CHAPTER XXIV-4

THE SPY BONY LABYRINTHS – ADDITIONAL RESULTS

Isabelle CREVECOEUR, Hélène ROUGIER & Linda BOUCHNEB

Abstract

Computer-assisted techniques allow us to access the innermost parts of bones and, particularly the inner ear in the petrous temporal bone. This structure is of significant interest in anthropology since it is related to locomotor behaviour and basi-cranial morphology. Moreover, its morphology has a strong genetic component. Therefore, this structure provides a strong basis for assessing phylogenetic relationships between hominid groups.

The Spy 1 skullcap includes two well-preserved petrous portions enclosing complete left and right bony labyrinths. The Spy 10 right petrous pyramid is broken off antero-medially, and the cochlea is missing, but the left inner ear is intact.

This chapter aims to present a descriptive and comparative study of the Spy bony labyrinths. The Spy specimens are compared to a wide sample of extant humans, European and African Upper Palaeolithic modern humans, early anatomically modern humans from Qafzeh and Skhul, and 23 Western Asian and European Neandertals (including four fossils from early stages of the lineage).

Univariate statistical analyses of identified labyrinthine traits that characterise Neandertals show some overlap between modern human and Neandertal variation ranges. Multivariate analyses allow us to go further in the interpretation of the results. We used Discriminant Analysis to determine the posterior probability that the Spy specimens belonged to each pre-defined comparative group. The results show a clear distinction between past and present modern human samples as compared to the Neandertal pattern. Both Spy bony labyrinths significantly align with the latter.

INTRODUCTION

Among many human remains, the excavations at Spy in 1886 yielded two Neandertal partial crania (Fraipont & Lohest, 1887). Spy 1 and Spy 10 represent the Neandertal individuals Spy I and Spy II, respectively (see Rougier *et al.*, this volume: chapter XIX), and they have been dated to ca. 36,000 ^{14}C BP (Semal *et al.*, volume 1: chapter XVI). As such, they represent important individuals in the stormy debate over the relationships that Neandertals and early modern humans may have had in Europe at the time of the Middle to Upper Palaeolithic transition. Defining their anatomical characteristics is thus of great interest. The crania Spy 1 and Spy 10 include well-preserved petrosal bones enclosing almost complete right and left bony labyrinths. The interest of this structure in anthropology lies in its correlation with locomotor behaviour and basi-cranial morphology, and also with its strong genetic component (Spoor *et al.*, 1994; Spoor, 2003).

The bony labyrinth reaches its adult size between the 17th and 19th weeks of gestation (Jeffery & Spoor, 2004). Since individual post-natal influences are absent or minimal, this structure provides an important potential source for assessing phylogenetic affinities between hominin groups. Hublin *et al.* (1996) investigated phylogenetic variation between the immature temporal bone from Arcy-sur-Cure, probably associated with a Châtelperronian layer, and other *Homo* taxa. They identified a number of traits that distinguish Neandertals from both *Homo erectus* and modern humans, although there is a degree of overlap in the morphological variation (Ponce de León & Zollikofer, 1999; Spoor *et al.*, 2003).

Since the initial publication of articles dealing with the phylogenetic importance of the primate bony labyrinth (Spoor, 1993; Spoor & Zonneveld, 1994), the inner ears of numerous fossil specimens have been studied in detail (e.g. Thompson & Illerhaus, 1998; Spoor *et al.*, 2002a, 2002b; Rook *et al.*, 2004; Viola *et al.*, 2004; Urquiza *et al.*, 2005).

Although several dimensions of the Spy bony labyrinths have already been published by Spoor *et al.* (2003), there has so far been no specific description of their morphometrical characteristics. The aim of this chapter then is to provide a complete descriptive and comparative study of the two Spy bony labyrinths, and to assess their affinities with the Late Pleistocene human groups and a sample of recent modern humans.

MATERIALS AND METHODS

The Spy 1 and Spy 10 temporal bones include well-preserved petrosal bones, with only their apices missing. They enclose complete right and left bony labyrinths except for the right one of Spy 10. The entire cochlea is broken off in the latter (Figure 1). On Spy 1, both cochleae are partially matrix-filled. The labyrinths of Spy 10 are matrix-free.

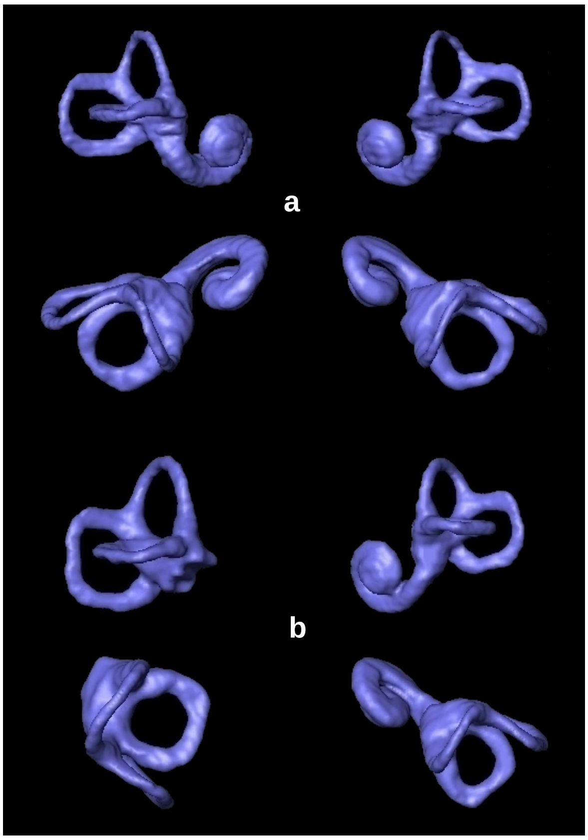

Figure 1. 3-D reconstruction of the right and left bony labyrinths of Spy 1 (a) and Spy 10 (b) in lateral and superior views.

The bony labyrinths of Spy were scanned using a Siemens Volume Zoom CT scanner. The scans were made in the axial plane, parallel to the lateral semicircular canal, using a slice spacing of 0.2 mm and a pixel size of 0.212891 mm for Spy 1 and 0.199219 mm for Spy 10.

In order to avoid overflow of the CT number scale, we used a wide window for the evaluation of the images. The four Spy labyrinths were investigated, and the measurements of the left and right sides were averaged. In order to be consistent with a previously published reference work (Spoor *et al.*, 2003), all linear and angular measurements of the labyrinth were taken from planar reformatted images in the transverse and sagittal planes according to the CT-morphometric method described in Spoor (1993) and Spoor & Zonneveld (1995, 1998). The CT thresholding protocol used for the linear measurements is the half-maximum height method (Ullrich *et al.*, 1980; Coleman & Colbert, 2007). All of the measurements were made using ImageJ (2005), and volumes were segmented and reconstructed with AMIRA 3.1 (2002) software (Figure 1, Table 1).

The Spy labyrinths were compared to a sample from Western Asian and European Neandertal specimens (NEAND, n = 23), including four from early stages of the lineage, Middle Palaeolithic modern humans from Qafzeh and Skhul (MPMH, n = 11), early and late Upper Palaeolithic modern humans (UPMH, n = 8) and extant modern humans (EMH, n = 134) (ST1). They were scanned and measured following the same technique as for the Spy specimens. The extant human sample included two main groups: the database published by Spoor (1993) and a sample of 100 modern humans collected by one of the current authors (L.B.) at the Erasmus Hospital of Brussels (Belgium). Adjusted Z-Scores (Maureille *et al.*, 2001) were computed to compare the measurements of Spy to the means and standard deviations of each of the comparative groups (Table 1). This method, which is based on the Student's t-test, has the advantage of taking into account the size of the comparative groups and maximises the range of variation for small-sized samples.

	Spy 1	*Spy 10*	*NEAND*			*MPMH*			*UPMH*			*EMH*		
			M	*Sd*	*N*	*M*	*Sd*	*N*	*M*	*Sd*	*N*	*M*	*Sd*	*N*
ASCw	6.55	5.78	6.20	0.50	22	7.06	0.50	11	7.22	0.38	7	6.82	0.42	134
LSCh	5.48	4.88	4.90	0.43	22	4.31	0.51	11	4.81	0.20	6	4.49	0.46	134
ASC-R	3.21	2.85	3.00	0.20	23	3.32	0.20	11	3.33	0.21	8	3.25	0.20	134
PSC-R	3.18	2.93	2.81	0.21	23	3.03	0.16	11	3.04	0.30	8	3.17	0.26	134
LSC-R	2.75	2.50	2.56	0.18	23	2.37	0.18	11	2.54	0.22	8	2.34	0.20	134
CO-R	2.25	2.19	2.25	0.15	21	2.45	0.12	11	2.36	0.11	7	2.26	0.11	134
SLI	52.08	58.24	62.39	8.01	23	53.01	6.22	11	41.30	8.87	8	50.70	7.06	134
ASCh/w	95.94	97.40	93.17	5.07	23	88.50	6.90	11	87.27	5.74	7	90.50	4.50	134
PSCh/w	106.03	102.59	100.23	10.73	23	99.67	7.87	11	107.41	8.13	7	104.98	7.22	134
LSCh/w	99.04	95.14	91.95	7.52	23	83.35	9.65	11	92.59	5.74	7	92.08	6.21	134
COh/w	125.36	125.64	132.91	13.37	21	129.72	7.71	11	141.54	8.70	7	134.06	8.07	134
ASC %R	35.08	34.44	35.80	1.28	23	38.08	1.30	11	37.46	1.38	8	37.10	1.16	134
PSC %R	34.79	35.33	33.61	1.75	23	34.74	1.61	11	33.99	1.42	8	36.16	1.63	134
LSC %R	30.13	30.22	30.57	1.31	23	27.19	1.59	11	28.43	0.95	8	26.74	1.72	134
ASCtor	18.32	14.72	22.91	5.92	22	14.92	5.56	11	13.61	2.50	7	16.14	4.48	134
PSCtor	-10.91	-15.89	-10.84	5.51	22	-4.85	6.33	10	-13.30	5.37	7	-10.24	4.75	134
LSCtor	3.83	4.09	1.94	5.05	22	1.00	4.02	11	3.52	3.29	7	1.97	3.99	134
APA<LSCm	41.81	45.20	44.53	5.40	22	39.17	5.76	11	35.18	3.56	6	40.35	4.44	134
LSCm<FC3	85.79	81.58	85.85	8.98	19	76.86	7.47	6	73.17	5.39	7	72.26	7.67	129
VC<LSCm	146.85	141.21	148.74	7.76	21	153.83	5.38	11	154.91	7.75	7	150.36	5.09	134
LSCm<PPp	62.00	68.50	68.39	8.51	15	60.53	5.09	5	57.50	12.06	6	59.87	8.65	120

	*Adjusted Z-Score**							
	Spy 1				*Spy 10*			
	NEAND	*MPMH*	*UPMH*	*EMH*	*NEAND*	*MPMH*	*UPMH*	*EMH*
ASCw	0.336	-0.461	-0.726	-0.325	-0.408	**-1.150**	**-1.553**	**-1.244**
LSCh	0.661	**1.035**	**1.297**	**1.098**	-0.016	0.506	0.134	0.434
ASC-R	0.520	-0.262	-0.255	-0.100	-0.355	**-1.061**	-0.978	-0.982
PSC-R	0.855	0.415	0.204	0.025	0.263	-0.284	-0.158	-0.477
LSC-R	0.525	0.957	0.410	**1.038**	-0.147	0.326	-0.073	0.407
CO-R	-0.011	-0.739	-0.390	-0.062	-0.194	-0.947	-0.595	-0.325
SLI	-0.620	-0.067	0.514	0.099	-0.250	0.377	0.807	0.540
ASCh/w	0.264	0.480	0.617	0.607	0.403	0.575	0.721	0.770
PSCh/w	0.261	0.363	-0.069	0.074	0.106	0.166	-0.243	-0.168
LSCh/w	0.455	0.730	0.459	0.566	0.204	0.548	0.181	0.248
COh/w	-0.271	-0.254	-0.760	-0.546	-0.261	-0.237	-0.747	-0.528
ASC %R	-0.272	**-1.035**	-0.728	-0.882	-0.512	**-1.255**	-0.923	**-1.159**
PSC %R	0.326	0.015	0.240	-0.426	0.476	0.167	0.402	-0.257
LSC %R	-0.161	0.829	0.758	0.997	-0.127	0.855	0.800	**1.024**
ASCtor	-0.374	0.274	0.768	0.245	-0.666	-0.017	0.180	-0.161
PSCtor	-0.006	-0.424	0.182	-0.071	-0.441	-0.772	-0.197	-0.601
LSCtor	0.180	0.315	0.038	0.235	0.205	0.345	0.071	0.269
APA<LSCm	-0.242	0.206	0.725	0.166	0.060	0.469	**1.095**	0.551
LSCm<FC3	-0.003	0.465	0.957	0.892	-0.226	0.246	0.638	0.615
VC<LSCm	-0.117	-0.582	-0.425	-0.349	-0.465	**-1.053**	-0.723	-0.909
LSCm<PPp	-0.350	0.104	0.145	0.124	0.006	0.565	0.355	0.504

* Significant differences ($p < 0.05$) between Spy values and the group means are indicated in bold.

Table 1. Bony labyrinth measurements of Spy 1 and Spy 10.
Definitions and abbreviations of all measurements are derived from Spoor & Zonneveld (1995).
The mean (M), standard deviation (Sd) and number of specimens (N) of each comparative sample are shown.

In order to characterise the affinities of Spy 1 and 10, we performed a Discriminant Analysis to compute a function that best discriminates specimens among predefined groups. The posterior probability of belonging to each comparative group was then assessed based on the squared Mahalanobis distances to the group's centroids. We used Statistica (2002) and SPSS (2003) to perform these analyses.

UNI- AND BIVARIATE RESULTS

Absolute dimensions of the semicircular canals

The dimensions of the anterior canal of Spy 1 (ASC-R) are included in the variability of the comparative groups. Spy 10's anterior canal radius of curvature lies at the inferior limit of the variation range of all of the comparative groups except for the Neandertals. This is related to the width of the canal (ASCw), whose value is excluded from the variability of the modern human groups.

As for the posterior canals, the curvature radius (PSC-R) of both Spy 1 and Spy 10 is within the variation range of all of the comparative groups.

Regarding the characteristics of the Neandertal vertical semicircular canals (the anterior and posterior canals), Hublin *et al.* (1996) noticed their low values as compared to modern humans. The results above show that this trait is present only in the anterior canal of Spy 10.

The curvature radius of Spy 1's lateral canal (LSC-R) is above that of the extant human range and nearly corresponds to the upper limit of the MPMH range. It is related to its height (LSCh), which lies outside of the upper limit of all of the modern human samples variation. The lateral canal curvature radius of Spy 10 is included in all of the comparative samples variation.

Shape of the canals

Spoor *et al.* (2003) showed that the height / width proportions of the anterior canal (ASCh/w) of Neandertals are different from those of modern humans, with a less circular shape. This pattern is found on Spy 1, but it is very attenuated, and it is clearer on Spy 10, with the width of its anterior canal (ASCw) being excluded from the ranges of the modern human groups and a height / width ratio in the upper half of their ranges.

The shape of the lateral semicircular canal of Spy 1 is almost circular and stands in the upper part of the variation of the modern human comparative samples; Spy 10 does not stand out of any of the comparative sample ranges for this measurement. The shapes of the posterior semicircular canals of Spy 1 and Spy 10 are not noticeable as compared with any of the samples.

Regarding the torsion of the various canals (ASCtor, PSCtor, LSCtor), Spy 1 and Spy 10 show angles that are included in all of the modern human comparative groups. Moreover, the torsion angle of their anterior canal (ASCtor) is closer to the mean of the extant modern humans than to the Neandertal mean. The individuals from Spy lie in the lower half of the Neandertal range for this variable. A more pronounced torsion of the anterior canal had been noted among Neandertals by Spoor *et al*. (2003).

Relative proportions of the canals

Figure 2 shows a graphical representation of the relative proportions of the semicircular canals (ASC %R, PSC %R, LSC %R) in Spy 1 and Spy 10 as compared with the modern human and Neandertal patterns. Spy 1 and Spy 10 follow the derived Neandertal condition (Spoor *et al.*, 2003), namely, relatively smaller vertical canals and a larger lateral canal. This is illustrated by the relative values that are excluded from the range of some of the modern human comparative groups (Spy 1: ASC %R below the MPMH range, and LSC %R almost equal to the upper limit of the EMH range; Spy 10: ASC %R below the MPMH and EMH ranges, and LSC %R above the EMH range). Lastly, both vertical semicircular canals of Spy 1 and Spy 10 show similar proportions.

Cochlea

The dimensions (CO-R) and the shape (COh/w) of the Spy 1 and Spy 10 cochleae are within the inferior half of the variation range of the comparative samples (Table 1).

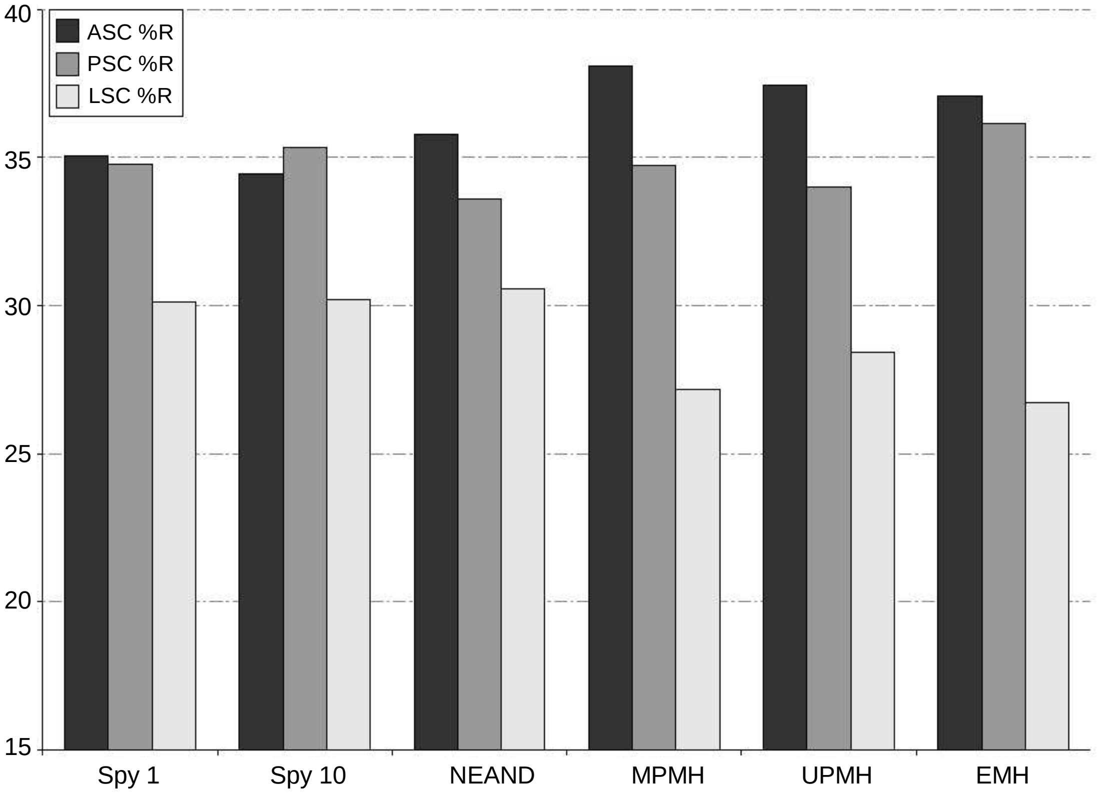

Figure 2. Graphic representation of the relative proportions of the semicircular canals of Spy 1, Spy 10, Neandertals (NEAND), Middle Palaeolithic modern humans (MPMH), Upper Palaeolithic modern humans (UPMH) and extant modern humans (EMH). Dark grey columns = ASC %R; grey columns = PSC %R; light grey columns = LSC %R.

Shape of the labyrinth

The sagittal labyrinthine index (SLI) of Spy 1 shows a low value as compared to the Neandertal variation, which means that its posterior semicircular canal is positioned more superiorly than the mean of this group. It is closer to the means of the Middle Palaeolithic and extant modern humans. As such, it does not show the low position characteristic of Neandertals. On another hand, Spy 10 shows the Neandertal pattern with a high index, closer to the Neandertal mean than to that of the modern human groups. The differences among the groups are not statistically significant; they show only tendencies, as shown by Spoor *et al.* (2003).

Regarding the correlation between the position of the posterior canal (SLI) and its size (PSC-R), Spy 1 follows the modern pattern with a moderately-sized posterior canal in a high position, whereas Spy 10 follows the Neandertal pattern, with a small canal in a low position (Figure 3). Neandertals are remarkable because they show an inverse correlation between the size and position of the posterior canal as compared to the one observed for fossil and extant hominoids (Spoor *et al.*, 2003). However, Figure 3 confirms the observations of Spoor *et al.* (2003) regarding the existence of an important overlap between the extant modern human and Neandertal distributions for uni- and bivariate dimensions.

Spy 1 possesses an angle between the ampullar line and the lateral canal (APA<LSCm) that is included in the variation range of all of the comparative groups. The inclination of the ampullar line is moderate as compared to the Neandertal mean, although it belongs to the upper half of the Upper Palaeolithic variation range. The characteristic of the UPMH having a low inclination fits the results of Spoor *et al.* (2003) and of Bouchneb & Crevecoeur (2009). The value of the angle for Spy 10 is similar to the Neandertal mean. Neandertals are characterised by a more pronounced inclination of the am-

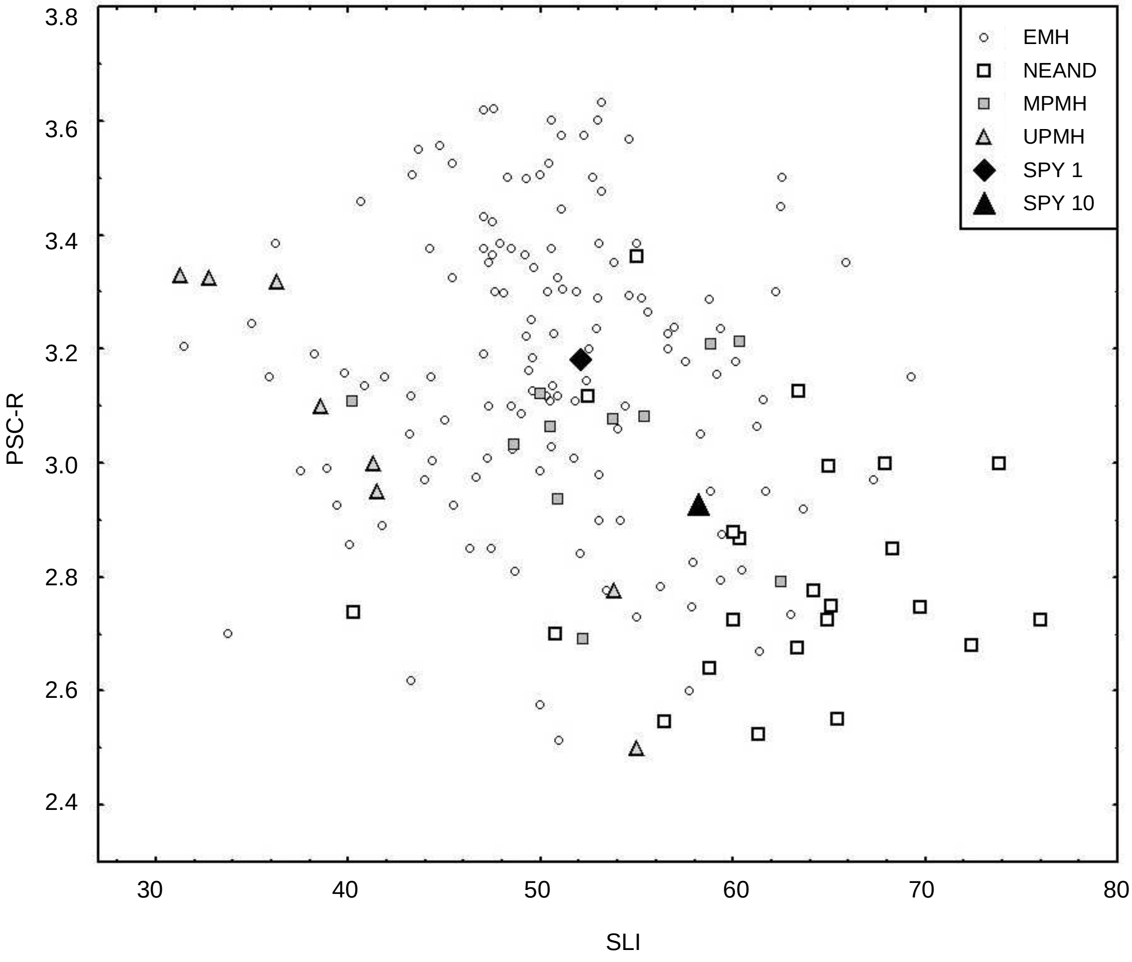

Figure 3. Bivariate plot of the curvature radius of the posterior canal (PSC-R) versus the sagittal labyrinthine index (SLI). Comparative group denominations are the same as in Figure 2.

pullar line with regard to the modern human comparative groups. The value of Spy 10 is excluded from the UPMH range.

The angle between the vestibulo-cochlear line and the lateral canal (VC<LSCm) is more closed on Spy 10 than on Spy 1, which corresponds to a cochlea in a more inferior position on the former rather than the latter. The value of Spy 10 lies close to the lower limit of the range of the modern groups, and it is even excluded from the variation range of the MPMH. The Neandertal mean is smaller than the modern human means but, among groups, differences are not statistically significant.

The angle between the lateral canal plane and the third part of the facial nerve canal (LSCm<FC3) of Spy 1 is identical to the Neandertal mean. Neandertals show a more vertical orientation of this part of the facial nerve canal as compared to modern humans. The value for Spy 1 is thus situated close to the upper limit of the variation range of the extant and UPMH groups. Regarding Spy 10, the angle is slightly smaller than the Neandertal mean and is included in the upper half of the modern human variation range.

The position of the lateral canal of Spy 1, as compared to the posterior petrosal surface (measured by the LSCm<PPp angle), is included in the variability of the comparison groups with an angle closer to the modern human means than to the Neandertal mean. Conversely, Spy 10 corresponds to the Neandertal mean, which accounts for a more open angle as compared to the modern human comparative groups.

MULTIVARIATE ANALYSIS

In order to determine the posterior probability that Spy 1 and Spy 10 belong to each of the comparative samples, we performed a Discriminant Analysis. This analysis was carried out on twenty-seven relative and absolute dimensions, among which eleven were selected by the stepwise method to discriminate among groups (LSC %R, LSCm<FC3, SLI, ASCw, LSCh, VC<LSCm, ASCtor, CO-R, PSCw, LSCtor, PSCtor). The selected variables express the dimensions and shape of the different areas of the labyrinth and are not strictly correlated. The result of the classification matrix and the posterior probabilities of Spy 1 and Spy 10 are shown in Table 2.

The percentages of accurate classification for the original (91.14 %) and cross-validated (83.50 %) grouped cases represent a very good validation of the *a priori* groupings. The Middle and Upper Palaeolithic modern human samples show a reduction of correct classifications for the cross-validated procedure due to the small number of specimens.

Spy 1 and Spy 10 have a significant posterior probability (respectively, p = 0.9810 and p = 0.9979) of belonging to the Neandertal group, and the latter shows the most robust grouping in cross-validation.

The multivariate analysis clearly shows the existence of a Neandertal pattern that is different from extant and fossil modern humans. The individuals from Spy unambiguously show this global pattern, and it is worth noting that the posterior probabilities that other Neandertals belong to their group are all between 0.98 and one, except for two individuals: Biache-Saint-Vaast 1 (p = 0.805) and La Ferrassie 3 (p = 0.655).

DISCUSSION AND CONCLUSIONS

Studies of the bony labyrinths of hominoids have emphasised the phylogenetic interest of this structure (e.g. Spoor & Zonneveld, 1995; Rook *et al.*, 2004). Research on the bony labyrinth within the genus *Homo* has highlighted the derived status of some characteristics in Neandertals (Hublin *et al.*, 1996), although there is a significant overlap with the variability of the other fossil and extant human groups (Spoor *et al.*, 2003).

The detailed study of the inner ear structures of the two adult Neandertals discovered at Spy brings new insight that complements observations of the internal and external morphologies of the Spy 1 and Spy 10 crania (*cf.* Balzeau, this volume: chapter XXIV-2; Grimaud-Hervé & Holloway, this volume: chapter XXIV-3; Rougier *et al.*, this volume: chapter XXIV-1).

Univariate analyses show that the Spy inner ears present some characteristics that have already been noted for Neandertals (Hublin *et al.*, 1996; Spoor *et al.*, 2003). On Spy 1, these are a lateral canal of significant height and radius that is proportionally large relative to the vertical canals, and a marked angulation between the planes defined by the lateral canal and the third part of the facial nerve canal. On the other hand, Spy 1 does not show the disposition characteristic of Neandertals with regard to the position and size of its posterior semicircular canal.

Spy 10 is remarkable as compared to modern humans because of its narrow and anteroposteriorly flattened anterior canal, its lateral canal, which is proportionally larger than the vertical canals, its posterior canal, which has a rather low position and is of moderate dimensions, and

	N	*Percentage of correct classification*		*Posterior probabilities*	
		Original grouped cases	*Cross-validated grouped cases**	*Spy 1*	*Spy 10*
NEAND	18	100.00	88.90	**0.9810**	**0.9979**
MPMH	5	100.00	60.00	0.0000	0.0000
UPMH	6	100.00	66.70	0.0004	0.0000
EMH	129	89.15	84.50	0.0187	0.0021
Total %	***158***	***91.14***	***83.50***	*1.0000*	*1.0000*

* In cross-validation, each case is classified by the functions derived from all cases other than that case.

Table 2. Classification matrix of the Discriminant Analysis on eleven variables.

the strong inclination of its ampullar line and its posterior petrosal surface as compared with the plane of the lateral semicircular canal.

These results show that the two individuals from Spy do not present the exact same pattern. Both possess Neandertal characteristics of the bony labyrinth, but they do not exhibit the same pattern of expression for these traits. Univariate analyses show some degree of overlap between the comparative groups for the whole set of variables. Expanding the comparative study by means of multivariate statistics, as suggested by Spoor *et al.* (2003), has allowed us to both define the affinities of the bony labyrinths of Spy 1 and Spy 10 and to emphasise the presence of a clear Neandertal pattern among all of the members of this group. Spy 1 and Spy 10 share this set of discriminant Neandertal features.

ACKNOWLEDGEMENTS

We are grateful to all of the curators and scientists who made original specimens available for this study: J.-J. Hublin from the Department of Human Evolution, Max Planck Institute (Leipzig), S. Louryan from the Erasmus Hospital (Brussels), B. Maureille from the UMR 5199 PACEA-A3P (Bordeaux), D. Grimaud-Hervé and H. de Lumley from the IPH (Paris), Y. Rak and B. Arensburg from the Tel Aviv University, E. Poty from the *Université de Liège*, M. Toussaint from the DGATLP, *Ministère de la Région Wallonne*, P. Semal from the Royal Belgian Institute of Natural Sciences (Brussels), P. Périn and C. Schwab from the *Musée des Antiquités Nationales* (St-Germain-en-Laye), P. Vermeersch and P. Van Peer from the *KULeuven*. We would like to deeply thank F. Spoor, who allowed us to use his extant human and fossil database and trained one of us (L.B.) on the morphometric CT-measurement method. In addition, we thank N. Jeffery for his calculator tool. This study has been supported in part by the *Projet Transition, volet Recherche Région Aquitaine (convention 20051403003AB)*, the Irene Levy Sala Care Archaeological Foundation, the GDR 2652 of the CNRS, the TNT project (The Neanderthal Tools, IST 6th framework), the Spy Action 1 project (Research project MO/36/012, Belgian Science Policy) and MARS (IST project I2/2F/212, Belgian Science Policy).

BIBLIOGRAPHY

AMIRA^{TM}, 2002. Amira 3.1. Zuse Institute Berlin (ZIB).

BOUCHNEB L. & CREVECOEUR I., 2009. The inner ear of Nazlet Khater 2 (Upper Paleolithic, Egypt). *Journal of Human Evolution*, **56** (3): 257-262.

COLEMAN M. N. & COLBERT M. W., 2007. Technical note: CT thresholding protocols for taking measurements on three-dimensional models. *American Journal of Physical Anthropology*, **133** (1): 723-725.

FRAIPONT J. & LOHEST M., 1887. La race humaine de Néanderthal ou de Canstadt en Belgique. Recherches ethnologiques sur des ossements humains, découverts dans des dépôts quaternaires d'une grotte à Spy et détermination de leur âge géologique. *Archives de Biologie*, **7**/1886: 587-757.

HUBLIN J.-J., SPOOR F., BRAUN M., ZONNEVELD F. & CONDEMI S., 1996. A late Neanderthal with upper Palaeolithic artefacts. *Nature*, **381**: 224-226.

IMAGEJ, 2005. ImageJ for Windows. Version 1.34.

JEFFERY N. & SPOOR F., 2004. Prenatal growth and development of the modern human labyrinth. *Journal of Anatomy*, **204**: 71-92.

MAUREILLE B., ROUGIER H., HOUËT F. & VANDERMEERSCH B., 2001. Les dents inférieures du Néandertalien Regourdou 1 (site de Regourdou, commune de Montignac, Dordogne): Analyses métriques et comparatives. *Paléo*, **13**: 183-200.

PONCE DE LEÓN M. S. & ZOLLIKOFER C. P. E., 1999. New evidence from Le Moustier 1: computer-assisted reconstruction and morphometry of the skull. *Anatomical Record*, **254**: 474-489.

ROOK L., BONDIOLI L., CASALI F., ROSSI M., KÖHLER M., MOYA SOLA S. & MACCHIARELLI R., 2004. The bony labyrinth of *Oreopithecus bambolii*. *Journal of Human Evolution*, **46**: 349-356.

SPOOR F., 1993. *The comparative morphology and phylogeny of the human bony labyrinth*. Utrecht, Monograph Utrecht University: 145 p.

SPOOR F., 2003. The semicircular canal system and locomotor behaviour, with special reference to hominin evolution. *Courier Forschungsinstitut Senckenberg*, **243**: 93-104.

SPOOR F., ESTEVES F., TECELÃO SILVA F. & PACHECO DIAS R., 2002a. The bony labyrinth. *In*: J. ZILHÃO & E. TRINKAUS (ed.), *Portrait of the artist as a child: the Gravettian human skeleton from the Abrigo do Lagar Velho and its archeological context*. Trabalhos de Arqueologia, **22**: 293-296.

SPOOR F., HUBLIN J.-J., BRAUN M. & ZONNEVELD F., 2003. The bony labyrinths of Neanderthals. *Journal of Human Evolution*, **44** (2): 141-165.

SPOOR F., HUBLIN J.-J. & KONDO O., 2002b. The bony labyrinth of the Dederiyeh child. *In*: T. AKAZAWA & S. MUHESEN (ed.), *Neanderthal Burials. Excavations of the Dederiyeh Cave, Afrin, Syria*. Tokyo, The Tokyo University Press: 215-220.

SPOOR F., WOOD B. & ZONNEVELD F., 1994. Implications of early hominid labyrinthine morphology for the evolution of human bipedal locomotion. *Nature*, **369**: 645-648.

SPOOR F. & ZONNEVELD F., 1994. The bony labyrinth in *Homo erectus*: a preliminary report. *Courier Forschungsinstitut Senckenberg*, **171**: 251-256.

SPOOR F. & ZONNEVELD F., 1995. Morphometry of the primate bony labyrinth: a new method based on high-resolution CT. *Journal of Anatomy*, **186**: 271-286.

SPOOR F. & ZONNEVELD F., 1998. Comparative review of the human bony labyrinth. *Yearbook of Physical Anthropology*, **41**: 211-251.

SPSS Inc., 2003. SPSS for Windows. Version 12.0.

STATSOFT FRANCE, 2002. *Statistica (logiciel d'analyse de données)*. Version 6.

THOMPSON J. L. & ILLERHAUS B., 1998. A new reconstruction of the Le Moustier 1 skull and investigation of internal structures using 3-D-µCT data. *Journal of Human Evolution*, **35** (6): 647-665.

ULLRICH C. G., BINET E. F., SANECKI M. G. & KIEFFER S. A., 1980. Quantitative Assessment of the Lumbar Spinal Canal by Computed Tomography. *Radiology*, **134**: 137-143.

URQUIZA R., BOTELLA M. & CIGES M., 2005. Study of a temporal bone of *Homo heildelbergensis*. *Acta Otolaryngologica*, **125**: 457-463.

VIOLA B., SEIDLER H. & ZUR NEDDEN D., 2004. Computer tomographic investigations of the OR-1 petrosals. *In*: A. P. DEREVIANKO (ed.), *Obi-Rakhmat Grotto.* Novosibirsk, Institute of Archaeology and Ethnography, SB RAS Press: 100-106.

AUTHORS AFFILIATION

Isabelle CREVECOEUR
Linda BOUCHNEB
CNRS
PACEA, UMR 5199
Allée Geoffroy St Hilaire
CS 50023
33615 Pessac cedex
France
i.crevecoeur@pacea.u-bordeaux1.fr
l.bouchneb@free.fr

Isabelle CREVECOEUR
Hélène ROUGIER
Earth and History of Life
Royal Belgian Institute of Natural Sciences
29, Vautier Street
1000 Brussels
Belgium

Hélène ROUGIER
Department of Anthropology
California State University Northridge
18111 Nordhoff Street
Northridge, CA 91330-8244
USA
helene.rougier@csun.edu