

CHAPTER XXIV-3

ENDOCASTS

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Abstract

These two endocasts of the fossil hominids retrieved from Spy allow us to study morphological variation in the same population. Detailed descriptive analysis has been done, with comparative morphometrical analysis. The results have been compared with European hominid endocasts remains from the same time period in order to highlight variation of the human brain in this group.

Cranial capacity has been estimated, based on completed reconstruction and water displacement techniques. Spy I was 1,305 ml, while Spy 10 yielded a volume of 1,553 ml. The endocranial shape is low, long and broad, similar to other endocasts from the Middle Palaeolithic of Western Europe. Cerebral asymmetries with left occipital and right frontal petalias are present. It is likely that the difference in volumes between the two Spy endocasts represents sexual dimorphism. The vasculature pattern is very poorly represented with scarce ramifications and no anastomoses. The presence of the spheno-parietal sinus has been noted. The encephalic surface is not well preserved, but the frontal and parietal cerebral convolutions show some minor relief and shape similar to those observed on other Neandertals, such as a rounded first parietal convolution or oval supramarginalis gyrus. However, major sulci, e.g. the central or Rolandic fissure, the Sylvian, parieto-occipital, and lunate sulci, or the limbs of the posterior portion of the Sylvian fissure cannot be unambiguously identified. All of these morphological characters are considered as autapomorphies for this Neandertal population.

INTRODUCTION

Both fossil hominids from Spy (Spy I and Spy II) have been recognised as representative of the Neandertal lineage based on external and internal morphology, but an exhaustive morphological description of endocranial features has never been done. A short description and analysis was provided by Holloway (1981). The endocasts of Spy (Spy 1, representing individual Spy I, and Spy 10, representing Spy II) are discussed and compared with Preneandertals, *Homo neanderthalensis*, and *Homo sapiens* samples in order to provide endocranial characterisation of both these specimens, improve the description of Neandertal endocranial autapomorphies, and emphasise differences between *Homo neanderthalensis* and *Homo sapiens*, although the question of true species differences remains moot.

The preservation of the Spy hominids is quite good. Physical endocasts were directly obtained from internal cavity of the skulls, and the quality exactly reproduced the internal sur-

face of the cranial bones. Cranial portions from Spy 1 and 10 are relatively complete and undistorted, except for the left parieto-fronto-temporal area of Spy 1 which is not preserved. The hemispheric surface of Spy 1 was not well preserved, and was covered with sediment. The left extremity of encephalic rostrum was absent, as were the inferior parts of these frontal lobes on both Spy endocasts. Two sets of endocasts have been used for morphological and metrical analysis, the first one housed in Columbia University in New York had been reconstructed by one of us (Holloway, 1981) and allows estimation of a majority of measurements; the second one from the Royal Belgian Institute of Natural Sciences in Brussels, which is in very good quality.

MATERIAL

Our comparative material is constituted of most of the ancient European fossil hominids, *Homo neanderthalensis* contemporaneous of Spy, and two modern *Homo sapiens* samples.

Fossil hominid endocasts (*Muséum national d'Histoire naturelle de Paris*; Columbia University, New York; Royal Belgian Institute of Natural Sciences, Brussels).

Spy 1 and 10 were compared to Arago 21 + 47 reconstituted with the Swanscombe 1 occipital, Ehringsdorf 9, Swanscombe 1, Biache-Saint-Vaast 1, Reilingen 1, Gibraltar 1, Gibraltar 2, Teshik-Tash 1, La Chapelle-aux-Saints 1, La Ferrassie 1, Le Moustier 1, La Quina 5, Neandertal 1, Combe Capelle 1, Předmostí 3, Předmostí 4, Předmostí 9, Předmostí 10, Cro-Magnon 3, Brno 3, Dolní Věstonice 1, Dolní Věstonice 2.

Modern population (*Muséum national d'Histoire naturelle de Paris*) n = 105

595, 713, 723, 726, 727, 728, 729, 730-2, 731, 732-3, 733, 748, 749, 753, 754, 755, 764, 784, 788, 789, 794-3, 798-2, 800, 808, 1294-2, 1489, 1490, 1865, 3635, 3662, 3663, 3664, 3665, 3666, 3667, 3668, 3669, 3670, 3671, 3672, 3673, 3674, 3675, 3676, 3677, 3678, 3679, 3680, 3681, 3682, 3683, 3684, 3685, 3686, 3687, 3688, 3689, 3690, 3691, 3692, 3693, 3694, 3695, 3696, 3697, 3698, 3699, 3700, 3702, 3703, 3704, 3705, 3706, 3707, 3708, 3709, 3775, 3827, 3828, 4362, 4815-2, 5720, 5733, 9843, 9844, 9852, 9853, 9854, 10109, 10111, 10112, 10113, 10114, 12033, 19246, 21413, 24636, 24940, 24942, 25027, 25536, 25620, 27429, 30189, 30195.

METHODS

Morphological characters such as asymmetry (petalias), imprints of circumvolutions and vascularisation (venous sinuses and middle meningeal system) have been closely described.

A traditional metrical study (ST1, SF1) has been performed on 128 specimens including 23 fossil hominids (*Homo neanderthalensis* as well as some Preneandertals and anatomically modern *Homo sapiens*) and 105 extant humans (Table 1).

Cranial capacity has been estimated directly by immersion of endocasts in water, and the result corresponds to the average of three

immersions. As any encephalisation quotient (EQ) must include a calculation of body weight, the incomplete post-cranial bones do not permit a reliable calculation of EQ.

Principal components analysis has been performed to synthesize information contained in the 10 variables which were selected with regard to the preservation of the endocasts. The measurements taken for this analysis were widths (WME, WBE, WCBE), average hemispheric length (LME), total height (HBBE), partial heights (HGQE and HBRE), and sagittal chord of each cerebral lobes (CFR, CPA, COC). These 10 variables have been used on 32 specimens including 23 fossil hominids and 10 extant humans.

In our 3D geometric morphometric study, particular care has been taken to choose the maximum of common landmarks preserved on the Spy endocasts (ST2 and SF2).

MORPHOLOGICAL RESULTS OF ENDOCRANIAL DESCRIPTION OF THE SPY HOMINIDS

Vascularisation

Cranial dural sinuses

Spy 1 exhibits the left sphenoparietal sinus preserved in its superior part, and its diameter is 3.8 mm. Clearly imprinted, its sigmoid course is situated anteriorly to the coronal suture, ending in a large arachnoideal granulation of 14 mm in diameter. The right sphenoparietal sinus is preserved in its final part going into a small arachnoideal granulation of 5 mm in diameter. The superior sagittal sinus is visible in the anterior part of the parietal bones showing sagittal suture impressions. It disappears to be again apparent between the occipital lobes. Considering the sagittal sinus orientation near the confluence, it flows into the well-developed left transverse sinus. The right transverse sinus is less enlarged but shows clearer margins; it is not positioned under the left one as usual, but at the same level. The left sigmoid sinus is strongly developed in its inferior portion, more than the right one which is thinner (7 mm and 10 mm for the left one).

<i>Specimens</i>	<i>Attributed taxon</i>	<i>2D Traditional</i>	<i>2D PCA</i>	<i>3D A</i>	<i>3D B</i>
Arago 21 + 47 – Swanscombe 1	Preneandertals	X		X	X
Ehringsdorf 9	Preneandertals	X			
Swanscombe 1	Preneandertals	X			
Reilingen 1	Preneandertals	X			
Gibraltar 1	Neandertals	X			
Gibraltar 2	Neandertals	X			
Spy 1	Neandertals	X	X	X	X
Spy 10	Neandertals	X	X	X	X
Teshik-Tash 1	Neandertals	X	X	X	X
La Chapelle-aux-Saints 1	Neandertals	X	X	X	X
La Ferrassie 1	Neandertals	X	X		
Le Moustier 1	Neandertals	X	X		X
La Quina 5	Neandertals	X	X	X	X
Neandertal 1	Neandertals	X	X	X	
Combe Capelle 1	anat. mod. <i>Homo sapiens</i>	X	X		X
Předmostí 3	anat. mod. <i>Homo sapiens</i>	X	X	X	X
Předmostí 4	anat. mod. <i>Homo sapiens</i>	X	X	X	X
Předmostí 9	anat. mod. <i>Homo sapiens</i>	X	X	X	X
Předmostí 10	anat. mod. <i>Homo sapiens</i>	X	X	X	
Cro-Magnon 3	anat. mod. <i>Homo sapiens</i>	X	X		
Brno 3	anat. mod. <i>Homo sapiens</i>	X	X	X	
Dolní Věstonice 1	anat. mod. <i>Homo sapiens</i>	X			
Dolní Věstonice 2	anat. mod. <i>Homo sapiens</i>	X	X	X	X
595	<i>Homo sapiens</i>	X	X	X	X
713	<i>Homo sapiens</i>	X	X		
723	<i>Homo sapiens</i>	X	X		
726	<i>Homo sapiens</i>	X	X		
727	<i>Homo sapiens</i>	X	X		
728	<i>Homo sapiens</i>	X	X		
729	<i>Homo sapiens</i>	X	X		
730-2	<i>Homo sapiens</i>	X	X		
731	<i>Homo sapiens</i>	X	X		
732-3	<i>Homo sapiens</i>	X	X		
92 others (material)	<i>Homo sapiens</i>	X			

Table 1. List of studied hominids.

On Spy 10 the right endocranial surface is the best preserved side with clearer imprints. Relief of spheno-parietal sinus is well marked with a sinuous course. Its diameter is 4.9 mm with less marked relief than the left side where its diameter is smaller (4 mm) and where it goes to a

nearly oval arachnoideal granulation of 18 mm in length. The superior sagittal sinus is visible for a short distance on the anterior and middle areas of the parietal lobe and is again apparent under the occipital lobes at the confluence where it turns into the right lateral sinus which is clearly visible

until it reaches the transverse portion. The left one is less apparent and inferiorly situated. The lateral sulcus presents no relief given its smooth surface. Unlike Spy 1, the sagittal sinus is going to the right transverse sinus, implying that the left occipital lobe was more developed.

Middle meningeal system

The middle meningeal system, situated in the dura mater, leaves direct imprints on the inner table of the endocranial surface. Comparisons between taxonomic groups are interesting concerning the variation of this anatomical character. The importance of the anterior and posterior meningeal branches sets has been analysed in relation to the covered encephalic surface, even if there is no close established relation between this vascular system and the encephalisation phenomenon. One of the features con-

sidered is the origin of the obelic branch which can be from either the bregmatic, lambdatic, or from both branches.

On Spy 1 (Figure 1), the middle meningeal system is very poorly represented, with scarce ramifications and no anastomosis. On the left hemisphere, the middle meningeal common vessel is well marked at the base of the temporal lobe. It is subdivided in two branches, an anterior one which has a horizontal frontward course, while the second one is divided into two inclined upwards and backwards courses. These are barely preserved at this level. On the upper part, no ramification is noted, just the extremity of the speno-parietal sinus is observed. On the right hemisphere of Spy 1, the base of the middle meningeal system is well preserved and exhibits a subdivision between anterior and posterior branches. The anterior one proceeds forwards and upwards on the 10 mm pre-

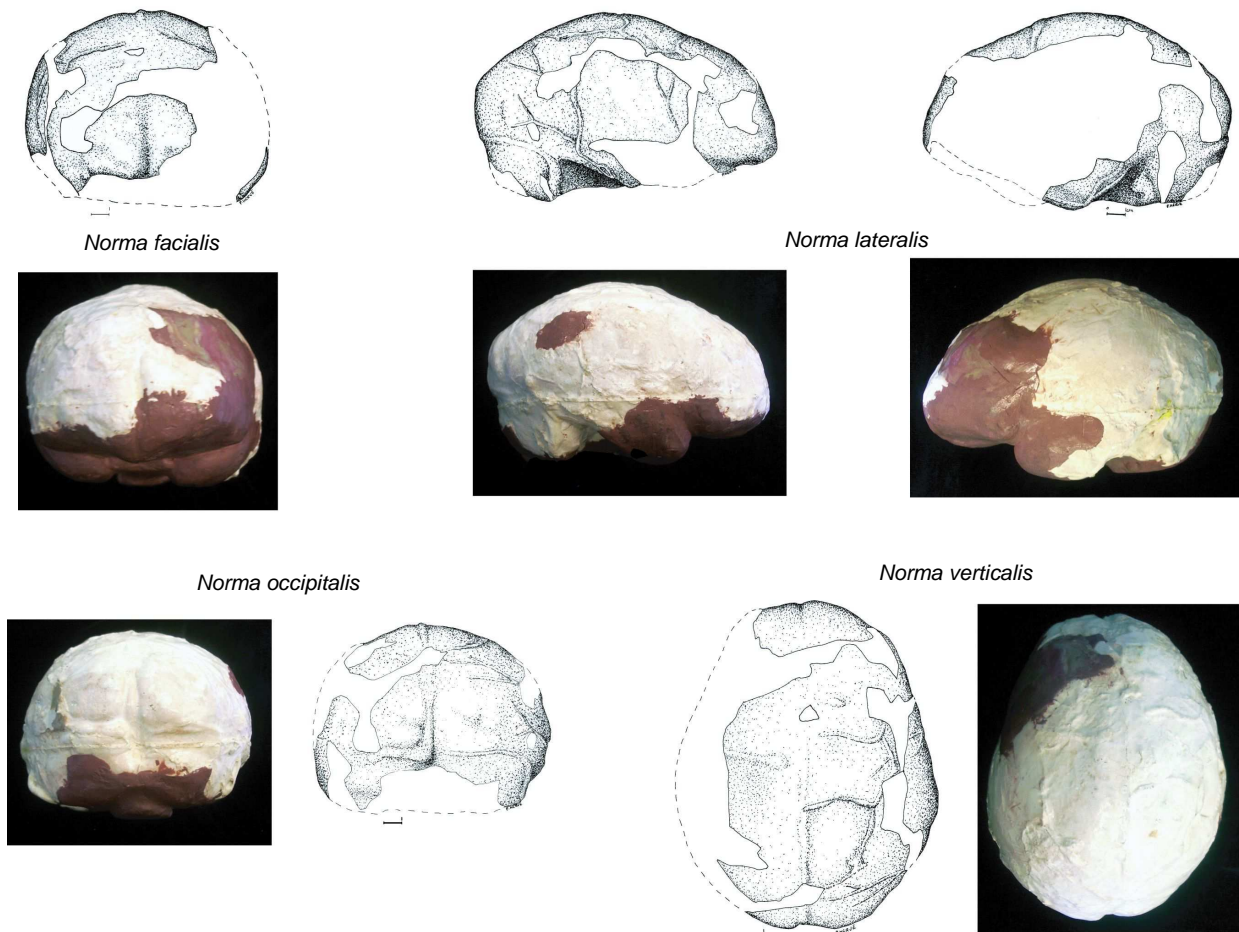


Figure 1. The Spy 1 endocast.

served portion. It is again apparent on the middle encephalic preserved portion where it is clearly imprinted and subdivided after 21 mm. On the superior preserved portion, it is divided into two branches: the anterior one corresponds to the sphenoparietal sinus and gives a strong ramification which is subdivided into two very well marked branches which corresponds to the obelic branch. Its extension is very large and covers the encephalic surface from postcentral gyrus to the posterior part of the supramarginal lobule, which is nearly the totality of the right parietal lobe. The posterior branch is apparent on the inferior portion of the temporal lobe with a sinuous course going 40 mm posteriorly. It is then divided in two branches, an anterior one, subdivided itself going to the lambdatic region with clear ramifications. The posterior one is also divided into two short ramifications which are going to the base of occipital lobes.

On Spy 10, the anterior and posterior right middle meningeal imprints are clearly marked with thin ramifications. The vascular system is poor, without any anastomosis. The anterior branch seems more developed than the posterior one, even if it seems that the two obelic branches are present, individualised from the anterior and posterior rami. The anterior system shows more numerous posterior and thin ramifications which cover the posterior frontal lobe until the middle area of parietal lobe and have very well marked ramifications from anterior edge where one of these ramifications can be seen as corresponding to the sphenoparietal sinus. The obelic vessel of the posterior branch is well marked and ascends towards the vertex. This posterior system with the lambdatic branch and its ramifications covers all of the posterior area of the parietal lobe including the anterior part of the occipital lobe. Some very thin ramifications of the anterior branch seem to reach the posterior ones and perhaps constitute an eventual anastomosis. On the left hemisphere, the imprints are more marked but less numerous. The obelic branch has been noticed from lambdatic branch. The anterior ramus is divided twice into two branches which exhibit thin relief, less developed from those of the lambdatic one. The posterior branch is more developed, constituted by the obelic and lambdatic branches which are both ramified at their extremities. The middle meningeal pattern is more reduced on the left hemisphere.

On both Spy hominids, the middle meningeal system is not well developed, with scarce ramifications and almost no anastomosis; this pattern is commonly observed on representatives of *Homo neanderthalensis* and is probably autapomorphic.

Encephalic imprints

The anterior frontal convolutions are not totally preserved on Spy's endocasts, being best preserved on the right hemisphere of Spy 1. The orientation of the first frontal convolution that is preserved allows us to conclude that the encephalic rostrum was short and large. Anteriorly, the interhemispheric fissure is deep and wide on both hominids. The convexity of the left frontal lobe seems less marked than the right on Spy 10. The imprint of central sulcus is unclear in the midsagittal region, so that the pre- and postcentral convolutions breadths could not be estimated on Spy 1. This is more marked on Spy 10, situated 38 mm behind endobregma. The Sylvian valley is not preserved on both endocasts from Spy. The terminal part of this sulcus is rectilinear, slightly inclined upwards, close to the horizontal plane on the right hemisphere of Spy 1. The course of this sulcus is too often interrupted to have a correct idea of its general orientation, but its extremity seems placed in inferior position, which is in accordance with Spy 1. Some depressions attributed to occipital sulcus are apparent, more deeply marked on the right lobe of Spy 1, but of equal intensity on both occipital lobes of Spy 10.

Spy 1 (Figure 1)

Even if the frontal breadths cannot be determined because of hazy depressions corresponding to the frontal sulcus on both hemispheres of Spy 1, the observation of preserved frontal portions lets us suppose that the left part of encephalic rostrum was much more developed. The right Broca's cap surface is badly preserved with many small cracks and exhibits well-marked anterior branch of the lateral sulcus, which is inclined upward and frontward.

The left inferior and median regions of frontal and parietal lobes are not present. The hemispheric surface allowing observations is re-

duced to a large band (around 60 mm) along the interhemispheric fissure. The central fissure region is badly preserved. Relief of sagittal suture is observed along the interhemispheric fissure from bregma to lambda, integrated into the left and right of the first parietal convolution. The endocranial surface, covered with small bumps (results of sediment) does not allow us to distinguish vascular imprints.

On the right hemisphere, the first parietal convolution breadth decreases from 31 mm to 19 mm posteriorly. The inferior parietal lobule is well individualised (23 mm), but exhibits weak internal relief. The posterior limit of supra-marginal gyrus is clearly marked. Even if its surface is not preserved in totality, its shape appears oval. The superior relief of angular gyrus is weakly developed, individualised from the supra-marginal one by a depression.

The occipital lobes are better preserved, and depressions corresponding to limits of convolutions are deeply impressed. As the sagittal sinus is going into the left lateral sinus, the right occipital lobe is larger. The occipital lobes are separated by the sagittal sinus which is 5 mm large. Cerebral regions corresponding to the superior portion of the temporo-cerebellar excavation are preserved on both hemispheres, but this opening is greater on the right. The cerebellum is not completely preserved on the reduced surface, and therefore provides no observations.

Spy 10 (Figure 2)

On both hemispheres of *Spy 10*, the anterior part of the frontal lobes is covered with small bumps, separated by strongly impressed depressions.

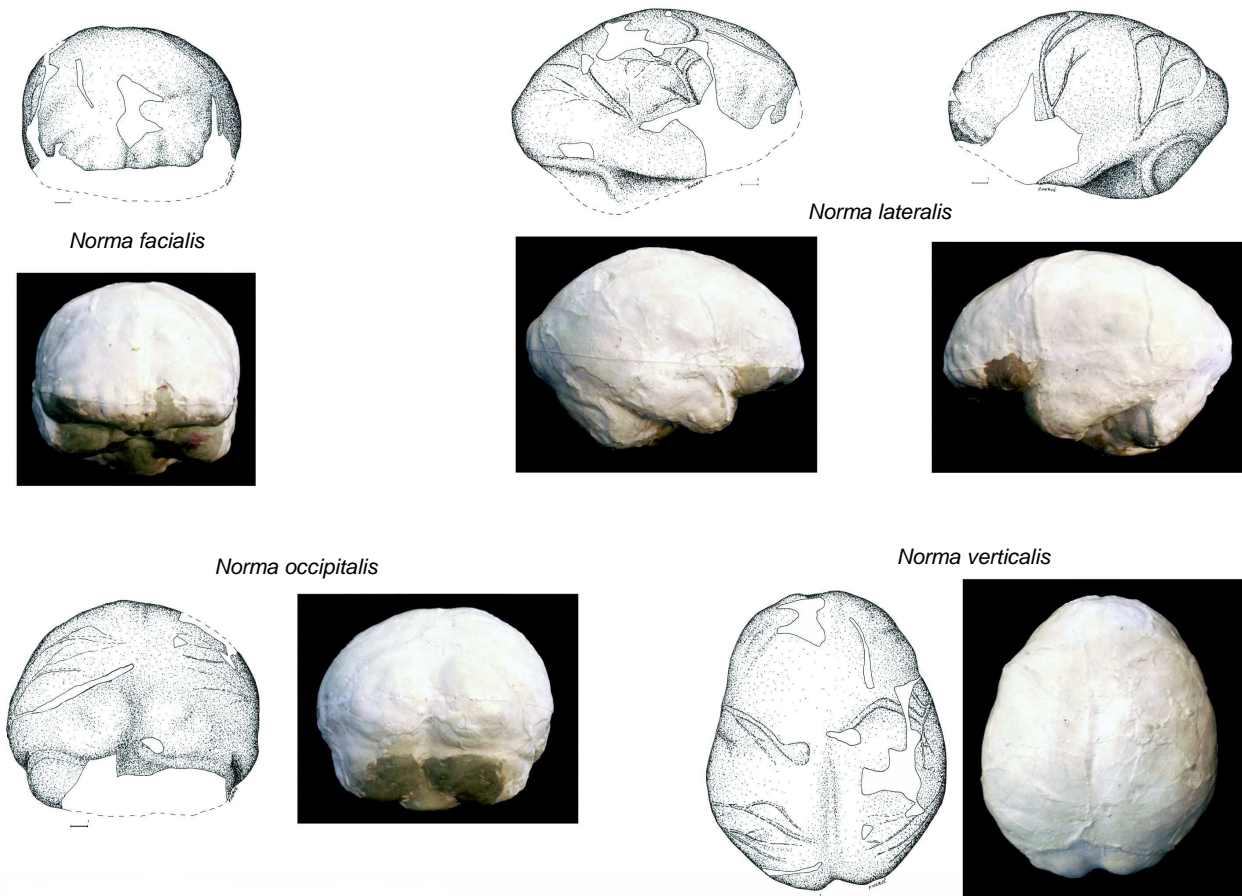


Figure 2. The *Spy 10* endocranial cast.

The first right frontal convolution is wider than the left. The orbital and triangular parts of the left third frontal convolution are very clearly separated by the vertical anterior branch of lateral sulcus. The relief of orbital part is marked and well individualised. The preserved surface of the triangular portion is clearly convex but shows reduced dimensions, as one of opercular part is not preserved, so areas 44, 45 are present with 47 missing. On the right frontal lobe, a reduced frontal surface is preserved, exhibiting well marked depressions corresponding to the frontal sulcus between convolutions.

Hazy depression corresponding to central sulcus allows us to determine the precentral (15 mm) and postcentral (16.5 mm) convolutional breadths.

On the right, sediment covers interparietal sulcus region and we cannot estimate the first parietal convolution breadth, although its relief is strongly convex. The Sylvian valley as anterior and medial parts of lateral sulcus, are not preserved. Only the posterior portion is visible on the reduced part and is horizontally oriented and rectilinear. It delimits the base of the second parietal convolution which is very well individualised with clear relief (19 mm diameter) which is situated along the anterior ramus of the middle meningeal system. The edges of the supramarginal gyrus are more diffuse but its shape is elongated, being an oval outline of this anatomical formation. It is not possible to determine the level of its junction with the angular gyrus. It is on this large and weak marked relief ($L = 42$ mm, $h = 38$ mm) that the maximal endocranial breadth has been measured.

On the left hemisphere, the inferior frontal lobe and the Sylvian valley are not preserved. The orbital part of the third convolution is nearly preserved in totality, separated from the anterior portion of the triangular part (only preserved) by the anterior ramus of the lateral sulcus with a vertical orientation.

The base of the left second parietal convolution (20 mm diameter) is less individualised than on the right lobe. The first parietal convolution breadth is decreasing posteriorly from 30 to 20.5 mm. The edges of the supra-marginal gyrus,

although with weak relief, are still distinct suggesting an oval shape. Nevertheless, angular gyrus is very clearly delimited and its relief is at the level of the maximal endocranial breadth position ($L = 32$ mm, $h = 40$ mm).

The temporo-cerebellar cleft is more open on the left hemisphere and depressions separating the occipital convolutions are well impressed. The occipital lobes are joined and situated under the parietal lobes.

The cerebellum, preserved on the reduced surface of the left hemisphere, does not allow any meaningful morphological observation.

METRICAL RESULTS

Univariate and bivariate dimensions

The cranial capacity values (Table 2, SF3) show increasing values from Preneandertal fossil hominids to *Homo neanderthalensis*. Preservation state of only three anatomically modern *Homo sapiens* specimens allows this estimation, and the obtained average is high, more than extant *Homo sapiens*. The decreasing value of absolute cranial capacity concurs with results from Martin (1995, 1996) who established a relation with technical progress noticed during this chronological period and made the connection with low-energy food. While this is always the purpose of such studies, it does emphasise the absence of any clear relation between the absolute value of cranial capacities and behavioural abilities.

Values of Spy 1 and 10 (ST3) are reported and analysed with the comparative fossil hominids groups (SF4 and SF5).

With respect to the main endocranial measurements, Spy 1 exhibits smaller values than Spy 10 closer to Gibraltar 1 and La Quina 5. Its hemispherical length is similar to the Preneandertal mean, the widths (estimated, because of a large left gap) and total height show intermediate values between Preneandertals and *Homo neanderthalensis* groups. Spy 10 shows greater dimensions, all comprised in *Homo neanderthalensis* variation, near specimens like La Chapelle-aux-Saints 1, La Ferrassie 1 or Le Moustier 1.

<i>Specimens</i>	<i>Direct</i>	<i>References</i>	
Ceprano 1		1,000 1,185 1,057 1,180 to 1,220	Clarke, 2000; Ascenzi <i>et al.</i> , 1996, 2000; Mallegni <i>et al.</i> , 2003
Arago 21 + 47 – Swanscombe 1	1,080		
Sima de los Huesos 4		1,390	Arsuaga <i>et al.</i> , 1993
Sima de los Huesos 5		1,125	Arsuaga <i>et al.</i> , 1993
Petralona 1		1,200	Stringer <i>et al.</i> , 1979; Seidler <i>et al.</i> , 1997
Swanscombe 1		1,325	Ovey, 1964
Ehringsdorf 9	1,370		
Biache-Saint-Vaast 1		1,200	Vandermeersch, 1978; Stringer, 1984
Reilingen 1	1,401	1,430	Dean <i>et al.</i> , 1998
Steinheim 1		1,163 to 1,214 950 1,140	Weinert, 1936; Ruff <i>et al.</i> , 1997; Prossinger <i>et al.</i> , 2003
Gibraltar 1	1,280		
Saccopastore 1		1,174 1,094	Sergi, 1944, 1948; Manzi <i>et al.</i> , 2001; Bruner & Manzi, 2008
Saccopastore 2		1,300	Sergi, 1944, 1948; Manzi <i>et al.</i> , 2001
Guattari 1		1,350	Recheis <i>et al.</i> , 1999
Spy 1	1,304	1,305	Holloway, 1981
Spy 10	1,536	1,553	Holloway, 1981
Teshik-Tash 1	1,515		
La Chapelle-aux-Saints 1	1,620		
La Ferrassie 1	1,670		
Le Moustier 1	1,650		
La Quina 5		1,350	Boule, 1909; Holloway, 1981
Neandertal 1		1,408	Boule, 1909; Holloway, 1981
Combe Capelle 1	1,570		
Předmostí 3	1,680		
Předmostí 9	1,720		
Extant <i>Homo sapiens</i>	m = 1,520	Variation Coefficient = 4.2; Max = 1,940; Min = 1,190; N = 103	

Preneandertals		<i>Homo neanderthalensis</i>		Anat. mod. <i>Homo sapiens</i>		Extant <i>Homo sapiens</i>	
Average	1,284	Average	1,511	Average	1,657	Average	1,520
VarCoef	13.8	VarCoef	10.6	VarCoef	4.7	VarCoef	4.2
Max	1,401	Max	1,670	Max	1,720	Max	1,940
Min	1,080	Min	1,280	Min	1,570	Min	1,190
N	3	N	7	N	3	N	103

Table 2. Cranial capacity in ml.

The occipito-cerebellar projection, which is so informative for most ancient fossil hominids, is not available for *Homo neanderthalensis* and *Homo sapiens* samples because of high vari-

ation coefficients. A great difference observed between both Spy hominids is the result of transverse sinuses protruding on Spy 1. Spy 10 is in *Homo neanderthalensis* variation.

An analysis of the sagittal chord of each cerebral lobe (frontal = CFR, parietal = CPA and occipital = COC) shows that the smallest is the parietal chord on all fossil hominids, with great variation coefficient in Preneandertals and *Homo neanderthalensis*, which is decreasing on anatomically modern *Homo sapiens*. Only extant *Homo sapiens* exhibits a shorter occipital chord with weak variation coefficient which is the expression of stability of this character.

Principal components analysis (2D)

Principal components analysis was applied to the endocast variables where the two first components reach 69.8 % of total variance. According to the first component (45.4 % of total variance) the specimens' position is the result of a strong weighting of the following variables: LME, HGQE, CPA and COC (ST4). Specimens

projecting on the positive side of PC1 have longer endocasts with high HGQE, longer occipital chords and short parietal sagittal chord; the three taxonomic groups are distinguished along the axis (SF6). The second component (24.4 % of total variance) is clearly related to the development of parietal lobes area (CPA), in relation to the reduction of the occipital one (COC). The low values of total or partial heights on Neandertals is best emphasised in PC2-PC3 (SF7). On the second component, the distinction between Neandertal specimens and *Homo sapiens* is very clearly demonstrated. The increasing of total and partial heights is in close relation with the development of parietal sagittal border and parietal area development. The third component (14.7 % of total variance) differentiates the hominid sample essentially with maximal endocranial breadth (WME), with that one measured to parietal lobes (WBE), and to frontal ones

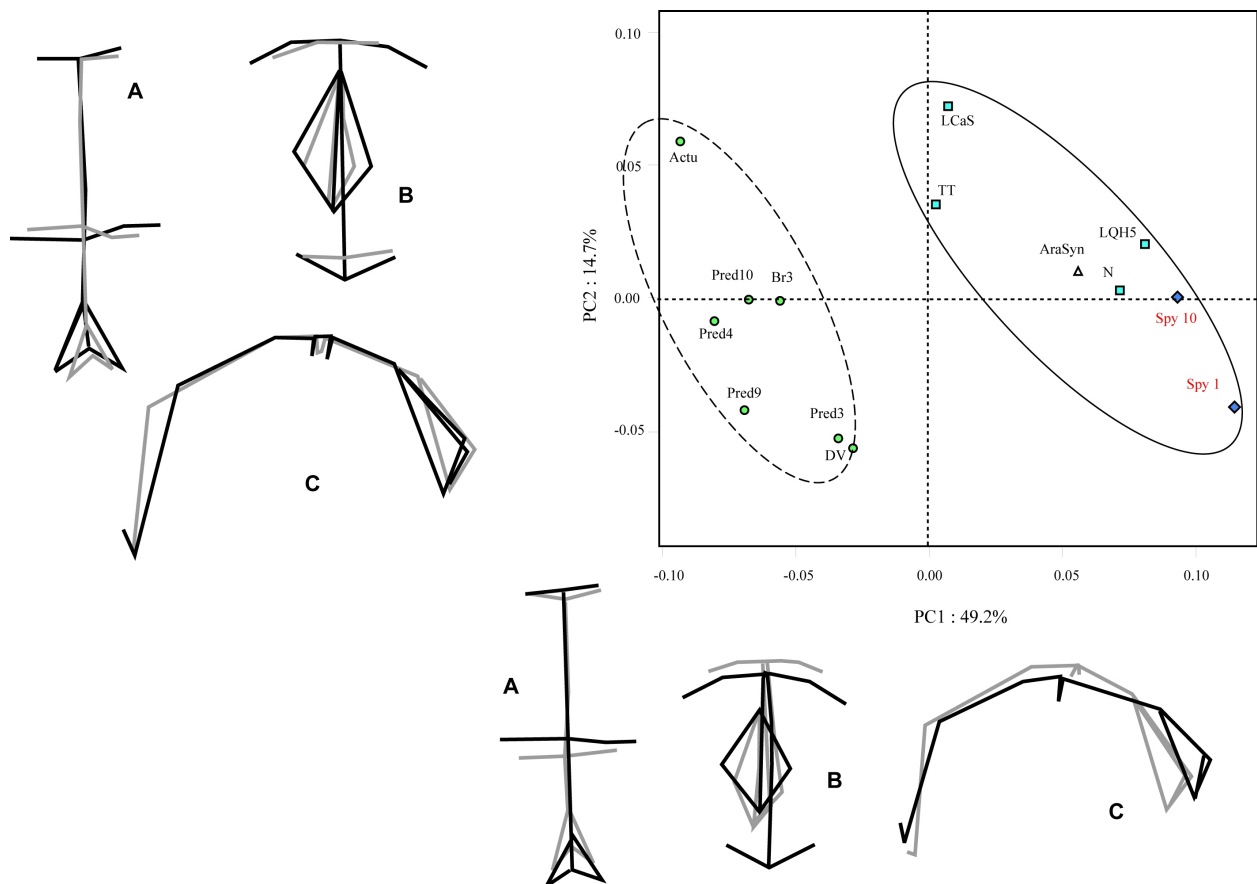


Figure 3. A Analysis: PCA scores with 14 variables and 14 specimens (superior (A), frontal (B) and lateral (C) views).

at Broca's cap area (WCBE), and also, but with lighter weight, with the frontal and occipital sagittal lobes borders (CFR, COC).

Morphometrical analysis (3D)

Two Procrustes superpositions have been done, the first one (A) which considers x, y, z coordinates of 14 lateral and sagittal landmarks for 14 fossil hominids (Figure 3), the second one (B), with 14 left lateral landmarks for 13 specimens (Figure 4). These two analyses are chosen because of the preservation of fossil specimens especially from Spy. By using Procrustes superposition, size differences and non-informative parameters are deleted. New data, called Procrustes "residuals" are generated. These in turn are re-dimensioned by principal components analysis (PCA) to concentrate a maximum of variance in accordance with first components and be free from 7 lost by superposition (Baylac, 1996).

Multivariate covariance analysis (MANCOVA) and multivariate regressions are also performed on components considering size and taxonomic attribution in order to test effects and interaction of these variables. Along the PCA axes, or according to the size, visualisation of the deformations is calculated by multivariate regressions. Thus, observed theoretical specimens can be observed situated in each extremity of axis: the projection of specimens to smallest values are in grey shading, and those ones to the greater values are shaded in black.

(A) Analysis: 14 specimens, 14 landmarks (sagittal and lateral)

According to the first analysis (A, Figure 3), fossil hominids tend to remain grouped with their taxonomic attribution. The endocasts from Spy are associated with classical Neanderthals as La Quina 5 and Neandertal 1. The shape

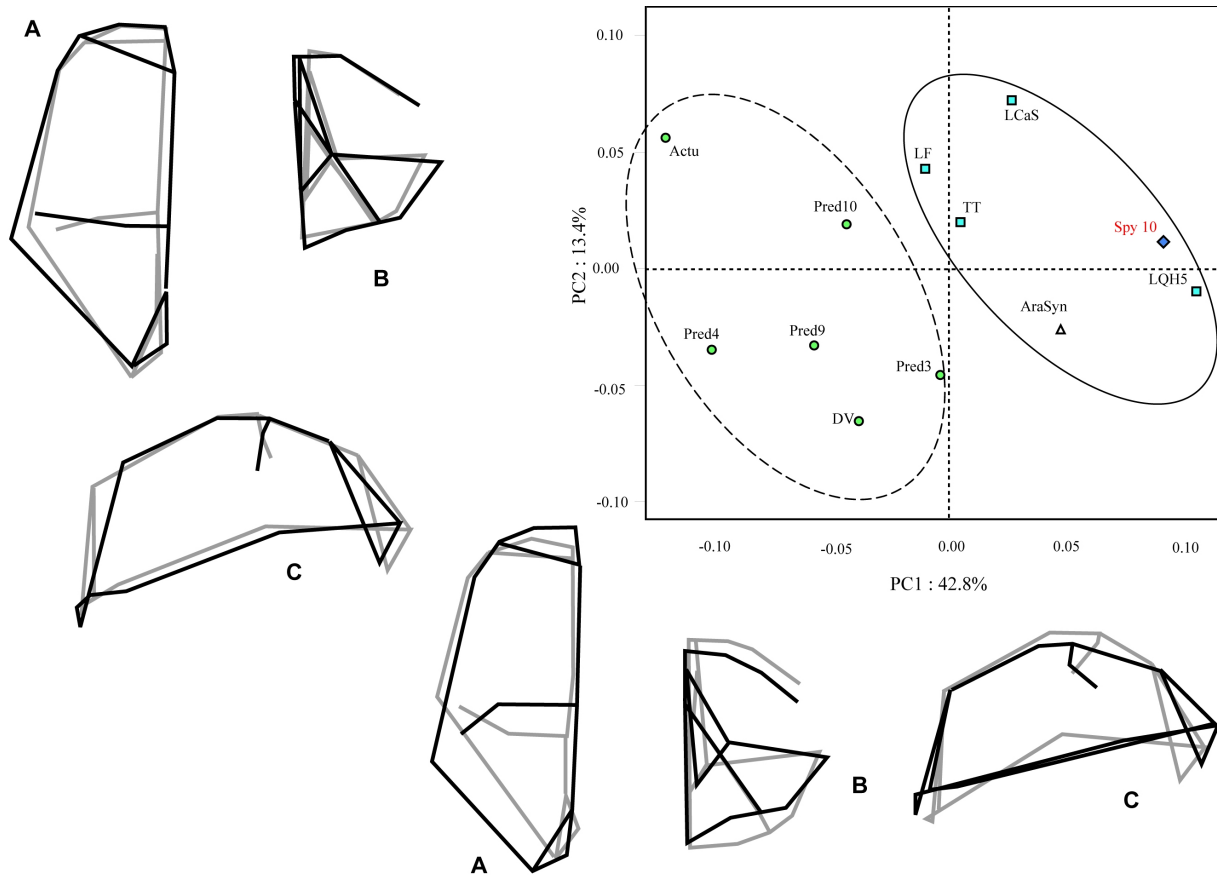


Figure 4. B Analysis: PCA scores with 14 variables and 13 specimens (Left superior (A), frontal (B) and lateral (C) views).

of the Neandertals endocasts is longer, lower, broader and less flexed than those of Upper Palaeolithic humans. In fact, the first graph, in superior view, shows the sagittal axis along the interhemispheric fissure between the encephalic rostrum and confluence sinuses, which seems longer simply because it is flatter. The breadths between the lateral points in the occipital region and the encephalic rostrum are similar, in contrast to the first parietal convolution breadth which is extending. This last character is confirmed in the frontal view with a lower position; the encephalic rostrum shape is significant with lateral points placed higher, showing a small protrusion of the first frontal convolution compared to Palaeolithic fossil hominids which constitute a line without angulation. The third graph, corresponding to a lateral view, confirms these observations, with the anterior and posterior encephalic Neandertal points externally placed, and joined to the superior part internally placed, compared to the *sapiens* group. This emphasises the elongated and lower endocranial shape on the Neandertals. From the results of the first MANCOVA A (ST5), done in relation with size, taxonomic attribution and their interaction, we can assess the existence of size differences as being statistically significant between and within taxonomic groups, when lateral and sagittal landmarks are uniformly placed.

(B) Analysis: 13 specimens, 14 landmarks (sagittal and left lateral)

According to Analysis B (Figure 4), fossil hominids are again grouped within their taxonomic attribution. Neandertal hominids are grouped in the superior right quarter. Spy 10 exhibits very strong morphological affinities with the Neandertal 1 and La Quina 5 specimens. Visualisation of endocranial shape confirms a shortening outline between *Homo neanderthalensis* and *Homo sapiens* with regard to the elevation of the superior part of the brain. The posterior position of the base of the first parietal convolution is observed on Neandertal endocasts. This morphological endocranial character is observed on the third part of the graph. The posterior rounding of the frontal lobes with anterior rounding of the occipital lobes is clearly visualised. From the results of the second MANCOVA B (ST5), of the two first principal components in relation with size, taxonomic attribution and their interaction, we can assess the

existence of size differences as statistically significant between and within taxonomic groups, which only considered the antero-posterior data concerning the left hemisphere.

DISCUSSION

The morphological and morphometrical features of Spy's endocasts are discussed and compared with some Preneandertals, *Homo neanderthalensis*, and *Homo sapiens* specimens in order to provide endocranial characterisation of both specimens, improve the definition of Neandertal endocranial autapomorphies, and emphasise the differences between *Homo neanderthalensis* and *Homo sapiens*.

Concerning vascularisation, the sphenoparietal sinus has been observed on both Spy hominids and on all studied *Homo neanderthalensis* with strongly marked relief, always situated on the precentral convolution. This sinus, really discrete on Swanscombe 1, is more marked on Ehringsdorf 9 and has not been observed on the *Homo sapiens* samples. This autapomorphy is clearly present in *Homo neanderthalensis* lineage, and clearly different from that of the *Homo sapiens* samples. This common presence of a sphenoparietal sinus has already been proposed as an autapomorphic trait by Gracia (1991), Grimaud-Hervé (1991), Saban (1995), Arsuaga *et al.* (1997) and Bruner (2003).

The superior sagittal sinus travels to the right transverse sinus in 62 % of the time in *Homo neanderthalensis* (Spy 1, Teshik-Tash 1, Gibraltar 1, La Quina 5, La Ferrassie 1 and Saccopastore 1 (according to Bruner & Manzi, 2008) and in 80 % within extant modern humans, strongly suggesting that the left hemisphere was more developed on these fossil hominids. This aspect of asymmetry is observed on all studied specimens.

The middle meningeal system observed on the Spy endocasts is very poor, with different patterns according to the side of the brain. The anterior set is a little more developed on the right hemisphere on Spy 10, while the posterior set has a small predominance on the left and right sides of Spy 1. Nevertheless, these

differences are weakly marked and the two branches are nearly equivalent, with the obelic branch coming from the lambdatic one. The principal vessels are strongly marked with considerable relief, and with very scarce ramifications and almost no anastomoses. In the *Homo neanderthalensis* sample, no trend appears in the development of the middle meningeal branches. They are nearly equivalent on both Spy hominids, Le Moustier 1, Neandertal 1, the left hemisphere of La Chapelle-aux-Saints 1, Saccopastore 1 (according to Bruner & Manzi, 2008) and Krapina 6 (Bruner *et al.*, 2006), and the right hemisphere of Gibraltar 1. The posterior branch is more developed on Krapina 3 (Bruner *et al.*, 2006), and the anterior branch is predominant on Teshik-Tash 1, La Quina 5, La Ferrassie 1, the left hemisphere of Gibraltar 2 and the right one of La Chapelle-aux-Saints 1.

Homo neanderthalensis does not exhibit any clearly defined trend for this feature or the development of the middle meningeal system being more ramified on one or the other hemisphere. It clearly appears to be a regression of complexity of middle meningeal pattern from Preneandertals such as Arago 47, Swanscombe 1, Reilingen 1, Biache-Saint-Vaast 1 and also Krapina 21 (Bruner *et al.*, 2003) to *Homo neanderthalensis*. The observed pattern is totally different on *Homo sapiens* endocasts with very numerous ramifications, which constitute anastomoses suggesting that the vascular system covers all the posterior frontal and parietal endocranial surface with dense squaring. Most of these exhibit a predominant anterior vascular set compared to the posterior one. While the general orientation of this pattern was nearly vertical on *Homo neanderthalensis*, it is definitely posteriorly oriented on *Homo sapiens*.

A comparative analysis of the brain shows a short and broad encephalic rostrum on all *Homo neanderthalensis* specimens. The difference between left and right first frontal convolution breadths cannot be observed on Spy. The right one is larger on Le Moustier 1, Neandertal 1, La Chapelle-aux-Saints 1 and Saccopastore 1 according to Bruner & Manzi (2008), and the left one is more developed on Arago 21 and Teshik-Tash 1, while equivalence is observed on both Gibraltar specimens, thus either trend is observed, the same for *Homo sapiens* samples. Anteriorly, a deep and

narrow interhemispheric fissure is observed in increasing order on Teshik-Tash 1, La Ferrassie 1, La Chapelle-aux-Saints 1, Spy 1, Neandertal 1 and Spy 10 which exhibits the largest depression.

On all *Homo neanderthalensis*, Broca's area exhibits depression from second inferior frontal sulcus. Unfortunately, comparison between left and right is not possible on Spy's hominids, but it is more developed on the right lobe of La Ferrassie 1, and on the left for all other specimens as observed on *Homo sapiens* in 70 % (16 % right and 12 % equivalence). The maximal frontal breadth is localised on the posterior region of Broca's areas.

The lateral sulcus is apparent on the Spy specimens which show a nearly horizontal and rectilinear course. The intensity of the depression is deep on La Chapelle-aux-Saints 1, and decreases on Neandertal 1, La Quina 5, Teshik-Tash 1, Spy 10, Spy 1, Le Moustier 1 and La Ferrassie 1 in this order.

Spy 1 and 10, as other *Homo neanderthalensis*, exhibit an intersection between the central sulcus and the sagittal border, situated at 2/5th of the anterior parietal chord, which is systematically observed, as the near equivalence of precentral and postcentral convolution breadths. The first parietal convolution is always very wide anteriorly with a strongly convex relief which decreases posteriorly.

The supramarginal gyrus limits are always more depressed along the lateral sulcus than the interparietal one, and it is always very distinct on all Neandertal specimens, showing an oval shape elongated in height, in relation to the transversal widening of the skull (Grimaud-Hervé, 2004a). The base of the angular lobule is distinct from the supramarginal one whose relief is less pronounced. This region is the position of maximal endocranial breadth, at the level of third temporal convolutions on Spy 10 and studied *Homo neanderthalensis*. It is different from the *Homo sapiens* samples with the upper localisation at the base of the supramarginal lobule.

The temporal lobes show significant height on *Homo neanderthalensis*. The occipital lobes, joined on Spy 10, are separated by a sagittal sinus breadth of 5 mm on Teshik-Tash 1 or

Spy 1, which increases on La Quina 5, La Chapelle-aux-Saints 1, and La Ferrassie 1 to 10 mm. These are always situated under the parietal lobes, that is to say in an anterior position but less marked than on the *Homo sapiens* samples.

In posterior view, the transversal endocranial outline is similar to that of the skull, with a low position of maximal breadth to angular lobules which gives a clear subcircular profile called “en bombe”.

In superior view, the asymmetry is clearly apparent on both Spy specimens (Holloway, 1981) and all *Homo neanderthalensis* specimens with right frontal and left occipital petalia pattern, defined by Holloway & De Lacoste-Lareymondie (1982) and Holloway *et al.* (2004), which include both the anterior-posterior and medial-lateral petalias, less marked for the anterior region on Spy 10 than Spy 1. This asymmetry is weakly marked on Saccopastore 1 (Bruner & Manzi, 2008), La Quina 5, Le Moustier 1, La Ferrassie 1, Neandertal 1 and Teshik-Tash 1. As noted by LeMay (1976, 1977), Galaburda *et al.* (1978), Holloway (1985) and Gilissen (2001), this pattern is classic modern *Homo* petalial pattern. A clear asymmetry on the width appears on Spy 10 with an enlarged left hemisphere, and this difference is observed on other Neandertals with a smaller difference than on *Homo sapiens* samples. Unlike height above maximal length which is higher on right hemisphere on Spy 10, no clear trend appears in *Homo neanderthalensis* and *Homo sapiens* samples.

In lateral view, the outline is elongated and lower than in *Homo sapiens*, but also regularly convex from frontal to occipital lobes, without depression to parieto-occipital lobes on both Spy 1 and 10, Gibraltar 1, Le Moustier 1 or La Chapelle-aux-Saints 1. Slight depression to this boundary has been observed on Saccopastore 1 (Bruner & Manzi, 2008), Teshik-Tash 1, Neandertal 1, La Ferrassie 1 and La Quina 5. The cerebellar lobes are mainly situated under parietal and temporal lobes which is a derived character compared to many anthropoid endocasts (but also compared with Asiatic *Homo erectus*, which exhibit occipital lobes in prolongation on parietal and temporal ones with cerebellar ones situated under the first ones).

Brain volume increases from Preneandertals to *Homo neanderthalensis*. The values of *Homo neanderthalensis* are similar to those from extant *Homo sapiens*, but somewhat lower than modern *Homo sapiens*, based on 3 specimens. It confirms the results obtained by Bruner *et al.* (2003) who conclude that “Neanderthals and modern humans reached comparable brain volumes, probably following independent structural trajectories” (but see Holloway, 1985; Holloway *et al.*, 2004 for slightly different values).

The results of traditional and more modern morphometrical analyses are convergent, showing enlargement of all the transversal diameters which in turn emphasises the frontal and parietal lobes’ expansion, which is also apparent on the encephalic rostrum shape between *Homo neanderthalensis* and *Homo sapiens* samples. These changes are in relationship to the increase of heights and the shortening of length, which is demonstrated by the rounding of the anterior and posterior cerebral regions which are clearly nearer each other on 3D analysis.

CONCLUSION

Concerning vascularisation, the presence of the speno-parietal sinus should be considered as an autapomorphy of *Homo neanderthalensis*. This anatomical character is not observed on anatomically modern *Homo sapiens*, extant *Homo sapiens* or Preneandertals where its imprint is very weak.

The middle meningeal pattern observed on the Spy endocasts and other *Homo neanderthalensis* is characterised by a truly reduced vascular system which might also be considered as an autapomorphy. The acquisition of this morphological feature is clearly apparent from the most ancient considered Preneandertals which exhibit developed middle meningeal system with ramified vessels which constitutes numerous anastomoses. This vascular pattern is less developed on the more recent endocast of Ehringsdorf 9 and this reduction is increasing through time to be reduced to a minimum vascular system on classical *Homo neanderthalensis*. The same phenomenon is observed on the *Homo erectus* lineage between the Kabuh layers’ hominids from Sangiran and

those which are more recent from Ngandong or Sambungmacan (Grimaud-Hervé, 2004b). The common feature between these two completely different populations is an environment with a restricted area. This pattern is totally different in *Homo sapiens* samples where the ramifications and anastomoses are covering the posterior frontal and the entire parietal lobes surface.

The encephalic rostrum clearly exhibits a regression on the Neandertal lineage between Preneandertals and *Homo neanderthalensis* which has to be considered as plesiomorphic (Grimaud-Hervé, 2005). This anatomical formation is still enlarged on *Homo sapiens* samples. Broca's area is more protruding, with more developed and convex relief on the left frontal lobe in the majority of *Homo neanderthalensis* and most of *Homo sapiens* (70 %). The maximal endocranial frontal breadth is localised in this anatomical region. The lateral sulcus is rectilinear and horizontally oriented on *Homo sapiens* samples, but it is weakly linear on *Homo neanderthalensis* and clearly incurved on Preneandertals. No trend concerning the lateral sulcus impression depth on preferential hemisphere appears on *Homo neanderthalensis*. It is more impressed on the left hemisphere in *Homo sapiens* samples. The junction between the central sulcus and the longitudinal fissure is situated more anteriorly in relation to endobregma and endolambda on Preneandertals than on *Homo neanderthalensis* and *Homo sapiens* samples. The trend of enlargement of the postcentral convolution appears between the Preneandertals (which exhibit larger precentral convolution) and *Homo neanderthalensis* where these breadths are nearly equivalent. These are also equal on *Homo sapiens* samples. The shape of the supramarginal gyrus can be considered as a *Homo neanderthalensis* autapomorphy with clearly defined relief and oval form elongated in height probably in relation with inferior transversal widening of the skull. This anatomical formation is less individualised on Preneandertals with a rounded shape than in *Homo sapiens*. Maximal endocranial breadth is localised at this level; it is placed

in an inferior position on angular gyrus in the Neandertal sample. These parietal morphological and metrical characteristics are clearly demonstrated on Spy 10. More noticeable difference concerns transversal shape in the posterior view which is clearly enlarged at the base and gives a subcircular profile. It is very different from that observed on Preneandertals, which is pentagonal with lateral walls of the parietal lobes convergent to the top, or on *Homo sapiens* where these parietal regions are parallel. The occipital and cerebral lobes position is derived, almost similar to *Homo sapiens*, contrary to the sagittal convexity outline which is clearly less elevated on *Homo neanderthalensis*.

An asymmetrical brain with right frontal and left occipital petalia pattern is clearly apparent on all *Homo neanderthalensis*; it is also present in 84 % of the extant *Homo sapiens* sample.

The encephalic and vascular changes observed on the endocasts studied are going gradually within the Neandertal's lineage from Preneandertals to *Homo neanderthalensis*. Morphological and morphometrical characters noticed on *Homo sapiens* appear to be definitively different. Their positions are particularly clearly expressed on 3D analysis where these lineages are separated on both directions which confirms different allometric trajectories.

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