SECTION 1 : THÉORIES ET MÉTHODES / THEORY AND METHOD
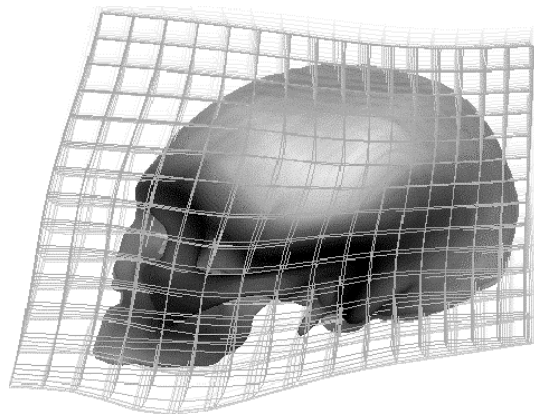
Colloque / Symposium 1.7

Three-Dimensional Imaging in Paleoanthropology and Prehistoric Archaeology

Edited by

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THE "VIRTUAL" ENDOCAST OF SACCOPASTORE 1. GENERAL MORPHOLOGY AND PRELIMINARY COMPARISONS BY GEOMETRIC MORPHOMETRICS

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Résumé: L'endocrâne du pré-Neandertal Saccopastore 1, obtenu par scannerisation CT de l'exemplaire original puis reconstruction virtuelle des volumes internes, est comparé avec d'autres hommes fossiles du Pléistocène Moyen et Supérieur. Les caractéristiques morphologiques générales sont analysées à partir d'une sélection de valeurs métriques par morphométrie géométrique. L'endocrâne de Saccopastore 1 présente des traits primitifs: platycéphalie, rostrum encéphalique, position de la largeur maximum, configuration du réseau méningé et des circonvolutions cérébrales, etc. En même temps, ces traits sont associés à des aspects de type Néandertalien, particulièrement quand on considère les largeurs, les structures occipito-cérébelleuses, la latéralisation et les asymétries. A partir d'une approche basée sur la morphométrie géométrique, la variabilité morphologique endocrânienne à l'intérieur du genre Homo apparaît être fortement liée à la taille, et, pour les faces latérales, à l'expansion des zones pariétales. Dans ce cadre général, le caractère plésiomorphe de l'endocrâne de Saccopastore 1 est resitué dans une perspective allométrique et l'hypothèse d'une pause dans l'évolution du cerveau (en dehors de son volume) pendant une grande partie de l'histoire naturelle du genre Homo est discutée brièvement.

Abstract: The endocast of the early Neandertal specimen Saccopastore 1 – obtained by CT-scanning of the original specimen and virtual reconstruction of the internal volumes – is compared with other fossil specimens ranging between Middle and Late Pleistocene. Features of general morphology are reported, together with a selection of metrical values and preliminary results of an ongoing geometric morphometric analysis. The endocast of Saccopastore 1 shows some primitive traits: platicephaly, encephalic rostrum, maximum breadth location, patterns of both meningeal system and gyrification system, etc. At the same time, these features are blended with derived Neandertal traits, particularly when width dimensions, occipito-cerebellar structures, as well as lateralisation and asymmetries are considered. From the multivariate approach based on geometric morphometrics, variability in endocranial vault morphology within the genus Homo appears to be size-related. In this general framework, the plesiomorphic appearance of the endocast of Saccopastore 1 is evaluated from an allometric perspective, and the case for stasis in brain evolution (but for its size) during great part of the natural history of the genus Homo is also briefly discussed.

INTRODUCTION

The fossil cranium known as Saccopastore 1 (Scp.1) was recovered in 1929 in the homonymous area now within Rome (Sergi, 1929, 1944), included in a gravel/sand deposit referred to the beginning of the Late Pleistocene, that is to about 100-120 ka (for a review of the literature, see Manzi & Passarello, 1991). It is well known that Scp.1, commonly considered a female specimen, exhibits a morphological pattern that appears consistent with its chronology, according to the so-called 'accretion model' for human evolution in Europe (Hublin, 1998). Clearly derived – i.e., Neandertal – traits are in fact blended with more archaic and less derived features (e.g., Condemi, 1992), including small cranial capacity (1174 ml was the best estimate obtained by Sergi, 1944) and marked platicephaly; this "mosaic" pattern is shared with Middle Pleistocene samples along the Neandertal lineage (compare Arsuaga et al., 1997). The fossil shows an extremely high level of mineralisation, and the endocranial cavity is partially filled by the geological matrix of inclusion.

The cranium has been recently CT scanned (Manzi et al., 2001) to allow, among other aims, the analysis of internal structures. In this framework, the endocast was reconstructed by computed assisted imaging techniques (Conroy & Vannier 1984; Zollikofer et al. 1998; Recheis at al. 1999; Spoor et al. 2000). In this paper, we report some notes on general morphology of the endocast of Scp.1 and a selection of metrical values, together with preliminary results obtained in comparing other fossil endocasts by geometric morphometrics. In perspective, this work is aimed to characterise the architecture of the Scp.1 endocranial morphology – and the decomposition of its shape – in the scenario of the evolution of the genus *Homo*. Clearly, the statistical power of this preliminary analysis must be increased by a larger sample, that will include other human *taxa*, samples, and specimens (Bruner, n.d.). Temporal areas must be added to the analysis, and a special attention should be paid to the cerebellar lobes (functionally linked to the parietal structures). Moreover, the approached based on geometric morphometrics will be extended to the superior view (which accounts for cerebral widths that, in turn, better characterise the Neandertal morphology) and/or to the three-dimensional space (for a description of the whole system).

MATERIALS AND METHODS

Scp.1 was scanned using a Tomoscan AUEP (Phylips), with sequential and contiguous 1 mm scans, 75 mA and 140 kV, and 0.49 mm pixel size (Manzi et al. 2001). The skull has been scanned by transverse planes, according to the Frankfurt horizontal. Data were exported as DICOM files. The high level of fossilisation, the stone matrix inclusions and the large depth of the layers caused marked streak artefacts and diffuse noise. Therefore, besides increasing the beam power (mA), a

filter was necessarily used to clean the signal. Data have been analysed using MIMICS 7.0 package (Materialise). Volumes have been segmented by thresholding the different CT numbers and following, in general, the "half maximum height" technique (Spoor et al., 1993).

Spatial coordinates of landmarks were analysed by Generalised Procrustes Analysis and Thin-Plate-Spline interpolation (Rohlf & Bookstein 1990; Bookstein 1991; Marcus et al. 1993; Rohlf 1993; Rohlf & Marcus 1993; Lynch et al. 1996; Marcus et al. 1996), using TPS softwares (Rohlf 1997, 1998a, 1998b, 2000a, 2000b) and the APS package (Penin, 2000). The landmarks were chosen in order to optimise the number of specimens available, and referred mainly to the vault profile in lateral view (Fig. 1). Two dimensional coordinates were collected without parallax distorsion from homologous landmarks (prerolandic and transverse sulci on midsagittal profile), points of maximum curvature (frontal and occipital poles, Broca area), and orthogonal projections from chords between the previous ones (frontal and parietal chords). The Scp.1 virtual endocast was compared with physical endocasts available at the Museum of Anthropology "G. Sergi" and the Istituto Italiano di Paleontologia Umana, in Rome. The comparative sample is composed by Trinil 2, Salé, Zhoukoudian III and XII, Arago (reconstruction), Neanderthal 1, La Chapelle-aux-Saints, and Guattari endocasts. Coordinates on comparative specimens were collected using a dioptograph and the tpsDig software (Rohlf, 1998c). The analysis based on the unweighted pair group method using arithmetic averages (UPGMA) was computed with PHYLIP 3.57c package (Felsenstein, 1989), and phenograms were elaborated by TREEVIEW (Page, 1996).

Fig. 2 - Transversal slice of Saccopastore 1 showing the stone matrix included in the endocranial cavity.

internal cavities. Even the endocranial surface is covered by sediment in various areas of the base and both the left and posterior walls of the braincase (Fig. 2), and particularly: the proximal areas of the right 3rd frontal circumvolution, the right temporal lobe, the cerebellar poles, and the occipital poles. Nevertheless, the cerebral surfaces are well preserved (especially those covered by the geological matrix), and the entire structure can be successfully reproduced (Fig. 3) except for some basal areas, where the sediment appears extremely interconnected with the fossil matrix.

The endocranial cavity is clearly asymmetric, with a strong dominance of the left hemisphere. The left frontal lobe is in fact slightly longer and broader, and the left parietal and occipital areas are definitely larger than the right ones in both the transvesal and coronal planes. Moreover, the maximum breadth is localised on the right at about mid-height of the hemisphere (temporo-parietal level), while on the left side it is placed forward and in a definitely lower position (base of the 3rd temporal circumvolution).

The frontal lobes show a marked encephalic rostrum, resembling the stage 1 described by Grimaud-Hervé (1997). The prefrontal circumvolutions are well defined, being more expressed on the left side, and the Broca area is clearly developed on the same hemisphere. The orbital circumvolutions are not identifiable, but they seem localised roughly on the orbital roofs, and not behind them. Cerebral impressions of the temporo-parietal areas are not easily discernible. The boss corresponding to the area of the angular and supramarginal gyri can be recognised on the left side, being the right one more rounded and smoother. Occipital lobes are only moderately developed, without any strong angulation with the parietal area. Cerebellar lobes, rather globular in shape, are placed anteriorly to the occipital poles, standing for the most part below the parietal area, reciprocally in contact and close to the mid-sagittal plane.
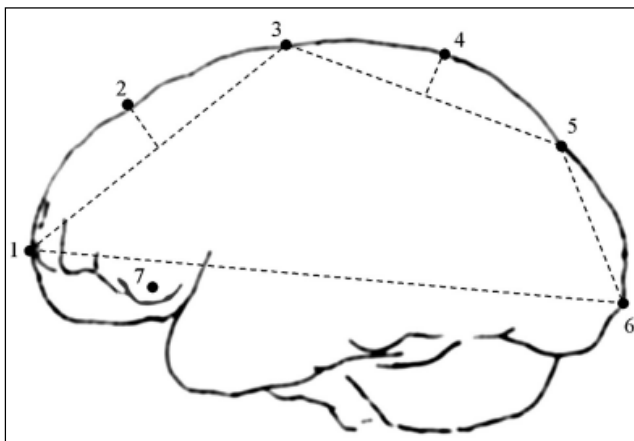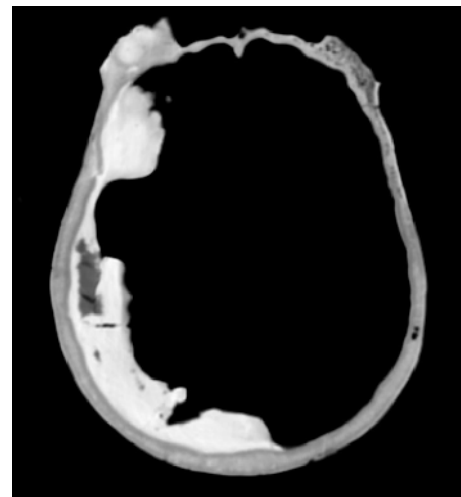

Fig. 1 - Landmarks sampled in lateral view. 1) most anterior point of the frontal pole; 2) orthogonal projection at the mid chord 1-3; 3) prefrontal sulcus; 4) orthogonal projection at the mid chord 3-5; 5) perpendicular sulcus; 6) most posterior point of the occipital lobe; 7) Broca area, at the boss between *pars opercularis* and *pars triangularis*.

RESULTS

General Morphology

Scp.1 is a heavily fossilised specimen (average HU = 3012±622); in addition, the geological matrix fills all the

As far as vascular relieves and sinuses are concerned, a marked wrinkle represents the anterior branch of the meningeal system on the left hemisphere, and it could be interpreted as a spheno-parietal sinus, being a smooth, unbranched and enlarging track
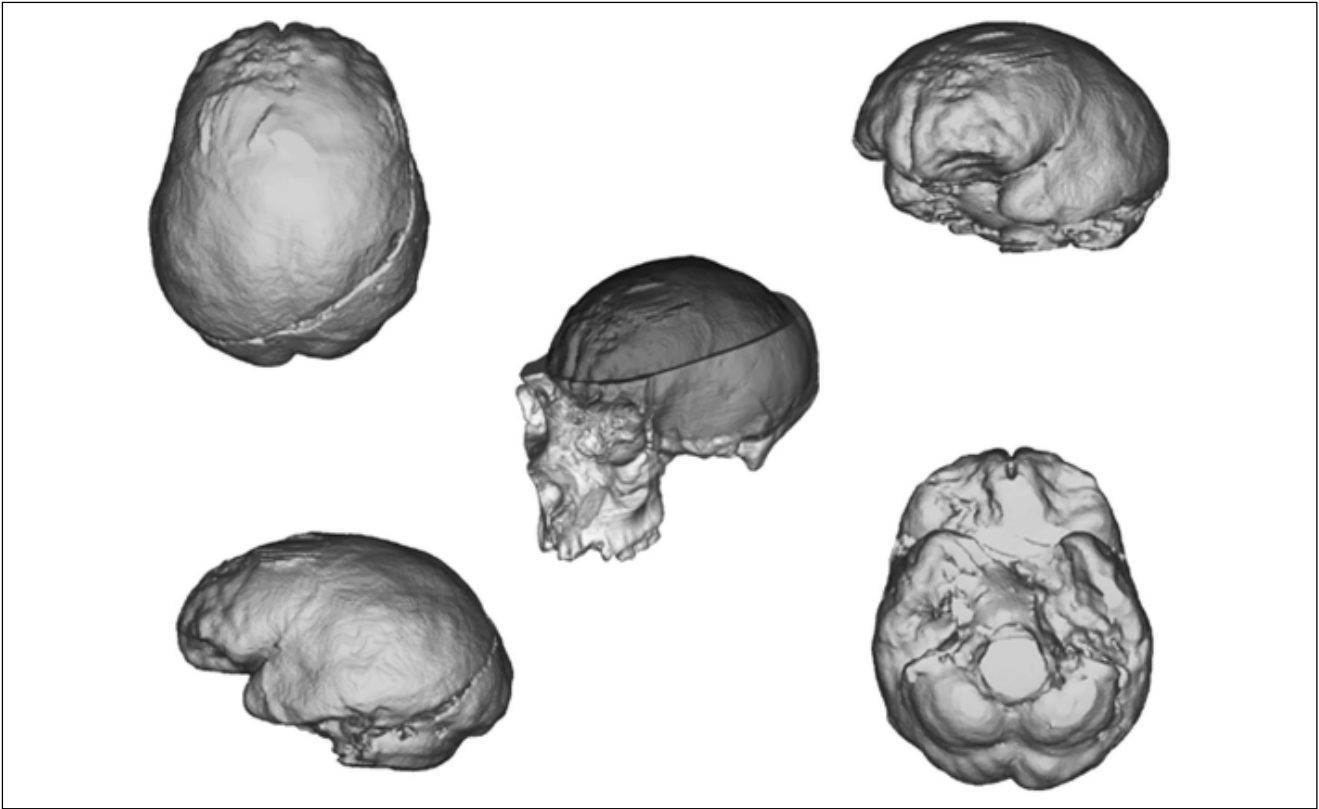
Fig. 3 - Virtual replicas of the Saccopastore 1 endocast.

that approaches the coronal suture; however, its superior end is not fully detectable, reaching the area of a large hole opened in the braincase. In these conditions, the occurrence of the Breschet sinus cannot be unquestionably assessed (D. Grimaud-Hervé, pers. comm.), but rather possible. On the right side, the anterior branch of the meningeal system is hardly noticeable, while the posterior one is more marked. The obelic (middle) ramus splits from the posterior one, branching at least once, and representing the most visible and large impression of the right meningeal system. The lambdatic wrinkle is marked but not branched. Whether this reconstruction of the fragmentary evidence observed on the right hemisphere is correct, Saccopastore 1 shows a configuration of Adachi type II (compare Falk, 1993). Anastomoses are not detected.

The superior sagittal sinus is clearly visible only in the interparietal region, showing a diameter of about 8 mm. At the *torcular herophili*, the sagittal sinus runs clearly into the right, well developed, transverse-sigmoid system. Conversely, the left transverse sinus is hardly detectable, and the area of the respective sigmoid sinus is not well preserved. No occipito-marginal system is noticed.

COMPARISONS: METRICAL DATA AND GEOMETRIC MORPHOMETRICS

Scp.1 has a rather small endocast, with an average hemispheric maximum length of 161 mm, maximum breadth of 131 mm, width at the Broca's cap of 102 mm,

and height (endobasion-endovertex) equal to 103 mm. In Figure 4, metrical values of Scp.1 are plotted with average values of fossil samples ranging between Middle and Late Pleistocene (data from Grimaud-Hervé, 1997). Scp.1 shows both hemispheric length and cerebral height clearly bracketed within the range of variability of specimens referred to *Homo erectus* (Sangiran and Zhoukoudian). Conversely, cerebral widths are close to values observed in the Ngandong sample, standing in an intermediate position between the European Middle Pleistocene sample, from one side, and Neandertals and modern humans, from the other. Anyway, when reported relatively to the exocranial dimensions, length and width measurements show values that are close to those expressed by Wurmian Neandertals.

In Fig. 5a, the specimens submitted to geometric morphometric analysis are plotted in the plane described by the first two principal components. As a result of the shape decomposition, these two principal components explain together 80.2% of the total variance. It should be noted in the plot the position of Scp.1, intermediate within the *Homo erectus* cluster, with respect to typical Neandertals such as Guattari, La Chapelle, and the Feldhofer calotte.

The PC1 (44.8% of variance) involves flattening of the posterior (parieto-occipital) areas (Fig. 5b), while PC2 (35.4%) relates to the relative reduction of the prefrontal region (Fig.5c). A multivariate regression of shape versus size (represented by the centroid size of the mid-sagittal contour) shows a significant and marked correlation ($R^2 = 0.79$) between absolute dimensions and these two PCs, almost equally involved in a size-related effect. A Partial
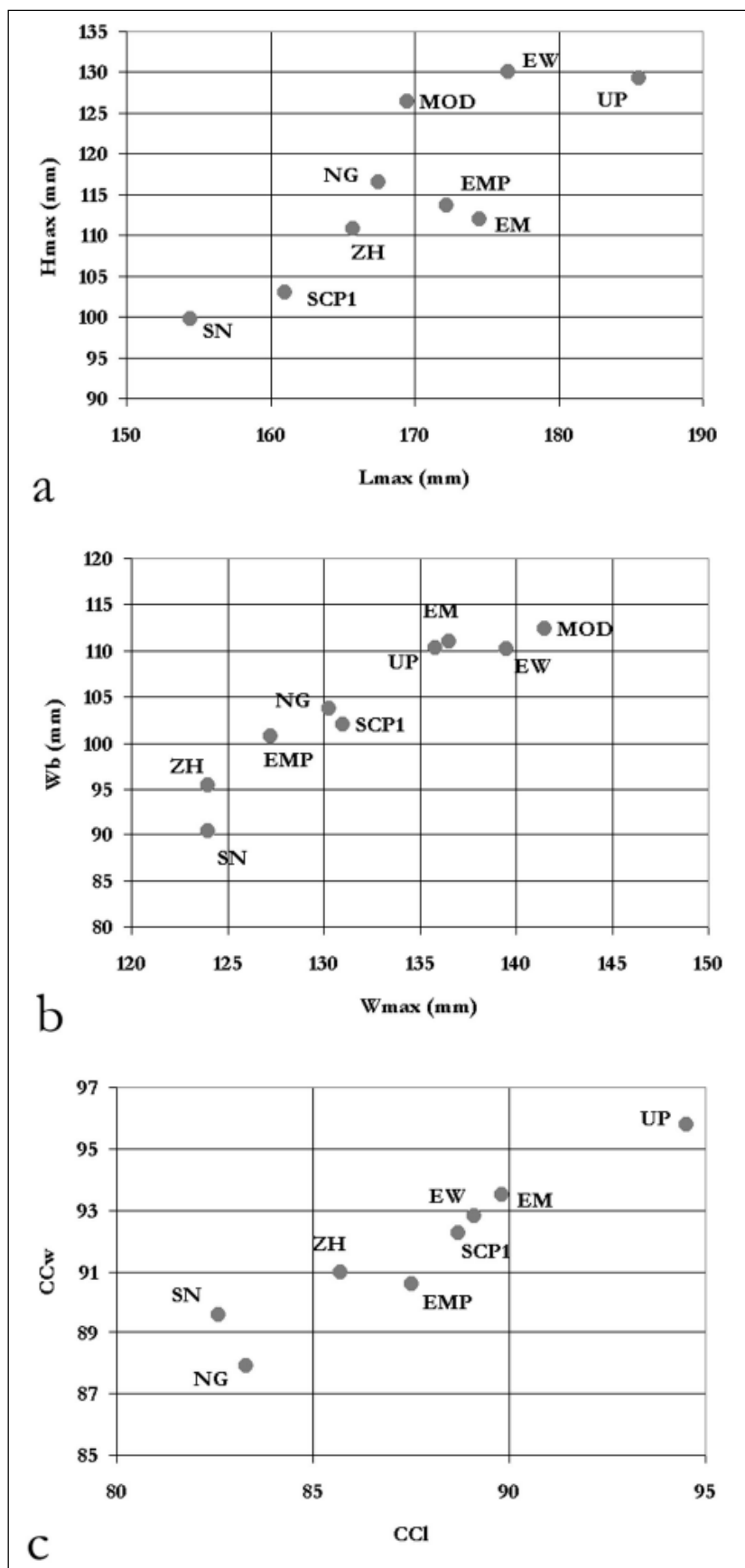
Fig. 4 - Comparison between endocranial dimensions of Saccopastore 1 and average values from other fossil samples (comparative samples and data from Grimaud-Hervé, 1997): a) average hemispheric length (Lmax) vs Endobasion-endovetrex height (Hmax); b) maximum width (Wmax) vs frontal width at the Broca's cap (Wb); c) cranio-encephalic length index (CCl) vs cranio-encephalic width index (CCw). *Legend* (fossil samples) – SCP1: Saccopastore 1; SN: Sangiran; ZH: Zhoukoudian; NG: Ngandong; EMP: European Middle Pleistocene; EW: European Würmian Neandertals; EM: early modern humans; UP: Upper Paleolithic; MOD: modern humans.
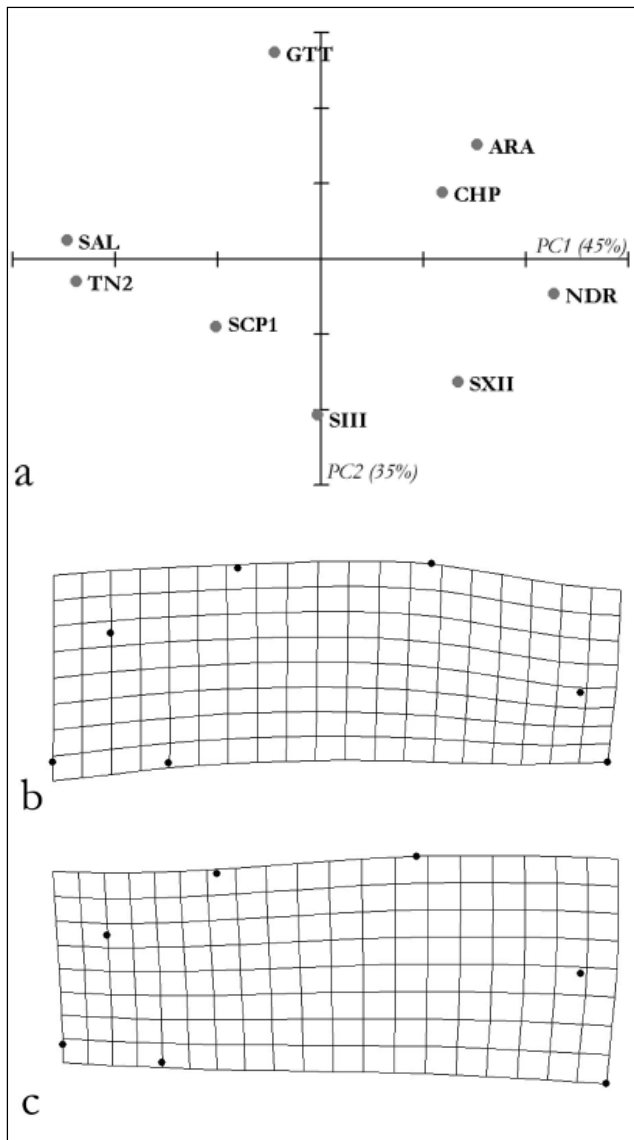
Fig. 5 - Plotting of the sample in the space of the first two principal components (a). Distortion grids showing the spline along the PC1 (b) and PC2 (c) are also reported. The basic configuration of landmarks is reported in Figure 1. *Legend* (fossil specimens) – SCP1: Saccopastore 1; SAL: Salè; TN2: Trinil 2; SIII: Zhoukoudian (Sinanthropus III); SXII: Zhoukoudian (Sinanthropus XII); ARA: Arago (reconstruction); NDR: Neandertal 1 (Feldhofer); CHP: La Chapelle-aux-Saints; GTT: Guattari 1.

Least Square regression of size on the entire set of shape parameters shows the same degree of correlation and globally discriminates the shape of small endocasts against larger ones.

An UPGMA procedure was then applied to the Procrustes distances obtained from the geometric morphometric analysis reported above. In the resulting tree (Fig. 6), Neandertal specimens describe a cluster that also includes the Arago reconstruction, while Scp.1 relates to *Homo erectus* variability and is closer to smaller specimens (such as Trinil and Salè). In a second analysis (not reported here) the confluence of sinuses (*torcular herophili*) was added to the landmarks: the same results were found, although Scp.1 moved closer to specimens from Zhoukoudian.
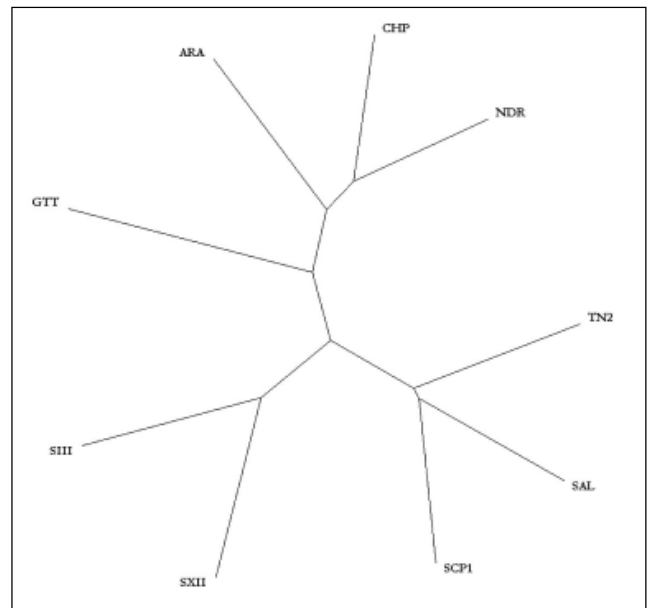

Fig. 6 - Unrooted tree resulted from an unweighted pair group method using arithmetic averages (UPGMA) analysis based on Procrustes distances; labels as in Figure 5.

DISCUSSION

It should be prudent when dealing with endocast morphologies based on reconstructions from CT-data (Zollikofer & Ponce de Leon, 2000). Yet, the virtual replica of Scp.1 appears complete and clear enough to allow a general description of the endocranial features, including size and both details and architecture of the shape. We can conclude that Scp.1 represents a useful test for this purpose, particularly when it is considered that it represents a specimen clearly within the Neandertal lineage, but with a brain scaled to the size of more archaic representatives of the genus *Homo*. As a matter of fact, the endocast of Scp.1 shows a mixture of features connecting the morphological patterns respectively observed in Middle and Late Pleistocene specimens.

For instance, although the shape of the frontal lobes seems to be of lesser importance during human evolution (Bookstein et al. 1999), Scp.1 shows a marked encephalic rostrum, that is considered a primitive feature shared within the *Homo erectus* hypodigm (Grimaud-Hervé, 1997). At the same time, diversely from what is reported for some large Middle Pleistocene specimens such as Petralona and Kabwe (Seidler et al., 1997), the orbital lobes in Scp.1 do not stand behind the frontal roof, but in a rather advanced position. Moreover, the frontal circumvolutions are well developed, including a large Broca area on the left side, and the ratio between frontal and parietal widths are fairly large when compared with Asian samples from Sangiran or Ngandong. Therefore – considering the common occurrence of strong platicephaly in Scp.1 as well as in specimens referred to *Homo erectus* – the expression of an encephalic rostrum could be viewed in relationship with the small endocranial heights, despite Scp.1 shows more derived traits in the frontal areas.

The occipital lobes are not stressed backwards as in the Asian clade, being rather continuous with the parietal outline and in close connection with the temporal lobes. The cerebellar lobes are globular and contiguous, while in *Homo erectus* they are more elliptical and detached (Grimaud-Hervé, 1997). This feature – already present in the Cranium 5 from Sima the los Huesos (EB, pers. obs.) – links Scp.1 to more derived configurations (Neandertals and modern humans), and could be in relationship with the longitudinal organisation of the whole system. During human evolution, all the posterior districts of the brain seem to have rotated gradually under the parieto-temporal areas. In Scp.1, as generally observed among Neandertals and (most of all) in modern humans, the cerebellar lobes lie almost entirely under the parietal ones, while in the Sangiran sample these are more posteriorly protruded (halfway between the parietal and the occipital areas); in more encephalized *Homo erectus* specimens, such as those from Zhoukoudian, the position is rather intermediate between these two extremes. Following such a process, along the general trend of human evolution, the cerebellar poles approach medially each other, changing the conformation of the entire cerebellum from a more longitudinal orientation to a little bit more transversal one.

Petalias are well developed in Scp.1. The global left dominance does not correspond to the more frequent right-frontal / left-occipital pattern (Holloway & de la Coste-Lareymondie, 1982), but it is nevertheless well expressed. The occurrence of cerebral asymmetries is another trend in human evolution – expression degree of petalias similar to Scp.1 have been found, without a marked gyral pattern, in small brained specimens such as Salé (Holloway 1981a) or the Indonesian *Homo erectus* clade (Holloway 1980, 1981b), but at a visual inspection lateralisation seems somewhat more developed in Scp.1. Actually, the asymmetries at the 3rd frontal circumvolution and at the supramarginal and angular gyri indicate an advanced level of lateralisation, with interesting functional consequences (Bradshaw, 1988).

The meningeal system is rather simple, and it is apparently similar to Asian (Zhoukoudian) and European (Arago) Middle Pleistocene specimens (Saban, 1995; Grimaud-Hervé, 1997), sharing a probable dominance of the posterior ramus, and lacking a complex branching pattern or the occurrence of diffused anastomoses.

In sum, the morphological pattern that can be observed dealing with the so far unknown endocast of Scp.1 appears peculiar and interesting for human evolution – *crucial* in connecting more archaic and more derived phenotypes. Strictly comparable with that of Scp.1 – characterised by the occurrence of a primitive encephalic rostrum and a simple meningeal structure, associated to a fully modern gyrification system and well developed cerebellar lobes – we have the pattern already described in Saccopastore 2, the less complete early Neandertal from the same site (Sergi, 1948).

Coming to the still preliminary comparative approach reported here, it should be observed that the main diameters (total length, width and height) set the position of Scp.1 – again – as an "intermediate" specimen between other fossil groups.

The endocast shows extreme platicephaly, closer to that expressed by the smallest specimens of *Homo erectus*, while the length is intermediate between those of small sized and larger sized Asian samples. The maximum width at the temporal lobe and at the Broca area, on the contrary, suggest a derived expansion which is typical of the Neandertal lineage. It must be stressed, however, that among Neandertals the maximum breadth is localised at the temporo-parietal area, while in *Homo erectus* it arises more inferiorly, properly in the temporal lobe (Holloway 1980). In Scp.1 it is parieto-temporal on the right and fully temporal on the left. Anyway, if we compare the endocranial diameters with the corresponding external dimensions, the ratio is strictly comparable with that of the Wurmian Neandertals. It may be hypothesised that many of the resemblances between Scp.1 and specimens referred to *Homo erectus* may be the result of the small size and of a size-related morphological pattern (including the strong degree of platicephaly). At the same time, it is interesting to note that width figures (derived traits) and relative endocranial dimensions of length and height approach Scp.1 to the other Neandertals more than the absolute values.

Whether the results of the geometric morphometric analysis reported here will be confirmed by a larger comparative effort (Bruner, n.d.), it should be concluded that the variability of the endocast architecture among archaic representatives of the genus *Homo* – as far as the mid-sagittal projection of the superior profile is concerned – appears strongly dependent from cerebral dimensions. Size results correlated to 80% of the variance in shape. This allometric pattern seems to be shared by both *Homo erectus* and the Neandertals. We must assume that allometric trend is not only related to overall morphology, but it is also linked to the functional organisation of the brain system, including the expression of circumvolutions, venous sinuses and meningeal patterns.

In light of this analysis of the shape, Scp.1 shows – once more – features that are comparable with the range of variability of *Homo erectus*, sharing with specimens referred to this *taxon* both the extent of brain size and a marked platicephaly. In future dataset modern profiles will also be included giving a more precise results, in particular regarding the role of the parietal areas, which in modern populations are extremely developed. It must be stressed that parietal enlargement has a geometrical effect on the whole cerebral structure. As parietal areas increase, the functional cerebral axis (i.e. the orientation of the brain) changes, pulling down and forward the occipital, temporal and cerebellar lobes. This process involves a rotation of the rear structures under the parieto-temporal areas, while the temporal poles are pushed below the frontal ones. Thus, in *Homo erectus* the cerebral axis is fronto-occipital, whereas among modern humans the axis is fronto-parietal. This must be taken into account when an evolutionary perspective and an analytical context and formalisation of the geometry of the brain are considered (Bruner, n.d.). The role of a posterior parietal cortex development has been previously described as one of the principal factor related to the origin of human evolution itself (Holloway, 1995); it is probably associated to the perception of spatial relationships, processing of visual, auditory and somatic information, as well as to social communication.

Allometry is often the result of ontogenetic and small regulative variations, and it is generally not related to any deep reorganisation of the genome (Gould 1966; Shea 1992; Klingenberg 1998). Given the piece of evidence added so far by the study of the endocast of Saccopastore, and if we consider that specimens as diverse – both in terms of chronology and geography, but also in terms of morphology – as Scp.1 and Trinil 2 may share the same model of brain development, we should assume that evolutionary stasis occurred along the *Homo* lineages, at least before the appearance of modern humans.

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