

ORIGINAL ARTICLE

Fractal dimension of the middle meningeal vessels: variation and evolution in *Homo erectus*, Neanderthals, and modern humans

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Abstract

The middle meningeal vascular network leaves its traces on the endocranial surface because of the tight relationship between neurocranial development and brain growth. Analysing the endocast of fossil specimens, it is therefore possible to describe the morphology of these structures, leading inferences on the cerebral physiology and metabolism in extinct human groups. In this paper, general features of the meningeal vascular traces are described for specimens included in the *Homo erectus*, *Homo neanderthalensis*, and *Homo sapiens* hypodigms. The complexity of the arterial network is quantified by its fractal dimension, calculated through the box-counting method. Modern humans show significant differences from the other two taxa because of the anterior vascular dominance and the larger fractal dimension. Neither the fractal dimension nor the anterior development are merely associated with cranial size increase. Considering the differences between Neanderthals and modern humans, these results may be interpreted in terms of phylogeny, cerebral functions, or cranial structural network.

Keywords: *Paleoneurology, human evolution, box-counting, endocranium*

Introduction

The neurocranial development is largely based on a secondary bone deposition associated with brain enlargement and consequent cerebral pressure (Enlow 1990). This biomechanical system relies upon the dura layers and the connective tensors to shape the neurocranial morphology during brain expansion (Moss & Young 1960). Because of this tight relationship between soft and hard tissues, many cortical structures – circumvolutions, arteries, and venous sinuses – leave their traces onto the endocranial surface.

Paleoneurology concerns the study of the endocasts from fossil specimens (e.g. Holloway 1978; Falk 1987; Bruner 2003a), where morphological features can be detected and studied to develop hypotheses on physiological, functional, and evolutionary processes. In this paper we are mainly interested in the traces of the meningeal vascular system in *Homo erectus*, *Homo neanderthalensis* and *Homo sapiens*,

providing a method to quantify their respective branching patterns.

The middle meningeal vessels

The middle meningeal artery is the main vascular system detectable on the endocranial surface (Figure 1). It is a branch of the maxillary artery stemming from the external carotid, commonly entering the endocranium through the foramen spinosum (see Saban 1995; Grimaud-Hervé 1997). The phylogenetic origin of these vessels is still debated (Diamond 1991, 1992; Falk & Nicholls 1992; Falk 1993), as it could not be homologous within the anthropoids variability. The association with two parameningeal veins make the interpretation of these traces more hypothetical. Given these facts, the term *Middle Meningeal Vessels* (MMV) will be used in this paper, without any reference to the arterial versus venous interpretation of the traces.

This vascular system accounts for both energy requirements and possibly thermoregulation of cortical structures, and represents a major source of cerebral homeostasis. In general, the vascular system is divided into three main branches, approaching bregma (anterior, or bregmatic), obelion (middle, or obelic), and lambda (posterior, or lambdatic), respectively. Many attempts to quantify and classify the morphological variation of this network failed because of the irregular, heterogeneous, and complex nature of its geometry (see reviews in Marcozzi 1942; Grimaud-Hervé 1997; Bruner et al. 2003a).

Grimaud-Hervé (1997) described in an extensive analysis some major differences between extant and extinct human populations. Modern humans show a complex and very anastomosed vascular network, mainly originating from the anterior meningeal branches. The vascular reticulation is particularly developed at the parietal areas, also in Late Pleistocene samples such as those from Brno, Dolni Vestonice, and Predmost (Saban 1982). In contrast, Asian *Homo erectus* specimens (*Homo erectus sensu stricto*) are characterised by a less complex vascular system, lack of anastomoses, and more developed posterior traces. Furthermore, in modern humans the scarcely arborised posterior branch runs almost

orthogonal to the anterior and more developed ramus, while in *H. erectus* s.s. the two branches are almost parallel. Neanderthals show a more dominant anterior branch, but without increase in the branching level. Figure 2 shows the endocast and the main middle meningeal traces of Zhoukoudian 12 (*H. erectus*), La Ferrassie (*H. neanderthalensis*), and Combe Capelle (*H. sapiens*).

The study of the MMV morphological variability has been, till now, entirely based on descriptive analyses, and quantitative approaches to test hypotheses and study differences between groups are currently lacking.

Fractal geometry and vascular morphology

As soon as the fractal properties of many geometrical forms were rigorously described, the morphologists recognised a new and powerful tool to code a large part of the apparently fuzzy variation in many natural structures (Mandelbrot 1977, 1982). The possibility of a general abstract description of patterns of these forms in terms of mathematical tools mainly relies upon *self-similarity*, a peculiar property of a great number of disordered structures. Self-similarity means invariance of forms under multiplicative changes of scale, and one of the conspicuous consequences of this property is the rising of exceedingly fine grained structures generated by successive branching. As it is well known, self-similar forms are now generally called *fractals* after Benoit B. Mandelbrot (1977). Starting from Mandelbrot, the large number of repeated self-similar structures and branching structural networks found in organisms suggested the fractal geometry as a 'fourth spatial dimension' of the biological systems (West et al. 1999). For what concerns in particular morphometrics, explorative applications of fractal geometry range from the analysis of outlines (Slice 1993), to the description of the cranial sutural patterns (Arqués & Gibert 2002).

Arterial trees are irregular-shaped structures based on the principle of successive bifurcations, representing classical examples of self-similar forms. As Suwa

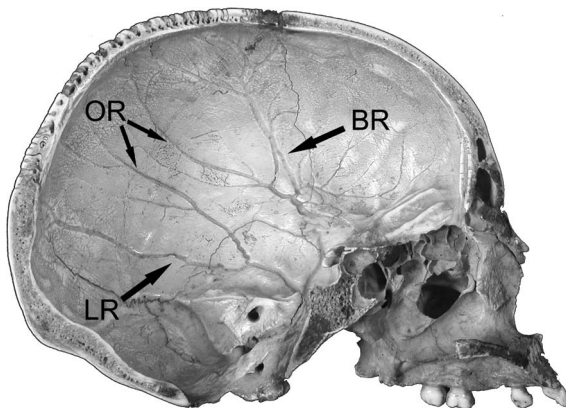


Figure 1. Traces of the middle meningeal vessels on the endocranial surface of a modern human skull (BR, bregmatic ramus; OR, obelic ramus; LR, lambdatic ramus).

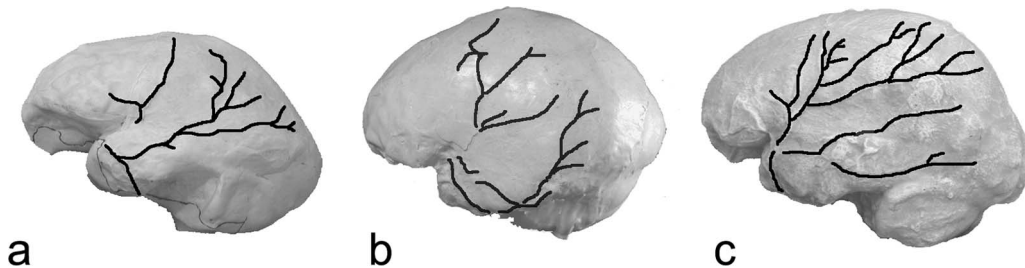


Figure 2. Endocasts from (a) Zhoukoudian 12 (*Homo erectus*, 300–500 kyrs bp – left side); (b) La Ferrassie (*Homo neanderthalensis*, 50 kyrs bp – left side); (c) Combe Capelle (*Homo sapiens*, 25–30 kyrs bp – right side reversed), showing the main traces of the middle meningeal vessels.

and Takahashi showed (1971), arteries and veins in mammalian vascular systems have been found to obey a suitable scaling law over a range of 20 bifurcations between heart and capillaries. This suggests that fractal – or pseudo-fractal – analysis (Zamir 1999, 2001a) seems the more suitable tool to investigate geometrical properties of these structures.

Vascular networks are rather heterogeneous in non-specialised organs, but they are organised in functional repeated units and packed in uniform patterns in specialised organs such as kidneys and lungs (Zamir 2001b). For what concerns in particular lungs, it is interesting to recall, as a final remark, that Mandelbrot (1982) hypothesised that the simple self-similar growth process that gives rise to the iterated structure of branches, is obtained not because of functional reasons, but as a result of the shortest growth-governing program, where each step repeats the previous one on a smaller scale. This remark suggests that fractal analysis could be considered not only as a possible quantitative approach, but also as a tool for a deeper understanding of natural phenomena.

As it is well known, the first step in the study of irregular geometries by means of fractal analysis is the description of their respective *fractal dimension* (Peitgen et al. 1992). The fractal dimension (FD), which describes the space-filling properties of the geometrical models, expresses the ratio between a self-bifurcating system and the relative surface covered. It can be calculated in several ways, including iterative methods such as the *box-counting* (see below). In anthropology, this approach has been successfully applied to test human sexual dimorphism from the interorbital morphology (Schiwy-Bochat 2001).

This paper is aimed at quantifying the traces of the middle meningeal vessels in modern and extinct groups of the genus *Homo* through the analysis of the fractal dimension, in order to describe and compare the variation and evolution of these vascular systems.

Materials and methods

Sample

Draws of the MMV from fossil specimens were collected from the literature (Saban 1995; Grimaud-Hervé 1997) and checked directly on the endocast collections at the Istituto Italiano di Paleontologia Umana (Roma), at the Museo di Antropologia G. Sergi, Università La Sapienza (Roma), and at the Institut de Paleontologie Humaine (Paris). The sample includes 54 hemispheres from 29 individuals (Table I), grouped into three operational taxonomic units: Asian *Homo erectus* ($N=22$), Neanderthals ($N=15$), and early modern humans ($N=17$). It is worth noting that ‘hemisphere’ is here used to indicate a single side of the endocranium, and not strictly the

Table I. Sample.

Taxon	Specimen
<i>H. erectus</i>	Ngandong 5
	Ngandong 7 ^a
	Ngandong 11
	Sangiran 2
	Sangiran 10
	Sangiran 12
	Sangiran 17 ^b
	Trinil 2
	Zhoukoudian 3
	Zhoukoudian 10
	Zhoukoudian 11
	Zhoukoudian 12
<i>H. neanderthalensis</i>	Engis 2
	Feldofer Grotto
	Gibraltar 2 ^b
	La Chapelle-aux-Saints
	La Ferrassie 1
	La Quina 5
	Le Moustier 1
	Tesik-Tash
<i>H. sapiens</i>	Brno 3
	Combe Capelle 1
	Cro Magnon 3
	Predmost 3
	Predmost 4
	Predmost 9
	Predmost 10
	Vestonice 1 ^b
	Vestonice 2

^aOnly right hemisphere.

^bOnly left hemisphere.

respective cerebral soft tissues. This term is commonly used in paleoneurology, mostly when describing the endocranial patterns of asymmetry (petalia) that directly depend upon the hemispheric development. Nevertheless, the term ‘hemi-endocast’ is probably more suited to indicate the two endocranial halves, and their respective moulds.

Some fossils lack the basal areas of the endocranium, missing the lower part of the MMV. These areas include in general the common arterial branch, and should not affect the fractal pattern. Nevertheless, a subset including only the complete MMV was also used to test the influence of such incompleteness.

The hemispheres have been also grouped considering the main vascular scheme, according to the classification by Adachi (1928). This is the simplest standard classification of the MMV, depending upon the derivation of the middle (obelic) branch from the anterior ramus (Adachi type I), from the posterior ramus (type II), or from both (type III). This general character accounts for the dominance of the anterior versus posterior branches, and it is a simple but rather repeatable and less subjective approach. This classification is frequently used to describe the variation of the middle meningeal vessels in extant and extinct hominids, being possibly involved in

phylogenetic differences. In contrast, the pattern of dominance of the vessels (anterior versus posterior) could be associated with structural signals. In both cases, the consequent relationship with the complexity of the network may represent an interesting topic.

Note that simple networks are easier to classify than those with more reticulated patterns. In the latter, only the major vessels must be considered to achieve a useful classification of the vascular systems.

Fractal dimension from box-counting

Imagine an abstract geometrical curve on a plane, generated by a process of many successive branching (a self-similarity process). Following the German mathematician Felix Hausdorff (1919), the length of this curve can be calculated as follows. Assume that N straight-line segments of length l are needed to step along the curve from one end to the other. To follow the finer and finer wiggles of the fractal structure, one needs shorter and shorter segments ($l \rightarrow 0$), and the product Nl , a reasonable candidate to measure the length, diverges to infinity. As Hausdorff

showed, however, the product Nl^{D_H} stays finite. In other words, there exists some critical exponent, $D_H > 1$, called the Hausdorff fractal dimension, that indicate that the length of the curve can be quantified by a well-defined homogeneous power law of l . However, in many practical cases, to follow the curve with straight-line segments is not the better way to measure its fractal dimension. Rather, it turns out to be more convenient to superimpose over the curve a square-grid of side s and account for the number $N(s)$ of boxes that cover the curve as $s \rightarrow 0$. It can be shown (Feder 1988) that as the grid lines become narrow, and therefore the number of boxes increases, the product Ns^D is finite as before, and $D > 1$ is the fractal dimension.

In the present study, draws of the MMV were converted into binary images. The final target of this explorative analysis was the quantification of the reticulation pattern, independently upon the section of each branch. Accordingly, the thickness of the vessels was assumed as constant. The vascular pattern was iteratively covered with a grid of square boxes of increasing/decreasing size (Figure 3). The number of

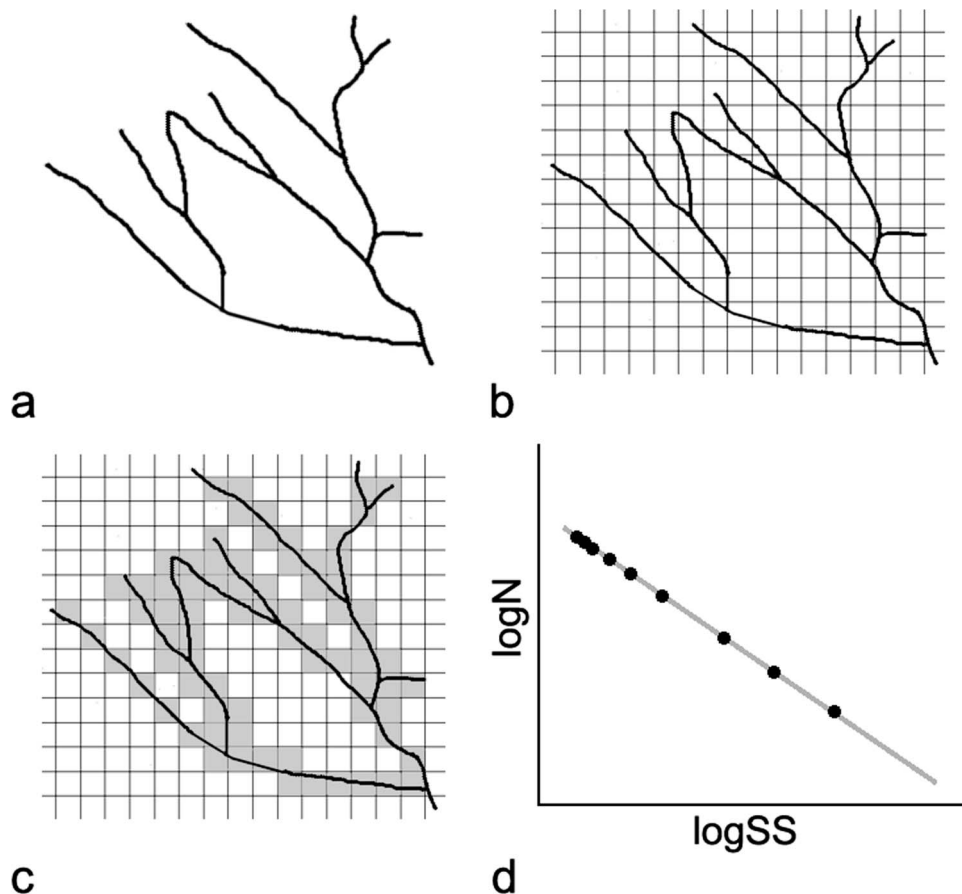


Figure 3. Box-counting applied to the middle meningeal network. The scheme of a middle meningeal vessel from a single hemisphere (a) is covered iteratively with square boxes increasing/decreasing the box size as to approach the limit of the fractal dimension (b). This limit describes the ratio between the linear growth and the respective surface covered (c), synthesising the space-filling property of the network. The fractal dimension is the absolute value of the slope from the log-log regression fit (d) between square size (SS) and number of squares necessary to cover the pattern (N).

boxes including at least one pixel of the image was reported at each given box size, into a bilogarithmic plot. The module of the slope from the resulting regression fit represented the fractal dimension. Iterations were performed from 1 to 256 pixels, with size increasing from 1 to 10 and subsequently each 10 steps, up to 32 values. Fractal Dimension 1.1 was used to compute the entire process (Bar-Ilan University – <http://ory.ph.biu.ac.il/SEP>). Differences between groups were tested through a non-parametric approach (Kruskal–Wallis and Mann–Whitney tests; $P < 0.05$).

Results

Figure 4 shows, for each taxon, the percentage of hemispheres represented in each Adachi category. The two branches give a comparable contribution to the parietal network in *Homo erectus*. Neanderthals show an increased influence of the anterior branch through a larger percentage of double obelic derivations. In modern humans there is a definite dominance of the anterior network.

Table II reports the descriptive statistics for the FD variation in the three taxa. There is no significant difference between the two extinct groups, while modern humans show significant higher values ($H_{2,54} = 19.60$, $P < 0.001$; Figure 5a). The standard

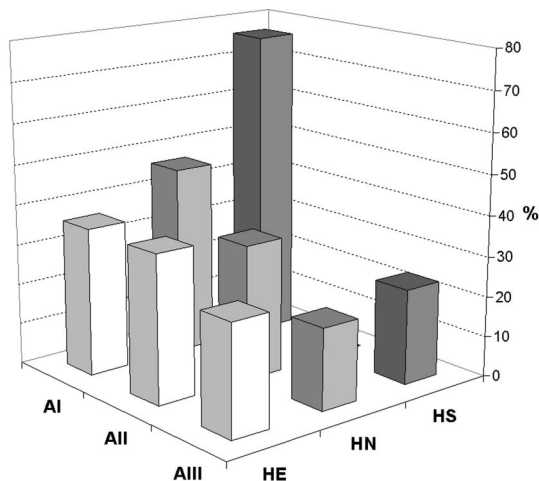


Figure 4. Prevalence of the three Adachi patterns (AI, AII, AIII) in each taxon (HE, *Homo erectus*; HN, *Homo neanderthalensis*; HS, *Homo sapiens*).

Table II. Descriptive statistics for the fractal dimension.

Species	N	Mean	St.Dev.	Q25	Median	Q75
<i>H. erectus</i>	22	1.29	0.06	1.25	1.27	1.33
<i>H. neanderthalensis</i>	15	1.29	0.06	1.25	1.28	1.33
<i>H. sapiens</i>	17	1.39	0.05	1.37	1.39	1.43

deviation is comparable for all the three groups, with the coefficient of variation slightly lower for the modern (3.4%) than for the non-modern (5.0%) distributions. No significant differences are found between left and right hemispheres, or considering only the hemispheres with complete MMV. Adachi type I and type III MMVs show higher FD compared with type II ($H_{2,54} = 20.10$, $P < 0.001$; Figure 5b). If modern humans are excluded, the pattern is similar but the difference between type I and type II is not significant anymore.

Discussion

Introducing a new tool in paleoneurology, this paper provides a methodological approach to quantify the degree of reticulation of the middle meningeal vessels, and to consider the observed changes between human extant and extinct groups.

Despite the importance of the MMV in the brain energy management, this anatomical system is scarcely known and investigated (Falk & Nicholls 1992). The first main difficulty is related to problems in availability of specimens, preparation of soft tissues, and analysis of metabolic functional correlates. A second problem is represented by the unconventional morphology of the arterial trees, rather difficult to quantify in terms of statistical and geometrical parameters.

Asian *Homo erectus*, Neanderthals, and modern humans, are frequently interpreted as three independent evolutionary entities of the genus *Homo*, associated respectively with human evolution in Asia, Europe, and Africa during the Middle Pleistocene (for discussions see Stringer 2002; Anton 2003; Manzi 2004). Compared with more archaic hominines, these three lineages underwent a process of encephalisation, resulting in an increase of absolute and relative cranial capacity (see Rightmire 2004). In particular, Neanderthals and modern humans reached comparable brain volumes, probably following independent structural trajectories (Bruner et al. 2003b).

The distribution of the MMV branches in these three taxa suggests a different balance between the anterior and posterior cerebral districts, as suggested in previous works (e.g. Grimaud-Hervé 1997). The Asian group shows an almost equivalent role of the anterior and posterior branches. This pattern has been hypothesised to be structurally related to platycephaly and occipital projection in *Homo erectus*, involving a larger percentage of posterior surface to support (Bruner 2004). Conversely, in Neanderthals and especially in modern humans the anterior branches play a more important role in the meningeal vascularisation. In the modern human sample considered in this analysis, not a single specimen was

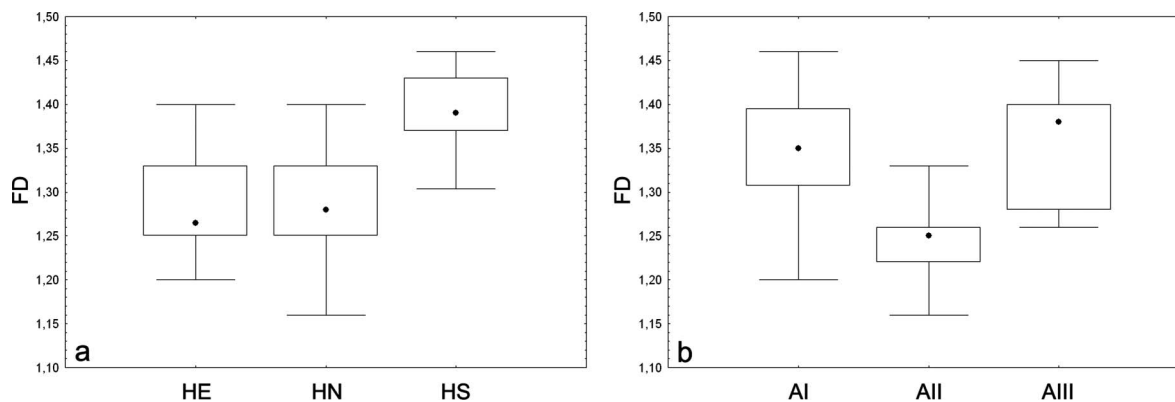


Figure 5. (a) variation of the Fractal Dimension (FD) in the three taxa (HE, *Homo erectus*; HN, *Homo neanderthalensis*; HS, *Homo sapiens*); (b) variation of the Fractal Dimension in the three Adachi patterns (AI, AII, AIII). Boxplots show median, interquartile, and range.

found to show a complete posterior dominance (Adachi type II), and this very low prevalence has been already described in living Europeans (Bruner et al. 2003a).

The obelic ramus has a great interest in paleoneurology for two main reasons. First, it covers the supramarginal and angular gyri, involved in important functional tasks as those recognised for the Wernicke area (i.e. language; see Stowe et al. 2005). Second, it covers the parietal areas, that have been hypothesised to play a fundamental role in human evolution in general and mostly in the evolution of modern humans, because of its morphological development and involvement in visuo-spatial integration (Bruner et al. 2003b; Bruner 2004). Although at present there is no recognised relationship between the distribution of the meningeal vessels and cortical functions, the correspondence between neural and vascular variations should be investigated further. In particular, the association between changes of the parietal shape and changes of the parietal network in modern humans deserves attention, mostly considering the lack of data on these topics and the current availability of computed biomedical approaches based on digital imaging techniques. Of course, apart from possible relationships with physiological correlates, primarily it must be assessed whether these arterial patterns are related to genetic/phylogenetic influences and/or structural endocranial constraints.

The application of the box-counting and the use of the fractal dimension to quantify the arterial network definitely supports the hypothesis of a species-specific branching complexity in *Homo sapiens*. In contrast, differences between Neanderthals and Asian *Homo erectus* in the degree of vascular branching are not evidenced. Considering that the cranial capacity in Neanderthals shows a similar range of variation than in modern humans, a correlation between encephalisation and vascular complexity is unlikely. In terms of reticulation

degree, these data suggest just the presence of one modern and one non-modern variation, as described also for the general endocranial structure (Bruner et al. 2003b). Furthermore, taking into account the distinctive ectocranial morphology of the anatomically modern humans (e.g. Lieberman et al. 2002), a gradual increase of complexity along the modern lineage seems improbable.

Nevertheless, considering the scarce information on the morphogenesis of many endocranial traits, some hypotheses may be further discussed. Actually, the traces detectable on the endocranial surface do not represent the entire morphological structures of the meningeal layers. The presence of a subarachnoidal space and cerebro-spinal fluid (see Peña-Melian 2000) accounts for a soft interface that easily separates the cerebral structures from the bony inner table. Furthermore, the extreme plasticity of the vascular systems and the biomechanical local environment (i.e. endocranial and cerebral pressure) act as a major structural determinant of the arterial and venous channels (Kimbel 1984; O'Laughlin 1996). Consequently, large vessels could leave but small traces on the endocranial surface, and small structures could conversely leave marked patterns depending upon local endocranial features (Campillo 2004).

Two main hypotheses therefore emerge to interpret the differences between the fractal dimensions in extinct and modern humans. First, the development of the arterial network in *Homo sapiens* can be related to higher metabolic requirements, finer thermoregulation, and/or specific and localised neuro-functional management. The complex parietal vascular network described in modern humans (e.g. Saban 1995) and the importance of the parietal cortical areas in the evolution of the modern brain shape (Bruner et al. 2003b; Bruner 2004) make this hypothesis rather interesting.

Alternatively, a different biomechanical environment can be hypothesised for extinct and extant human groups, involving a different distribution of

the cerebral pressure with consequent different effects on the relationship between meningeal soft structures and their endocranial bony traces. In this case, the less branched pattern in the endocranial surface of *Homo erectus* and *Homo neanderthalensis* could represent a lack of traces more than lack of vessels. Actually, these taxa show both a different skull architecture (Manzi et al. 2000; Bruner et al. 2004; Harvati et al. 2004) and ontogeny (Ponce de León & Zollikofer 2001; Manzi 2003; Ramirez Rozzi & Bermudez de Castro 2004) compared to modern humans. Their respective cranial functional matrices (*sensu* Moss & Young 1960) could be associated with different forces and vectorial growth with direct consequences on the patterns or cerebral pressure.

Clearly, both these processes (different neuro-functional context and different biomechanical environment) may have a role in characterising the vascular traces of the endocranial surface, and must be carefully considered.

On the relationship between anterior/posterior branch dominance, a higher fractal dimension in type I and type III Adachi patterns can be interpreted simply as a consequence of the higher percentage of modern humans in the first case, and of a double middle branch in the second one.

Beyond the methodological implications, it must be remarked that the patterns described for these three human groups are very general, and the actual variation of the genus *Homo* seems to be not so univocal. The European Middle Pleistocene parietal from Arago shows a rather developed vascular network, as well as the early Neanderthal parietal fragment Krapina 21 (Bruner 2003b) and the Biache skull (Saban 1979) of the last interglacial. Therefore, the studies on the morphology of the middle meningeal vessels must be further improved by considering a larger amount of extinct variability, exploring the structural relationships between endocranial soft and hard tissues, and improving the knowledge on the functional role of the middle meningeal system in living hominoids. Fractal analysis and box-counting represent useful techniques able to quantify differences between longitudinal and transversal samples, ontogenetic changes, and intra-population variation.

Acknowledgements

Henri and Marie-Antoniette de Lumley kindly allowed the study of fossil endocasts at the Institut de Paléontologie Humaine (Paris), under the supervision of Dominique Grimaud-Hervé. Aldo and Eugenia Segre encouraged the study of the endocast collection at the Istituto Italiano di Paleontologia Umana (Roma). This research is partially supported by the Istituto Italiano di Antropologia and by the Ministero per l'Istruzione, Università e Ricerca (MIUR).

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