Věstonice 3	EUP	REC*	<0·01	<0·01	0·31	0·69†
Dolní Věstonice 13	EUP	UP	0·01	<0·01	0·79†	0·20
Dolní Věstonice 14	EUP	UP	0·20	0·01	0·64†	0·15
Dolní Věstonice 15	EUP	UP	0·02	0·02	0·87†	0·09
Dolní Věstonice 16	EUP	UP	<0·01	<0·01	0·70†	0·30
Mladeč 2	EUP	REC*	<0·01	<0·01	0·48	0·52†
Mladeč 5	EUP	UP	0·24	<0·01	0·75†	0·01
Pavlov 1	EUP	UP	0·05	<0·01	0·86†	0·09
Předmostí 1	EUP	UP	0·02	0·02	0·85†	0·11
Předmostí 3	EUP	Nea*	0·16	0·54†	0·30	<0·01
Předmostí 4	EUP	UP	<0·01	<0·01	0·88†	0·11
Předmostí 7	EUP	UP	0·04	0·03	0·87†	0·07
Předmostí 9	EUP	UP	0·04	0·03	0·92†	<0·01
Předmostí 10	EUP	UP	0·01	<0·01	0·88†	0·11

*Incorrect classification according to *a priori* defined group.
†Highest values of the posterior probability classification.

specimens and none of the early modern human fossils.

The question nonetheless remains, in the context of the Šal'a 1 frontal bone being essentially similar to those of the Neandertals, whether it can be considered to exhibit a trend toward an early modern human morphological pattern (whether that of the Qafzeh-Skhul sample or that of the earlier Upper Paleolithic sample). Such an evolutionary assessment of the Šal'a 1 frontal bone depends in part on its chronological position. If it does indeed derive from last interglacial deposits (or slightly earlier ones), then its modest toral reduction most likely reflects a general pattern of facial robusticity reduction seen in the Neandertals *sensu lato* relative to their Middle Pleistocene ancestral populations (including samples like the Krapina one). This general facial reduction, in the context of maintained total facial prognathism and similar body size, has been previously documented (Smith & Ranyard, 1980; Trinkaus, 1987; Trinkaus & Smith, 1995), and it is likely that it is reflected as well in the supraorbital region [despite ambiguities regarding the functional role of the supraorbital torus (e.g., Hylander *et al.*, 1991)]. If, on the other hand, the Šal'a 1 frontal bone represents a late European Neandertal, from OIS 3, and was secondarily mixed with faunal indicators of the last interglacial, then its more modest supraorbital torus and evidence of lateral thinning (albeit in the context of Neandertal features such as orbital margin rounding and the absence of segmentation) might support a trend toward further facial reduction among late Neandertal populations [e.g., the Vindija sample and Saint Césaire 1 (Wolpoff *et al.*, 1981; Smith & Trinkaus, 1991; Wolpoff, 1999)]. However, even though the stratigraphic position and faunal associations of the Šal'a 1 frontal bone remain ambiguous, we feel that the available data make it more likely that Šal'a 1 derives from relatively early in the Late Pleistocene. In any case, given the stratigraphic uncertainties it remains inappropriate to use Šal'a 1 as firm support of models of late Neandertal facial reduction.

Conclusion

This morphological and morphometric reconsideration of the Šal'a 1 frontal bone, in its stratigraphic context, indicates that it is most likely that it represents a Late Pleistocene representative of the central European Neandertal sample. The interpretation of it as a "progressive Neandertal" by Vlček (1968, 1969) should be seen principally in the historical context of those statements, from a time period during which a distinction was made between "classic" Neandertals and "progressive" ones and the morphological heterogeneity of the "progressive Neandertal" sample was not fully recognized. The subsequent interpretations of Šal'a 1 as providing paleontological support specifically for the some degree of evolutionary continuity in central Europe between Neandertals and earlier Upper Paleolithic early modern humans are not corroborated by this analysis; such hypotheses need to be assessed principally on the basis of the morphology of the most recent Neandertals in the region and the subsequent populations of early modern humans and their inferred population dynamics (e.g., Duarte *et al.*, 1999; Smith *et al.*, 1999; Wolpoff *et al.*, 2001).

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The Zlatý Kůň–Koněprusy has been dated to the Late Upper Paleolithic since the paper was written. However using data of the individual will make only minor and not significant changes in the univariate analysis and comparison of supraorbital morphology and therefore will not affect evaluation of Šal'a 1 frontal.