



# Krapina and Saccopastore: Endocranial Morphology in the Pre-Würmian Europeans

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## Abstract

*The skulls of Saccopastore 1, Krapina 3, and Krapina 6, are sufficiently well preserved to allow the reconstruction of their endocranial casts. In addition, these specimens are useful to investigate the paleoneurological changes that occurred during the Mid-to-Late Pleistocene in Europe. The main features of their endocasts are described in this paper, and combined with some comparative metrics performed on the major endocranial diameters. The raw endocranial lengths and arcs characterize the specimens according to their general size, reflecting a generalized brain enlargement. Saccopastore 1 and Krapina 3 are rather similar for their raw diameters, and for showing a similar posterior dominance of the middle meningeal network. In contrast, Krapina 6 shows values that are more comparable with the Neanderthal range, and a more developed anterior ramus of the middle meningeal vessels. All the three specimens have the maximum endocranial width positioned over the temporal lobes, but no data are available for the general parietal development of the Krapina fossils. Because of the marked allometric component of the endocranial development in non-modern human taxa, and because of the limited preservation status of the Croatian specimens, the hypothesis of a gradual allometric variation from Middle to Upper Pleistocene in Europe (that is, between *Homo heidelbergensis* and Neanderthals) cannot be falsified by the present data. Future investigations should consider traits like the widening of the frontal lobes or the lateral development of the parietal surfaces to test the possibility of a more discrete transition after the Oxygen Isotopic Stage 6 in Europe.*

## INTRODUCTION

Neanderthals are presently one of the most studied and debated taxon among the extinct hominids, by virtue of their relative good fossil record (compared with other extinct human groups) and of their biogeographical context limited to Europe and Near East. Leaving aside the Asian evidence, also the Afro-European humans of the Middle Pleistocene are represented by excellent fossil samples (1). Accordingly, a large part of the paleoanthropological literature is devoted to the interpretation of the related evolutionary processes. Conversely, little information is currently available at the transition between the Middle and the Late Pleistocene, with a consequent gap in our ability to promote robust inferences on the evolutionary scenarios. Present theories provide quite interesting models for the European evolutionary continuum – including the chronospecies *Homo heidelbergensis* and *Homo*

*neanderthalensis*, whether the species rank will be recognised in both cases (2–3) – but they relies upon highly speculative hypotheses for the transitional passage(s) along this supposed lineage. The relationship between the two morphs have been hypothesized to be the result of a gradual anagenetic shift of characters known as the »accretion model« (4–6; *but see* 7). Nevertheless, genetic bottlenecks possibly related to climate changes could have involved more discrete steps, especially in the transition from Middle to Late Pleistocene Europeans, with interesting population dynamics still to be better understood.

As far as the encephalization process is concerned, the Afro-European Middle Pleistocene specimens show a significant increase in cranial capacity compared with their ancestors or with the synchronic Asian variability (8). Subsequently, the endocranial volume increases further among the Würmian Neanderthals. Considering the general brain shape, the endocranial morphology of the non-modern human taxa has been hypothesized to be largely the expression of a shared allometric trajectory (9–10). In this perspective, shape differences (widening of the frontal lobes, vertical development, parietal flattening) are interpreted as the result of the same structural model scaled at different sizes. Nevertheless, minor variations were hypothesized to be associated with specific human groups. In particular, Neanderthals display a certain development of the parasagittal parietal areas, which is not described in the Middle Pleistocene specimens (9), producing the well-known »*en bombe*« profile in rear view when both the ecto- and endocranial surfaces are observed. Anyway, the most relevant endocranial human characters (ranging from the hemispheric asymmetry to the expression of single circumvolutions), are already present in all these morphotypes, and the mentioned hypotheses remains to be to be further supported on a more robust statistical ground.

The more complete endocasts available to evaluate from a paleoneurological perspective the transition from the Middle to the Late Pleistocene in Europe are those of Saccopastore 1, Krapina 3, and Krapina 6. Saccopastore 1 (SCP1) was found in Roma (Italy) and has been dated to about 120 Ka (*for a recent review see* 11). The skull is rather complete and since its discovery it was described as an »early Neanderthal« (*e.g.*, 12–13). Further analyses confirmed this interpretation, both taking into account the ectocranial (14–18) and endocranial (9, 19) morphology. The human remains from Krapina (Croatia) are probably penecontemporaneous with the Italian fossil, showing also a similar phenotype (20–21). Both the Krapina 3 (KRP3) and Krapina 6 (KRP6) endocasts are known for their right side only, because of the incomplete preservation of these specimens (22).

This paper is aimed at comparing the endocasts of these three specimens within the framework of the non-modern human variation, trying to improve the available knowledge about the transition between Middle and Late Pleistocene in Europe. In particular, the general endocranial diameters and arcs are used to perform uni-

variate and multivariate metric comparisons, together with a description of the traces left by the middle meningeal vessels upon the inner endocranial walls.

## THE ENDOCASTS

The endocast of SCP1 was digitally reconstructed after computed tomographic analysis of the specimen (23–24). The endocranial cavity is partially filled with high-density geological matrix, that is easily removable through densitometric segmentation. Only the cranial base cannot be completely resolved from the infiltrations, leaving some areas of uncertain morphology at the temporal lobes and in correspondence of the clivus. Furthermore, the presence of two localized damaged areas (pick holes) on the frontal bone hampers the complete reconstruction of the respective surfaces. The digital endocast of SCP1 is shown in Figure 1. The right frontal lobe is slightly larger, whereas the left occipital areas are more developed than the counterpart. Both the proximal parts of the 3<sup>rd</sup> frontal circumvolutions and the supramarginal boss are more shaped on the left side, while the right parietal lobe is larger and more rounded in the right hemisphere. The maximum endocranial width is influenced by the marked asymmetry, but it is anyway localised in the area of the temporo-parietal junction. The cerebellar lobes are posterior to the brainstem, roundish and divergent, largely positioned under the temporal areas. The endocast underwent STL digital moulding and subsequent stereolithographic modelling with epoxy resins.

Since only parts of the right side of the endocasts of KRP3 and KRP6 are available (Figure 2), no information can be provided on cerebral asymmetries and differential expression of the cortical areas (*e.g.*, 25). The third frontal circumvolution (more visible and complete in KRP3) is fully developed. The maximum endocranial width is localized at the temporo-parietal boundaries, but no clear information is available on the morphology of the upper parietal and occipital areas. The cerebellar lobes, at least in KRP6, are positioned entirely under the temporal lobes.

## METRICS

### Main endocranial diameters and arcs

A basic set of variables was used to describe the major endocranial dimensions (*for a description of the variables and further details, see* 22): hemispheric length (HL), lateral arc (LA), dorsal arc (DA), maximum width (MW), bilateral maximum width arc (MWA). Comparative data were taken from Holloway *et al.* (22). Measures were averaged between the two hemispheres when available. Data for the Krapina specimens were re-sampled considering new improved values. Data from Saccopastore 1 and Sima de los Huesos 5 were directly sampled from the stereolithographic model and from a traditional cast of the stereolithographic model (courtesy of J. L. Arsuaga) respectively. Univariate comparisons were performed grouping the comparative sample as follows:

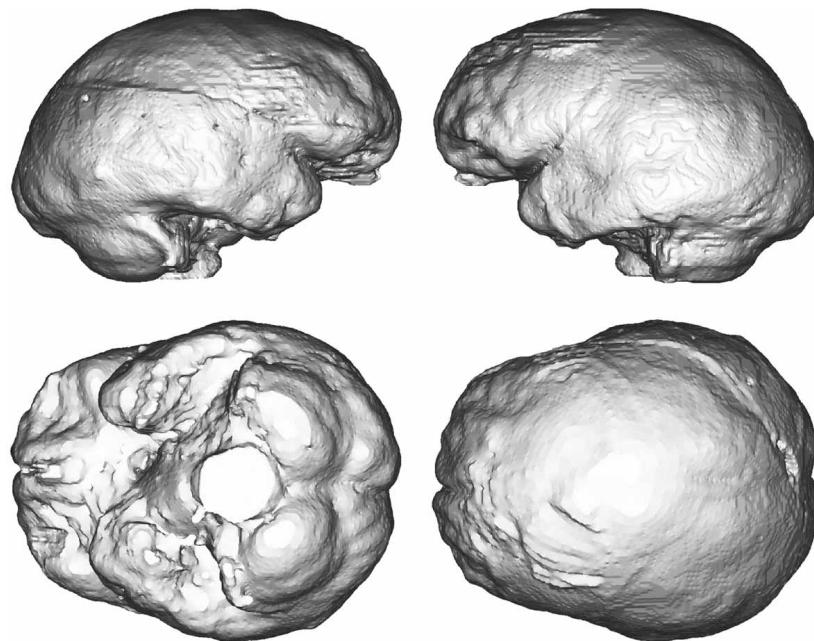


Figure 1. Digital endocast of Saccopastore 1.

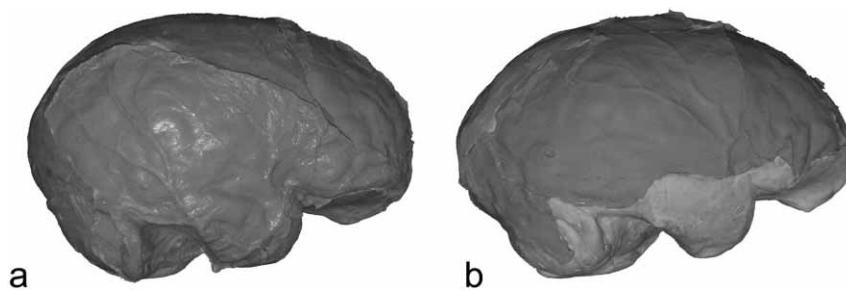
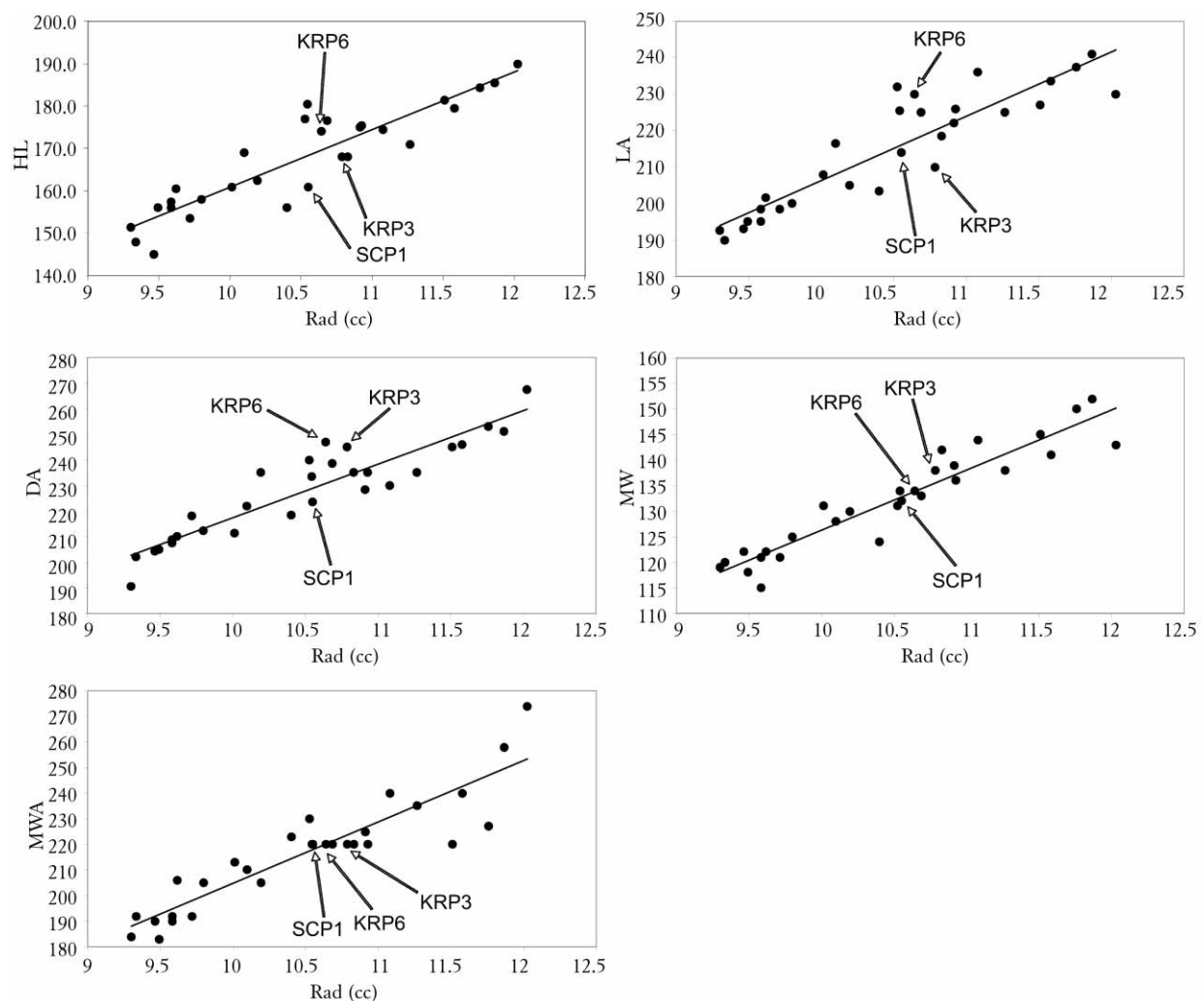


Figure 2. Right hemi-endocast of Krapina 3 (a) and Krapina 6 (b).

TABLE 1

Cranial capacity (CC), hemispheric length (HL), dorsal arc (DA), lateral arc (LA), maximum endocranial width (MW), and maximum width arc (MWA) for Saccopastore 1 (SCP1), Krapina 3 (KRP3), Krapina 6 (KRP6), and the variation – median (med) and quartiles (25th, 75th) – of the comparative samples: archaic *Homo group* (ARC), Afro-European Middle Pleistocene humans (HHE), and Neanderthals (NDR).

		CC	HL	DA	LA	MW	MWA
ARC (N=13)	med	890	158	210	199	122	192
	25 <sup>th</sup>	855	154	205	195	120	190
	75 <sup>th</sup>	1004	161	218	205	128	206
HHE (N=4)	med	1233	173	232	224	135	228
	25 <sup>th</sup>	1146	164	224	213	128	224
	75 <sup>th</sup>	1365	176	238	229	139	233
NDR (N=9)	med	1525	181	245	230	143	227
	25 <sup>th</sup>	1305	176	235	226	141	220
	75 <sup>th</sup>	1625	184	251	236	145	240
SCP1		1174	161	224	214	132	220
KRP3		1255	168	245	210	138	220
KRP6		1205	174	247	230	134	220



**Figure 3.** Linear regressions between each metric variables (in mm) and the cubic root of the cranial capacity. SCP1, KRP3, and KRP6 are labelled, and compared with the rest of the sample.

*Archaic humans* (ARC): less derived specimens (i.e., *H. ergaster/erectus*), including KNM-ER3733, KNM-ER 3883, WT-15000, Salè, Trinil 2, Sangiran 2, 10, 12, 17, Sambungmacan 3, Zhoukoudian 3E, 1L, 3L;

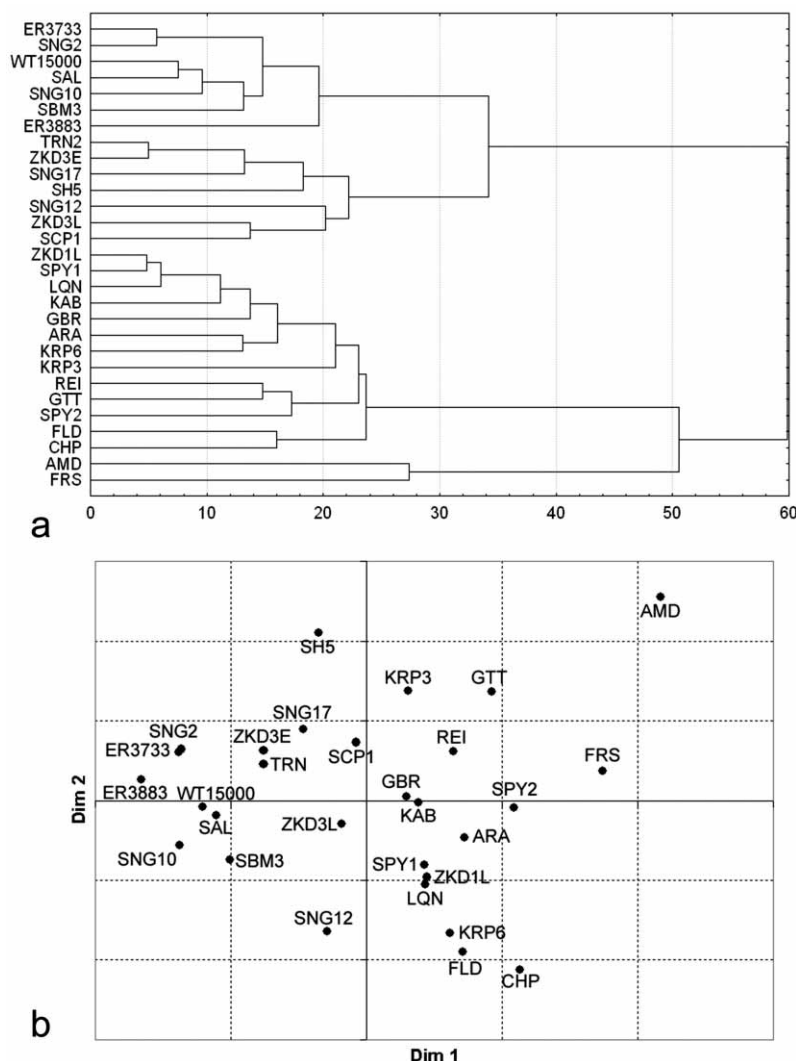
*Afro-European Middle Pleistocene* (HHE): specimens generally included in the *H. rhodesiensis/heidelbergensis* hypodigm, namely Kabwe, the Arago reconstruction, Reilingen, Sima de los Huesos 5;

*Würmian Neanderthals* (NDR): classic and Near-Eastern Neanderthals, including Amud, Feldhofer, Gibraltar 1, La Quina, Guattari, Spy 1, Spy 2, La Ferrassie, La Chapelle-aux-Saint.

Metric results are synthesised in Table 1. SCP1, KRP3, and KRP6 show endocranial volumes and hemispheric lengths comparable with the Middle Pleistocene variation, being this second measure rather larger in KRP6 and smaller in SCP1. The situation is similar for the lateral arc length, but with KRP6 showing a value comparable with the Neanderthal mean. Considering the dorsal arc, both the Krapina endocast show Neanderthal-like

values, while SCP1 displays a shorter length. In all three specimens the maximum width is rather intermediate between the distribution of the Afro-European Middle Pleistocene sample and the Neanderthals, while the arc width is intermediate between the archaic and more derived ranges.

Figure 3 shows the least-square regressions between each metric variable and the cubic root of the cranial capacity. Correlation coefficients range between 0.91 and 0.94 ( $p < 0.001$ ). No differences can be detected between the Neanderthal and the non-Neanderthal trajectories. Clearly, because of the limited sample size the statistical power of such grouped correlations is quite low, and beta errors (unrecognised existing differences) cannot be definitely ruled out. According to the residuals displayed on these bivariate regressions (that is, relatively to their cranial capacity), SCP1 shows a quite short hemispheric length, KRP3 a short lateral arc, and KRP6 a large lateral arc. Both the Krapina endocasts display a large dorsal arc. For the rest of the measures, these specimens do not show large departures from the linear prediction.



**Figure 4.** Raw endocranial variables are ordered using the Euclidean distance matrix: a) UPGMA cluster procedure (cophenetic correlation coefficient = 0.73); b) multidimensional scaling (stress = 0.0354). Labels: AMD: Amud; ARA: Arago (rec.); CHP: La Chapelle-aux-Saints; ER: KNM-ER; FLD: Feldhofer; FRS: La Ferrassie GBR: Gibraltar 1; GTT: Guattari; KAB: Kabwe; KRP: Krapina; LQN: La Quina; REI: Reilingen; SAL: Salé; SBM: Sambungmacan; SCP: Saccopastore; SH: Sima de los Huesos; SNG: Sangiran; SPY: Spy; TRN: Trinil; WT: West Turkana; ZKD: Zhoukoudien.

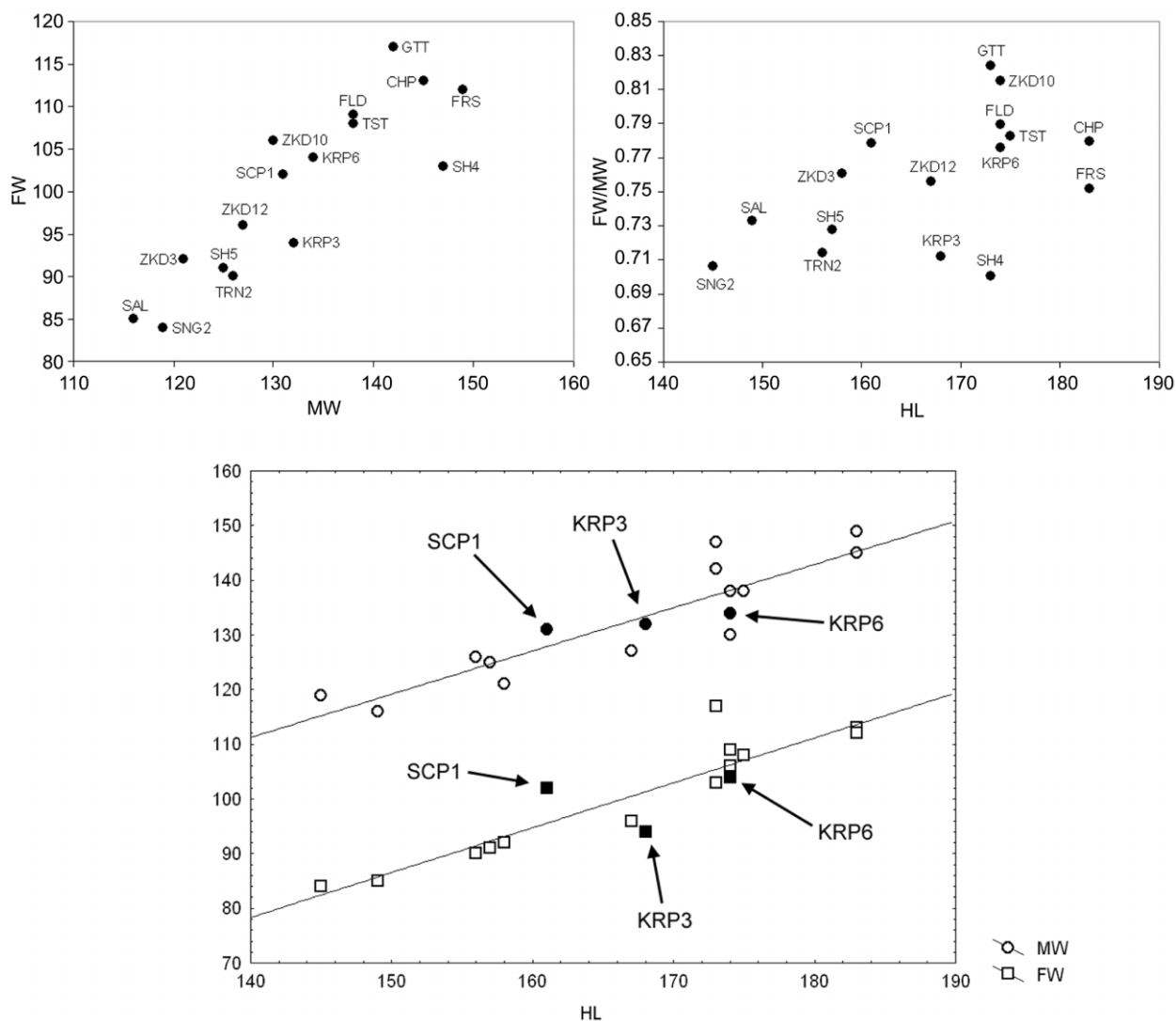
Using these data to cluster the specimens according to the Euclidean distances and the unweighted pair-group method through arithmetic averages (UPGMA) procedure, two main groups are obtained (Figure 4a). The first cluster includes the small-brained hominids (*H. ergaster/erectus*) plus SCP1 and Sima de los Huesos 5. The second cluster includes the large brained specimens (Neanderthals), plus Zhoukoudien 1L, Kabwe, Reilingen, and the Krapina endocasts. Within this second cluster, the two largest specimens (La Ferrassie, Amud) appear separated from the rest of the sample.

Visualizing the same Euclidean distances through multidimensional scaling, the morphological similarities are less constrained by the discreteness of the cluster procedure (Figure 4b). The first dimension separates more or less continuously the small from the large brained specimens, showing high correlation coefficients (0.95–0.97,

$p < 0.0001$ ) with all the variables used and with the cranial capacity (raw, log transformed, or cubic root). The second dimension accounts for intra-sample variation without grouping specimens according to their geographical, chronological, or phylogenetic distribution. KRP3 and SCP1 are close each other, at the borderline between the archaic and more derived groups respectively. In contrast, KRP6 is more internal to the Neanderthal range, comparable with the Feldhofer endocast. A Principal Component Analysis computed on the metric dataset loads almost the entire variability (89.7%) on the first size-related component, without improving the information available.

**Endocranial widths**

In view of the importance of the lateral widening of the frontal lobes, the frontal width at the Broca’s cap and the maximum endocranial width were sampled on the



**Figure 5.** Bivariate comparisons between frontal width (FW), maximum endocranial width (MW), their ratio (FW/MW), and hemispheric length (HL). Labels: CHP: La Chapelle-aux-Saints; FLD: Feldhofer; FRS: La Ferrassie GTT: Guattari; KRP: Krapina; SAL: Salé; SCP: Saccopastore; SH: Sima de los Huesos; SNG: Sangiran; TRN: Trinil; TST: Tesik-Tash ZKD: Zhoukoudien.

Krapina endocranium (doubling the value of the hemi-endocast) and compared with data published elsewhere (10). The values of SCP1, KRP3, and KRP6, fit well within the *Homo* variation, even if KRP3 shows a short absolute frontal breadth (Figure 5a). When these two diameters are regressed onto the hemispheric length, SCP1 shows positive residuals for both variables, while in KRP3 a relative short frontal breadth is evidenced (Figure 5b). Plotting the hemispheric length onto the frontal/maximum width ratio, SCP1 and KRP6 show different endocranial length but similar frontal widening, while KRP3 displays a very marked frontal narrowing (similarly expressed in the Sima de los Huesos 4 endocast – Figure 5c).

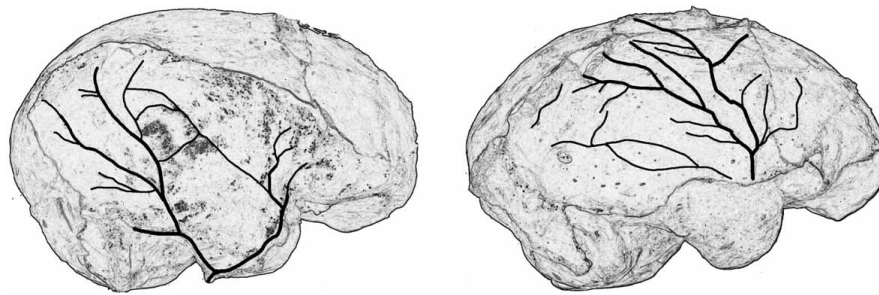


**Figure 6.** Drawings of the middle meningeal networks on the right hemisphere of Saccopastore 1.

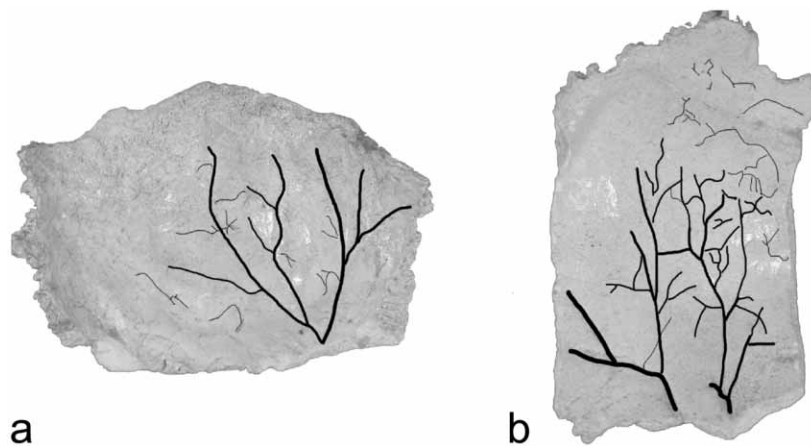
**MIDDLE MENINGEAL VESSELS**

Only the right meningeal networks will be described and compared here, because of the incompleteness of the

Krapina remains. The traces of the middle meningeal vessels are more clearly imprinted on the Krapina endocasts, while they are less visible on the SCP1 surface. Apart for a possible actual lack of meningeal imprints,



**Figure 7.** Drawings of the middle meningeal networks on the right hemisphere of Krapina 3 (left) and Krapina 6 (right).



**Figure 8.** Drawings of the middle meningeal networks on Krapina 19 (a; reversed image), and Krapina 21 (b). Not at scale.

this deficiency is related to both the limited resolution of the 1 mm tomographic section, and by the extension of the damaged area on the frontal lobes. Nevertheless, SCP1 clearly displays a dominance of the posterior vascular system (Adachi type II; *see e.g.* 26), that is more developed compared with the anterior ramus and includes the obelic branch running to the supramarginal area (Figure 6).

Similarly, KRP3 shows an evident dominance of the posterior network, with branching obelic derivation supporting the lower parietal surfaces (Figure 7a). In KRP3 a small vessel from the anterior ramus runs backward to meet the posterior network through some anastomoses. In this respect, it might be classified as Adachi type III (obelic branch derived from both anterior and posterior systems), but the dominance of the posterior vessels on the anterior ones is nevertheless well established. In general, the network is rather developed, even if not reticulated.

The endocast of KRP6 shows a more arborized meningeal network, even if no clear anastomoses can be detected (Figure 7b). In contrast with SCP1 and KRP3, it displays a clear dominance of the anterior branch (Adachi type I), that provides a long and bifurcated obelic ramus. The posterior vessels are scarcely recognizable.

In addition, we report the drawings of the vessels detected onto the endocranial surfaces of other remains from Krapina, namely Krapina 19 and Krapina 21 (Figure

8). The former is a rather complete left parietal, and it is hypothesised to be the counterpart parietal bone of KRP3 (21). It shows the anterior network of the middle meningeal system, which appears rather arborized, including a possible obelic derivation. The second fragment is an oblique portion of a right parietal bone, showing two main vascular rami, anastomized by a tiny and reticulated network.

Nor in SCP1 neither in the Krapina endocasts a clear speno-parietal sinus can be described, even if in the former a para-sagittal lacuna occurs close to a smooth and enlarged traces of the left middle meningeal network. However, the morphology of this trace is not easily recognizable, because of the weakness of the imprint and because of the damaged frontal area.

## DISCUSSION

A limited variation of the endocranial morphology in the genus *Homo* is commonly recognised when compared with the differences observed looking at the ectocranial surface (*e.g.*, 27). That is, although possibly very relevant because of the involvement of cognitive functions, cortical brain differences between extinct human groups may be quite subtle. If we exclude the modern variability (characterized by a marked parietal development), the superficial morphology of the brain in all the other human taxa may be just the result of allometric

variation, associated with surface/volume and connective tensors constraints (9–10). The metrics involved in the present analysis described the variation of the major endocranial diameters and arcs. Both bivariate and multivariate approaches stress that such metrics only rely upon size differences, without improving the information available on changes in shape. Actually, specimens can be ordered and separated only according to their raw dimension. This limit plus the mentioned strong size-related trajectory make these variables scarcely informative, at least when looking for discrete changes between the Middle Pleistocene humans and the Neanderthals.

Considering such a continuous variation, the SCP1 endocranium appears very flat and wide, as already suggested by more detailed analyses (19, 24). The Krapina endocrania do not show the same degree of platycephaly, being in contrast quite tall with respect to their size. KRP3 shows a marked narrowing of the frontal lobes compared to the maximum endocranial breadth, while KRP6 displays a very large lateral endocranial arc. Clearly, all these features do not depart from the general variation of the Mid-to-Late Pleistocene groups, even when their endocranial size is considered. Accordingly, there are no information at present to discard these peculiar features as idiosyncratic traits, without any phylogenetic relevance.

Taking into account this size-related trend, SCP1, KRP3, and KRP6 show intermediate values between the Middle Pleistocene and Neanderthal ranges. Particularly, SCP1 and KRP3 stands in a very borderline position, so that in the cluster procedure the first is grouped with the small-brained subsample, the second with the Neanderthals. Actually, their similar raw dimensions once more stress their overall phenetic resemblance, already noticed considering the ectocranial morphology (e.g., 14). KRP6, because its larger dimensions, better fit within the Neanderthal range.

Similar conclusions can be inferred according to the pattern of the middle meningeal traces. SCP1 and KRP3 show a clear dominance of the posterior network, more frequently described in small-brained hominids such as the Asian *Homo erectus*, while KRP6 displays a more developed anterior branch, prevalent in large-brained taxa as the Neanderthals and modern humans (28–29). It is well known, however, that the dynamics relating the middle meningeal vessels to their traces are rather elusive, and these traits must be used with caution, also when their large intra-group variation is considered (30–35). The fine network displayed by the Krapina 21 parietal fragment add further noise to this scenario, mostly considering that the orientation of the bone could match that network to the supramarginal area. Such parietal reticulation is common among modern humans, even if it has been also described in some archaic specimens like in the parietals from Arago or Biache Saint-Vaast (36–38).

In sum, according to the present paleoneurological data is not possible to falsify the hypothesis of gradual changes along the hypothesized *Homo heidelbergensis*-

*-neanderthalensis* lineage, which in turn might be related to allometric variations and increasing cranial capacity. Of course, the present analysis is limited by the state of preservation of the Krapina remains, that does not allow considerations on possible diagnostic traits. As a matter of fact, it has been hypothesized that SCP1 could show derived Neanderthal traits, including many ectocranial features (13, 17, 39) and a certain lateral development of the upper parietal areas of the brain (9, 19). Accordingly, the pre-Würmian European populations should be included within the Neanderthal variability, as the result of a possible bottleneck occurring during the Oxygen Isotopic Stage 6 (11). In SCP1, also the ratio between the frontal and maximum widths is extremely large, involving a general frontal widening generally expressed in Neanderthals and modern humans (10). Of course, it must be established whether or not this could be another allometric trait or a species-specific character (see 40), and the available hypotheses must be supported on more robust statistical frameworks.

Both the parasagittal parietal enlargement and the widening at the frontal lobes must be carefully considered in the paleoneurological record, in order to improve our knowledge on encephalisation during the transition between Middle and Late Pleistocene in Europe. It is worth noting that, although the Krapina endocrania do not allow appropriate considerations on their upper parietal volumes, in all the three specimens examined in this paper the maximum endocranial width is not localized at the temporal lobes, but more superiorly as in Neanderthals (41). Anyway, considering the large allometric component in the brain morphology and the marked noise due to individual variations, at present we cannot statistically reject the hypothesis of a gradual (anagenetic) evolution, and the alternative scenario (i.e., a sharp transition from *H. heidelbergensis* to the Neanderthals) must be interpreted just as an interesting hypothesis.

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