

## Fossil traces of the human thought: paleoneurology and the evolution of the genus *Homo*

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**Summary** – Paleoneurology is the study of brain evolution by means of the morphological and anatomical analysis of the endocranial traits and volumes. The reconstruction of the endocasts of fossil hominids allows inferences on functional anatomy, physiology, and phylogeny. Brain size and shape must be analysed within a structural context in which the relationships between each part is the result of a biomechanical and functional integrated system. This review on the main endocranial characters is aimed at synthesising some recent advances in human brain evolution, summarising the present knowledge on asymmetries, middle meningeal vessels, venous sinuses, and other related issues. Particular attention is focused on the development of the neurosciences, to allow the access to functional inferences. Computed tomography and virtual imaging supplied the more relevant improvement to the development of paleoneurology. The endocranial morphology does not represent the original brain anatomy, and the consequent results must be interpreted adequately. However, paleoneurology is the only available tool to analyse and understand human brain evolution.

**Keywords** – *Endocasts, Brain evolution, Genus Homo.*

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“Las cabezas humanas, como las palmeras del desierto, se fecundan a distancia.”  
(Santiago Ramón y Cajal - *Reglas y Consejos Sobre Investigación Científica*, 1898)

### Paleoneurology

Skull bones, mostly those involved in neurocranial anatomy, do not grow by self-expansion but in response to cerebral growth pressures (Moss & Young, 1960; Enlow, 1990). The growth of cerebral mass separates the bones at the sutures, inducing osteoblasts to “fill the gap” and promoting ectocranial bone deposition, while on the endocranial surface the osteoclastic processes allow a shifting of the bony elements. This correspondence between the inner table and brain makes the endocranial cavity a very useful mould of the cerebral surface and volume, as well as of supporting structures like vessels and dura systems. Thus inferences about cerebral anatomy can be made directly from paleontological remains. This approach is the basis of *paleoneurology*, namely the examination and analysis of natural or artificial endocasts reproducing details of the external morphology of the brain (Falk, 1987).

In this paper, some of the major topics of paleoneurological studies will be revised, in order to describe the general features of this emerging science. Encephalisation and brain size evolution will be briefly discussed. Then, the shape variability of the brain morphology in the genus *Homo* will be described, in order to consider the spatial relationships between the principal cortical districts. The evolution of asymmetries and circumvolutions will be analysed to approach the emispheric specialisation. The vascular patterns (middle meningeal artery, venous sinuses) will be described and interpreted. Some considerations on the functional and structural network of brain evolution will be then provided. Some recent advances in neontologic neurosciences are described to integrate the information from the fossil record. Finally, computed tomography and imaging techniques are introduced, with some additional methodological notes.

### Beyond the brain size

The first aim of hominid paleoneurology was clearly the analysis of brain size evolution. Primates show an autapomorphic high level of encephalisation, that is not developed by a metabolic increase (as in sea mammals) but by a reallocation of energy (Martin, 1981; Armstrong, 1983). Hominid evolution was based on an extreme expression of this process, that determined the main characterisation of this taxon. It must be considered that the human brain receives 20-25% of the basal metabolic power, compared with about 8% in non-human primates, and 4-6% in non-primates mammals (Leonard & Robertson, 1992).

There is still no agreement on the pattern involved, tested by gradual vs. punctuationalist models (Godfrey & Jacobs, 1981; Falk, 1987), but on a behavioural basis a discrete cultural “revolution” has not been clearly proved (McBrearty & Brooks, 2000). The first hominids barely departed from living African apes in cerebral volume (Tobias, 1995) and even after the radiation of the genus *Homo* there seems to have been a long successive stasis between 1,8 Ma and 600 ka, taking into account the body mass increase (Ruff *et al.*, 1997; Conroy *et al.*, 2000a). A linear model of cranial capacity increase proposed by Holloway hypothesises an early slight allometric trend in Australopithecinae, a successive size-unrelated brain enlargement in *Homo habilis*, a minor increase related to body size in *H. erectus* and a further gradual size-unrelated enlargement and reorganisation in subsequent *Homo* taxa (Holloway, 1995). An autocatalytic model is often used to explain brain enlargement during human evolution, describing a positive feedback between cerebral complexity and consequent socio-cultural factors.

After the emergence of anatomically modern humans, a decrease of brain size was related to a generalised gracilisation of the body structures (Henneberg, 1988; Ruff *et al.*, 1997). Table 1 shows some general reference values for cranial capacities of the main hominid groups. It must be stressed that an encephalisation process was operating

**Tab. 1 - Means and standard deviations of cranial capacity (cc) in some taxonomic groups (data pooled from Aiello & Dean, 1990 and Schwartz & Tattersall, 2002). N: number of specimen considered.**

	<i>N</i>	<i>mean</i>	<i>sd</i>
<i>Australopithecus</i> sp.	10	442	39
<i>Paranthropus</i> sp.	10	481	47
early <i>Homo</i>	8	654	96
<i>Homo ergaster</i>	8	835	123
<i>Homo erectus</i>	18	1026	141
Euroafrican Middle Pleistocene	15	1259	122
Neandertals	20	1427	173
Late Pleistocene modern humans	20	1488	112

in *Homo* as well as in *Paranthropus*, leading to a certain degree of evolutionary parallelism (Elton *et al.*, 2001). Figure 1 shows the cranial capacity in some specimens of the genus *Homo* plotted on a temporal axis.

The brain volume reorganisation was clearly related to changes in skull architecture, that was affected by allometric trends and structural constraints. For instance basicranial flexion, that represents a mechanism to control brain expansion in Primates, may have reached some functional limits, needing to be supported by other compensation processes for “spatial packing” (Ross & Henneberg, 1995; Jeffery & Spoor, 2002; but see McCarthy, 2001).

In Primates most of the life-cycle parameters are related to brain size (Harvey and Clutton-Brock, 1985), and in the human lineage the encephalisation process has necessarily required a reassessment of all the biological variables, such as longevity (see Bruner & Manzi, 2001a) or secondary altriciality (Foley & Lee, 1991; Begun & Walker, 1993). It must be stressed that the evolution of brain volume and its requirements is directly connected with ecological factors like diet, home range and social structure (Foley & Lee, 1991; Leonard & Robertson, 1992, 1994, 1997; Elton *et al.*, 2001), producing a complex biological network where causal relations are often confused and emergent functions are not easily interpreted.

As cautionary note, it must be remarked that the endocranial capacity does not represent exactly the brain volume, including the subarachnoidal interfaces that can account for 300 cc (Peña-Melian, 2000).

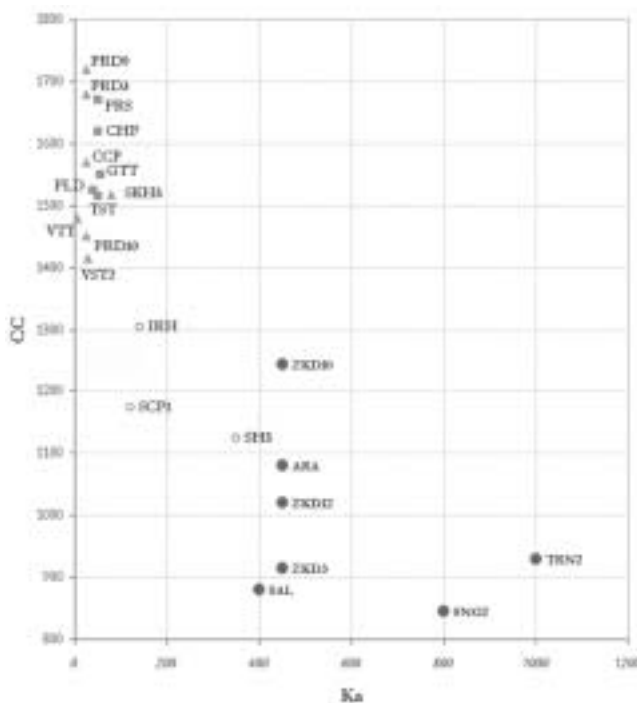


Fig. 1 - Cranial capacity (cc) plotted on chronology (*kilo annum*, ka) for some specimens included in the *Homo* radiation. ARA: Arago; CCP: Combe Capelle; CHP: La-Chapelle-aux-Saints; FRS: La Ferrassie; GTT: Guattari; IRH: Djebel Irhoud; PRD: Predmosti; SAL: Salé; SCP: Saccopastore; SH: Sima de los Huesos; SKH: Skhul; SNG: Sangiran; TRN: Trinil; TST: Tesik-Tash; VST: Vestonice; ZKD: Zhoukoudian; Black circles: *Homo erectus* s.l.; Squares: *Homo neanderthalensis*; Triangles: *Homo sapiens*; Empty circles: other specimens.

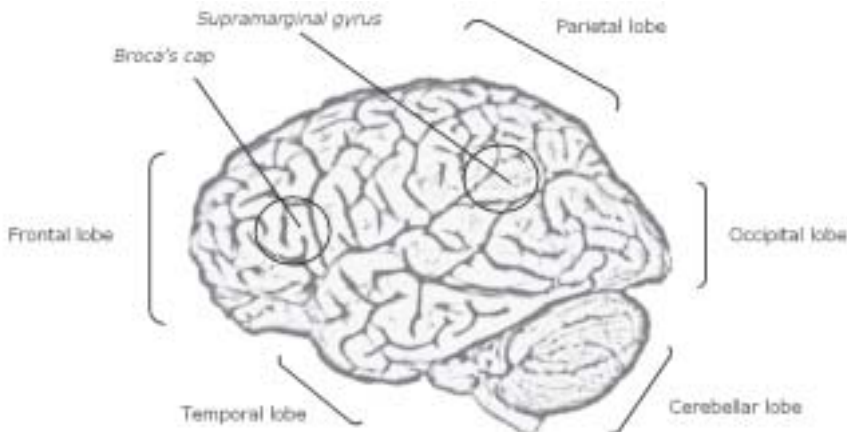
## Brain shape

The basic information available from an endocranial cast is the shape of the brain itself, namely the geometry of the entire structure, its general morphology, and the spatial relationships between each single cerebral districts (Fig. 2).

Much interest has been devoted to the frontal lobes, which have been hypothesised to be involved in higher cerebral functions such as consciousness, abstraction, planning, and language. It has recently been proposed that derived morphological features of frontal areas can be found very early in the human lineage, namely in the orbital structures of *Australopithecus*, but not in *Paranthropus* (Falk *et al.*, 2000). In contrast, a comparison between Middle Pleistocene and modern human variability in the frontal midsagittal endocranial profile has revealed no general shape differences (Bookstein *et al.*, 1999). In *Homo erectus*, the frontal width is relatively limited, especially at the base of the third circumvolutions (Broca's cap), and there is a marked encephalic rostrum due to the midline inclination and separation of the frontal lobes (Grimaud-Hervé, 1997). In more derived morphs, such as Neandertals and especially modern humans, the frontal width increases, with a consequent decrease of the rostrum expression. Usually, the frontal poles lie almost entirely onto the orbital plates. In some robust Middle Pleistocene specimens such as Petralona and Kawbe, the marked pneumatisation and the massive structure of the supraorbital areas push the frontal lobes almost behind the roof of the orbits (Seidler *et al.*, 1997). The whole volume is therefore tilted backward, as can be recognised by the orientation of the *crista galli*.

The brain's maximum width is located at the temporal base in *Homo erectus* and other Middle Pleistocene groups, between the temporal and parietal areas in Neandertals, and at the parietals in anatomically modern humans (Holloway, 1980; Grimaud-Hervé, 1997; Seidler *et al.*, 1997). Consequently, from the posterior view the more archaic specimens show the classic "tent-like" profile, while in Neandertals the upper parietal development leads to the *en bombe* morphology, and in modern humans towards a "housed" shape.

The occipital lobes project backward behind the parietal profile in more archaic brains, shifting under the parietal areas as brain size increases. In modern humans they are relatively reduced, and flattened against the temporo-parietal areas. KNM-WT 15000 (dated to about 1.5 Ma) and the other specimens included in the *Homo ergaster* hypodigm show an endocast quite comparable with those of Asian *Homo*



**Fig. 2 - Principal districts of the human brain. The area of the Broca's cap and the *supramarginal gyrus* (included in the Wernicke's area) are also indicated.**

*erectus*, but with a less developed frontal diameter and without the typical occipital projection (Begun & Walker, 1993).

The cerebellar structures are located under the occipital poles in archaic *Homo erectus*, under the parietals in more derived taxa and almost under the temporal areas in modern humans (Grimaud-Hervé, 1997). In Middle Pleistocene hominids the cerebellar lobes are elongated and quite separated, becoming tighter, more globular and approaching the midline in modern humans. A three-step model has recently been proposed for human cerebellar evolution (Weaver, 2002): non-allometric brain enlargement with cerebellar increase (early *Homo* and *H. erectus*), brain development without cerebellar evolution (from the Afro-European Middle Pleistocene to early modern *H. sapiens*), and a decrease in brain and body size with relative and absolute development of cerebellar structure (anatomically modern humans).

As size increases, a general closure and tightness of the interposing spaces (scissures, Sylvian valley, temporo-cerebellar valley) can be observed.

It is possible that during the human radiation an early derivation of frontal areas was followed by a late and gradual evolution of posterior districts (Falk *et al.*, 2000). In earlier hominids the principal differences may have been a reduction of the primary visual striate cortex, a reorganisation of the frontal lobe (mostly at the third frontal circumvolutions), and the expression of hemispheric specialisation (Holloway, 1995). Subsequently, the development of the posterior parietal cortex may have been related to an increase in visuospatial integration, as well as in sensory reception and social communication.

Plates I-III show the left lateral view of endocasts in different *Homo* taxa, from Arago (ARA), Combe Capelle (CCP), La-Chapelle-aux-Saints (CHP), Feldhofer (FLD), La Ferrassie (FRS), Guattari (GTT), Djebel Irhoud (IRH), Predmosti (PRD), Salè (SAL), Sima de los Huesos (SH), Skhul (SKH), Sangiran (SNG), Trinil (TRN), Tesik-Tash (TST), Vatte di Zambana (VTT), Vestonice (VST), Zhoukoudian (ZKD), and a recent human endocast with a marked brachymorphic morphology (RHE).

### Asymmetry and circumvolutions

The increase in brain complexity seems to be linked to the expression of cerebral asymmetries (Hellige, 1993). Volumetric differences between the two hemispheres are related to a relative hypertrophy of a district with respect to the opposite homologous side. An asymmetry due to the enlargement of a lobe (mainly frontal and occipital) with respect to the hemispheric counterpart is called *petalia*. Clearly, differences in macro- and microanatomy, as well as in metabolism, account for differences in function and cortical specialisation between hemispheres. Concerning general hemispheric dominance in *Homo sapiens*, the left hemisphere is often related to learning, analytical and sequential processes, such as the execution and coordination of movements or language organisation (syntax, decoding, producing), discrimination, categorisations and local dynamics, while the right side is linked to emotional systems, visuospatial processing, relational aspects and global dynamics. However it must be stressed that any function is composed of independently located sub-processes, and even if one hemisphere can dominate in a functional context, both sides are still involved in any task and thus are complementary.

In modern and fossil humans the most common and distinctive general pattern is a dominance of the right frontal and left occipital lobes, namely right frontal (RF) and left occipital (LO) petalias (LeMay, 1976; Holloway & De La Coste-Lareymondie, 1982).

Non-human primates show different degrees of cerebral asymmetries, but generally not as developed as in the human brain (Fig. 3). *Macaca* shows a RF petalia involving both the orbital and dorsolateral areas, with a possible associated LO development (Cheverud *et al.*, 1990a, 1990b; Falk *et al.*, 1990). The great apes present specific patterns, more marked in *Gorilla* with a LO dominance (Holloway & De La Coste-Lareymondie, 1982).

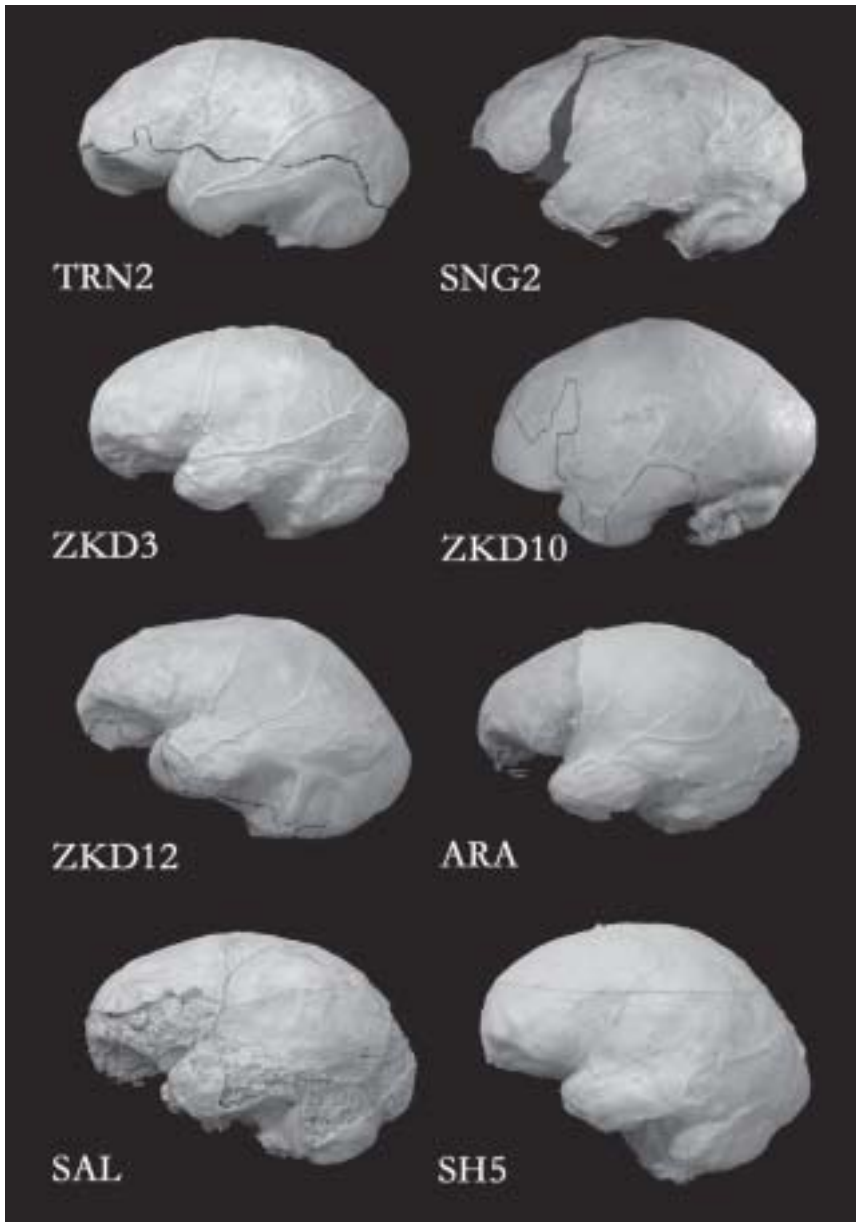


Plate I - Endocasts of fossil hominids (left lateral view).

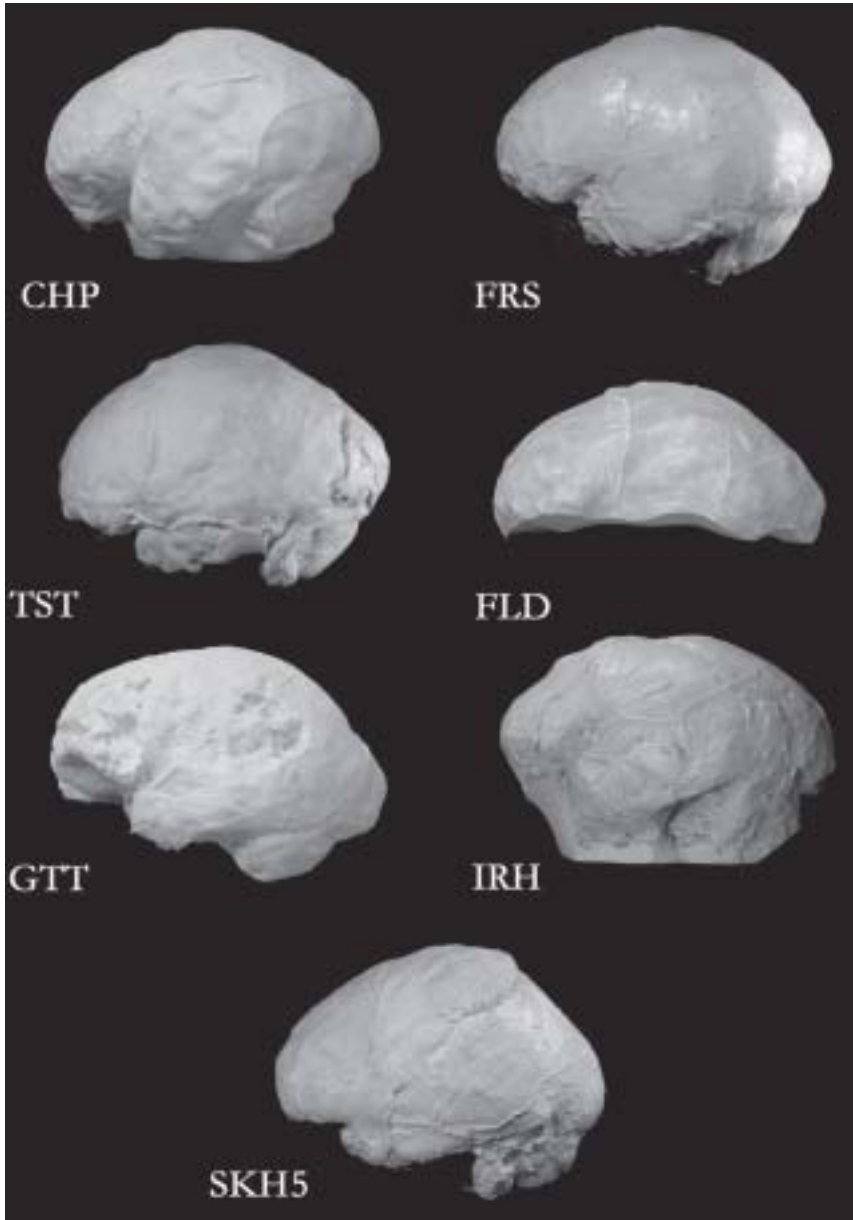


Plate II - Endcasts of fossil hominids (left lateral view).

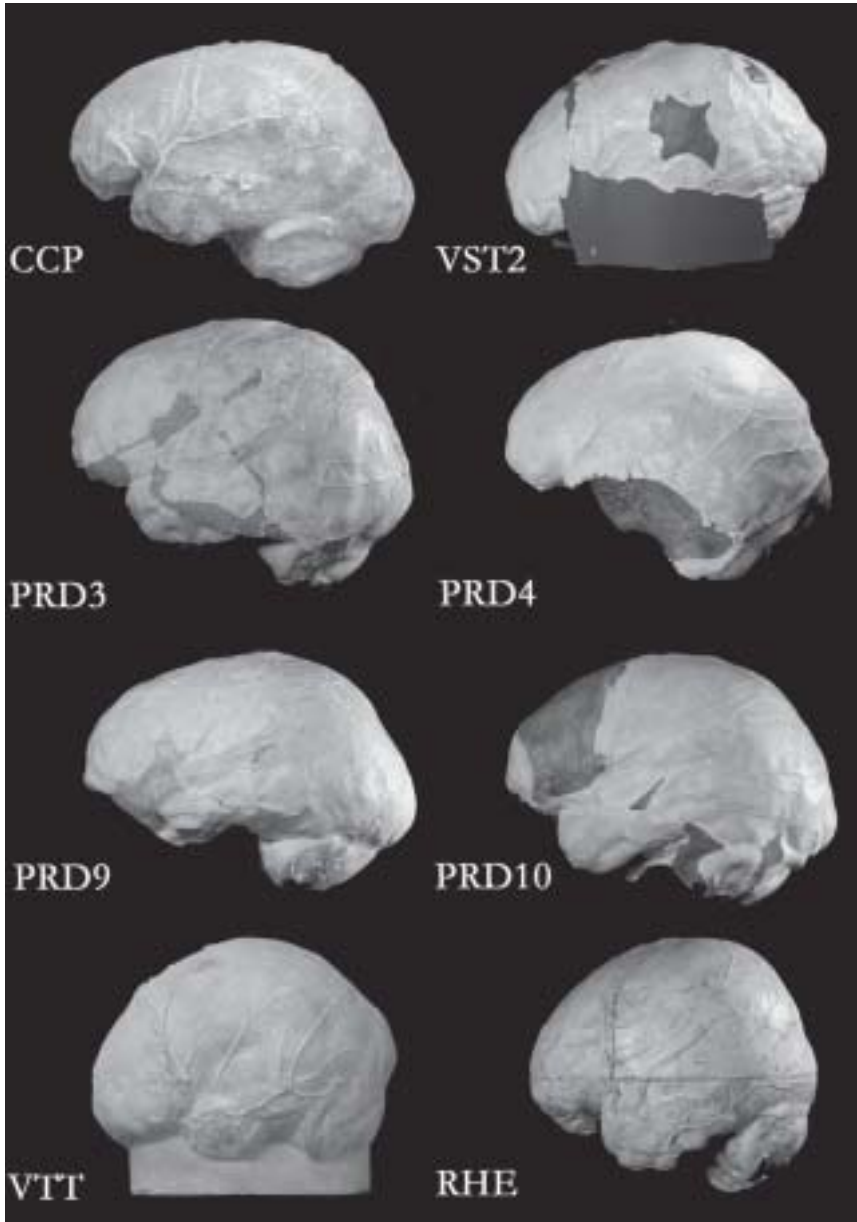
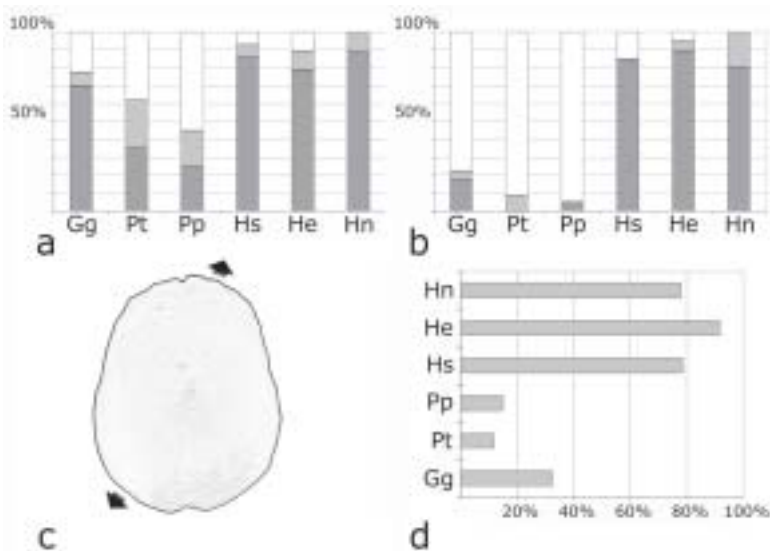


Plate III - Endocasts of fossil hominids (left lateral view).





**Fig. 3 - Cerebral asymmetries in Hominoidea: longitudinal occipital asymmetry (a), lateral occipital asymmetry (b), morphology (c) and prevalence (d) of right-frontal left-occipital petalias. Gg: *Gorilla gorilla*; Pt: *Pan troglodytes*; Pp: *Pongo pygmaeus*; Hs: *Homo sapiens*; He: *Homo erectus*; Hn: *Homo neanderthalensis*. a,b: Dark grey: left dominance; light grey: right dominance; white: no dominance. Data from Holloway & De La Coste-Lareymondie, 1982.**

Since brain asymmetries have been related to handedness (Galaburda et al., 1978), there have been many attempts to analyse the relationship between petalias and behavioural components. Right hand preference has been correlated to a left dominance of the structures located at the third frontal circumvolution. The same areas were identified by Paul Broca as the main centres of language production and integration (Broca's area). In general, while the right frontal lobe is larger both laterally and frontally, the left frontal lobe shows a larger expression of these circumvolutions, in particular the proximal tract (*pars opercularis*) and the middle one (*pars triangularis*). The *pars triangularis* shows left asymmetry in right-handers, while it is less asymmetric in left-handers. The *pars opercularis* is again left-dominant in right-handers and it is often right-dominant in left-handers (Foundas et al., 1998a). Left-handers generally show a smaller degree of asymmetry and frequently can present a left frontal-right occipital petalia (LeMay, 1977). A similar left dominance for right-handers and smaller asymmetry for left-handers has also been recorded in the precentral gyrus (Foundas et al., 1998b).

A second area of left dominance is the temporal planum, and in particular the supramarginal gyrus (LeMay, 1976; Bradshaw, 1988), included in Wernicke's area and related to speech integration. Consequently, the Sylvian scissure is straighter and longer in the left hemisphere, and this pattern is even present in the *Macaca* endocast (Falk et al., 1986).

Asymmetries in both Broca's area and the temporal planum have been found in modern apes (Gannon et al., 1998; Cantalupo & Hopkins, 2001). Thus, they represent shared characters in Hominoidea, and differences can be displayed only in the degree of expression.

All the features linked to brain asymmetry in modern humans have been detected in many fossil specimens of the genus *Homo* (Holloway, 1980, 1981a, 1981b;

Grimaud-Hervé, 1997), although there is a lesser expression of the circumvolution systems on the fossil endocasts. Thus it seems possible that the development of marked brain asymmetry was an early derivation during human evolution, and symbolic or visuospatial integration may have represented a major selective force (Holloway & De La Coste-Lareymondie, 1982). Many of the asymmetry patterns are expressed in non-human primates, and it is possible that such features are plesiomorphic characters that represented the substratum for a pre-adaptation to hemispheric specialisation in human evolution. Both speech and handedness (linked both to tool-making and communication) are serial, syntactic and manipulatory behaviours based on complex articulations of biomechanical patterns (Bradshaw, 1988, 1997; Hellige, 1993). The same areas involved in language production are activated by tongue or hand movements, and they are thus probably better linked to motor programming and praxis (e.g. Begun & Walker, 1993). In monkeys, it has been suggested that the asymmetry in Broca's cap could be related to gestures and vocalisation (Cantalupo & Hopkins, 2001). It is therefore possible to hypothesise some basic integration between the evolution of language and tools, as well as a "snowball effect" based on an autocatalytic model between the general primate asymmetry and social complexity, resulting in the extreme hemispheric specialisation of the human brain.

In summary, concerning asymmetries, in the genus *Homo* no particular trend can be defined except a general accentuation of some patterns already recorded in non-human primates. Generally, there is right-dominance for the anterior and middle areas, left-dominance for the occipital districts, and a more marked expression of the major circumvolutions in the left hemisphere (Grimaud-Hervé, 1997). What may be interesting in future perspectives is the development of a useful scoring procedure to quantify asymmetry, to analyse how and how much human asymmetries are the result of a clear hemispheric specialisation, or else an allometric structural stressing of a common pattern.

### **Vascular systems**

Because of the tight structural relationship between the brain and the inner table of the vault, the endocranial surface is a useful record of the pre-existent soft tissue, such as the arterial networks and the venous drainage. Of course, a trace is not the object itself, but a partial information. What can be detected on the bone is the trace of something that was there. In contrast, the presence of what cannot be detected cannot be excluded. The vascular vessels leave their traces proportionally to variables such as the endocranial local pressures, or the thickness of the interposing tissues (i.d. the dura layers). As stressed previously, the subarachnoidal spaces represent another marked volumetric interface between the brain and the endocranial wall (Peña-Melian, 2000). Therefore, in relation to different mechanic environments a trace will be stronger or lighter. Small vessels can leave marked traces, and large ones cannot even be recognised (Mannu, 1911; Kimbel, 1984; Zollikofer & Ponce de León, 2000).

These endocranial traces represent somehow "fossilised" physiological processes. The vascular network is related to the main cerebral functions and requirements, namely the energy supply and thermoregulation. Energy means metabolism, thus biochemical power and activation of neural processes. As stressed previously, in modern humans the cerebral metabolism account for the 20-25% of the total energy requirements, with consequently high thermal loads. At the same time, the brain is not capable of internal thermal control, except by regulation of the blood input and output through the vessels. In this context, the vascular systems on the endocast offer some additional physiological information useful to further functional approaches.

#### *Middle meningeal system*

One of the most visible marks on the endocranial surface is the trace of the middle meningeal artery. In humans, this is a branch of the maxillary artery, stemming from

the external carotid. The exact anatomical origin of the meningeal grooves is not still clear (Falk & Nicholls, 1992). The artery is firmly joined to a couple of parameningeal veins draining the diploe, the dura mater and the periosteum, that can form large sinuses (sphenoparietal and petrosquamous), and students do not agree about which vessel is the main source of the visible grooves. A direct communication between the meningeal artery and parameningeal veins has also been suggested, which could cause further confusion. For this reason, here the marks will be referred to in general as the Middle Meningeal System (MMS). An anterior network of the meningeal system supplies the frontal areas connecting the superior ophthalmic vessels, while the MMS represents a posterior network covering the fronto-temporal surfaces with veins draining into the pterygoid venous plexus (Saban, 1995). The MMS is generally formed by three branches: anterior (bregmatic), middle (obelic) and posterior (lambdatic). The anterior ramus is probably homologous to the anterior orbital branch of non-human primates, whose backward shift towards the middle cranial fossa and development is probably related to the increase of cranial capacity (Diamond, 1991, 1992; Falk & Nicholls, 1992; Falk, 1993). Tens of classification models have been proposed to describe the variability of MMS patterns, based on shape, surfaces, branching pattern or vessel origin, but there has been no agreement on a common and useful scheme to be employed. The simplest is that of Adachi: it classifies each MMS depending upon the origin of the middle branch which can derive from the anterior ramus (type I), from the posterior ramus (type II), or from both of them (type III). In modern human populations the type I morphology is observed in 44-45% of the cases (Falk, 1993; Bruner et al., 2003). It must be stressed that a clear attribution of a single specimen to a schematic MMS pattern is rarely possible, and classifications must refer to the general aspect and organisation of the meningeal vessels. Some early recognised characters of the modern MMS were the large development of the anterior branch, a probable dominance of the left system, and the lack of clear inter-population differences (Marcozzi, 1942; Bruner et al., 2003). There were early attempts by Weidenreich to show that the pattern in the human fossil species resembled the ape pattern, and there have been recent attempts to interpret the extinct human patterns as a *scala naturae* based on ontogenetic progresses (Saban, 1995). However it was soon clear that the extinct *Homo* morphotypes were not comparable morphologically or evolutionarily with those of extant non-human primates (Marcozzi, 1942; Falk, 1993).

The analysis of endocasts generally reveals an increase in the frontal network development and an increase in the complexity of the anastomotic system during human evolution (Saban, 1995). Anatomically modern samples like the ones from Brno, Dolni Vestonice and Predmostí are characterised by a marked development of the parietal grooves (Saban, 1982), although vascular anastomoses in the parietal areas have also been detected in the early Neandertal from Biache-Saint Vaast (Saban, 1979).

Some general trends and patterns can be used as simplified and useful indications of more complex variability (Grimaud-Hervé, 1997). Asian *Homo erectus* specimens show a dominance of the posterior branch with derivation of the obelic ramus (Zhoukoudian) or equivalence in anterior and posterior systems with a double origin of the middle segment (Trinil, Sangiran). In Neandertals there is an equivalence of the two branches, while in anatomically modern groups a dominance of the anterior branch with derivation of the obelic branch is the most common pattern (Fig. 4). The anterior ramus runs from the posterior regions of the frontal circumvolutions to the ascending parietal one in *Sinanthropus*, reaching the anterior regions of the parietal circumvolutions in some Middle Pleistocene specimens and approaching the supramarginal lobule in Neandertals. In anatomically modern humans this branch may reach the angular gyrus (Upper Pleistocene), and it covers from the posterior areas of the frontal lobes to nearly the entire parietal surfaces (present populations). In contrast the posterior ramus runs from the supramarginal lobule to the posterior region of the angular gyrus in Asian *Homo erectus*, while it is limited to the latter area



**Fig. 4 - Principal middle meningeal traces on the endocrasts of Zhoukoudian XII (left), La-Chapelle-aux-Saints (middle), and Combe Capelle (right). Combe Capelle has been flipped to show the more preserved right hemisphere.**

in other extinct groups and it is a single and non-branched ramus in modern humans. At the same time, the more it loses importance the more it shifts from parallel to the anterior branch to markedly oblique. Anastomotic systems seem to be more frequent after the Middle Pleistocene, although they are rare in Neandertals, who furthermore show poorly ramified branches with respect to their encephalisation features.

Generally, the more a taxon is encephalised, the more the anterior (bregmatic) branch dominates over the posterior (lambda) ramus, both in terms of complexity and parietal (obelic) supply (Saban, 1995; Grimaud-Hervé, 1997). According to the relation between surface and volume, an increase of the vascular system was expected on the surface to keep pace with a faster allometric increase of brain mass. This hypothesis seems not to be verified. Even if Neandertals show a more encephalised brain than the archaic specimens, an increase of the vascular network complexity is not detected by visual inspection. The branching pattern could be even less developed in many individuals. Whether or not this pattern is physiologically consistent must be further investigated. It must be considered that some taphonomic processes may have biased the detection of the vascular system.

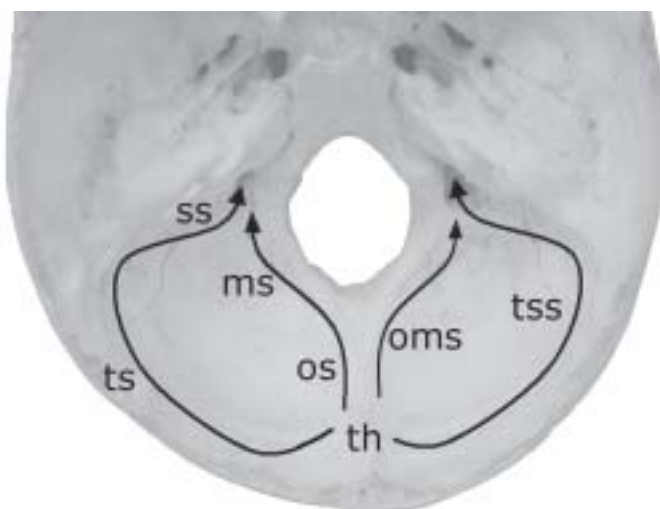
Considering that the vascular traces are not completely related to the original soft tissue, some differences in brain pressure or other physiological and histological variables could affect the result. Therefore, the presence of a more branched pattern and development of anastomoses seems unrelated to size, but instead mainly to the specific parietal expansion in modern humans. The meningeal vessels are extremely plastic to physiological and biomechanical variations, as can be demonstrated analysing the response to craniosynostotic or artificial skull deformations (O’Laughlin, 1996). In both cases, the MMS is subjected locally to the pressure of the deformation, and the vessels are then redirected to compensate for the blood flow in undistorted areas. Thus the presence of a specific branch, the enlargement of a ramus or the degree of arborisation can depend upon geometric and functional constraints on the whole structure. Therefore, we must assume that a large amount of the middle meningeal system variability is not related to specific functions or adaptive response, but may represent a structural (individual) consequence of the whole brain architecture. The analysis of the pattern matching between hemispheres could be a useful approach to this issue, showing the sensitivity of the same genetic background to the endocranial asymmetries. A close correspondence between hemispheres has been observed for the Adachi I and II patterns. In contrast, the Adachi III pattern on one hemisphere is often matched to a different pattern on the counterpart (Bruner *et al.*, 2003). The MMS pattern is probably a “index” of the brain shape, sensitive to the overall structural and functional balance. The Adachi III scheme is probably a “intermediate” and unbalanced phenotype, that easily shifts to another morphology according to some minor volumetric change.

Physiological activation of some networks by metabolic increase or the development of trajectories by minimum resistance pathways should play a major role throughout the morphogenetic processes. Different morphotypes can be therefore associated with specific brain shapes, independently of direct genetic influences or

even phylogenetic relationships. This sensitivity to the morphological environment makes these systems quite inappropriate in a systematic context, but more useful to delineate models of biomechanical and structural processes.

#### *Venous sinuses*

Catarrhines, contrary to most other mammalian taxa, show an endocranial venous drainage directed principally toward the internal jugular veins. A system of venous sinuses runs into the layers of the dura mater, representing the main system of regulation of the cerebral blood flow (see Kimbel, 1984; Saban, 1995; Grimaud-Hervé, 1997). The drainage is the result of a complex network in which the dura sinuses receive flows from the middle meningeal vessel as well as from the diploë, from the pericranium and from the cerebral vascular complex, by direct junctions, capillary nets and anastomoses. The superior sagittal sinus runs medially from the *foramen caecum* to the internal occipital protuberance, passing under the vault roof. In proximity to the internal occipital protuberance the superior sagittal sinus enlarges into a confluence of sinuses or *torcular herophili* (Fig. 5). This structure also receives the straight sinus from the cerebral volume and the two transverse sinuses running laterally through the occipital and parietal bones to the jugular fossae through the curved sigmoid sinuses (Transverse-Sigmoid System, TSS). Many attempts to classify different confluence patterns have not managed to agree on the frequencies of these traits (see Romagna-Manoia, 1911; Grimaud-Hervé, 1997). Marked variability, subjective interpretations and problems in dissection techniques have provided extremely different results (see Bruner *et al.*, 2003). Nevertheless, the most common pattern in human populations is an asymmetrical flow with the larger blood volume from the superior sagittal sinus flowing into the right transverse one (but see Navsa & Kramer, 1998). This asymmetry is probably a direct consequence of the petalia pattern, and it is clearly individual-specific. Even if the direction of blood flow is mainly from the sagittal sinus to the jugular veins, a double or inverted circulation in the transverse sinuses is a common physiological status (Kuroiwa *et al.*, 1995). A second but less common drainage network complementary to the TSS is the Occipito-Marginal System (OMS). One or two occipital sinuses pass from the confluence



**Fig. 5** - The venous drainage at the posterior fossa; ms: marginal sinus; oms: occipito-marginal system; os: occipital sinus; ss: sigmoid sinus; th: torcular herophili, or confluence of sinuses; ts: transverse sinus; tss: transverse-sigmoid system.

downward through the lower rim of the internal occipital crest and then pass laterally to the foramen magnum as marginal sinuses to join the jugular veins at the jugular fossa. This rare feature gained some attention when it was found in a presumed *Australopithecus* lineage (*A. afarensis* and the *Paranthropus* clade) with some inferential hypotheses about adaptations to upright posture (Falk & Conroy, 1983; Tobias & Falk, 1988). Analyses of modern populations have shown that, although this character is difficult to sample and record objectively in anatomical studies, the usual low frequency (around 6-7%) can be replaced locally by extremely high frequencies, reaching 30% of cases (Kimbel, 1984; Bruner *et al.*, 2003). The Atapuerca sample from Sima de los Huesos shows this trait on two out of four specimens preserving the foramen magnum (Arsuaga *et al.*, 1997). The Late Pleistocene sample from Predmostí, dated to about 26 ka, presents a frequency of 45%. Other OMSs have been detected in Brno III and in the Middle Pleistocene fragments from Vertesszöllos. Other fossil specimens show the common TSS, without any particular pattern or distribution (Hollaway, 1981a; Kimbel, 1984; Grimaud-Hervé, 1997).

Both the TSS and OMS develop during ontogeny, with the latter appearing later but generally decreasing after childhood. It has been assumed that both systems are adaptively equivalent, with a low frequency of the OMS that can increase following genetic isolation, interbreeding or epistatic population interactions (Kimbel, 1984). Furthermore, the presence of one of these two systems is not related to the absence of the other. In contrast, the absence of one of them necessarily requires the development of the second. It must be stressed that sinus asymmetry is less marked in apes, and an OMS is often present but not as developed as in humans.

Among the many other additional sinuses, particular attention must be paid to the speno-parietal sinus, or Breschet's sinus (Fig. 6), running coronally from parieto-sagittal arachnoid granulations or lateral lacunas to the cavernous sinuses, and draining the dural, meningeal, diploic and anterior cerebral veins (Grimaud-Hervé, 1997). The anterior parameningeal veins could be extremely developed (great anterior vein) and easily be incorrectly identified as a speno-parietal sinus (Saban, 1995). In general, an artery has a mark enlarging downward, arborised and with a more defined border, while a sinus shows a gradual enlargement approaching the vault, little or no arborisation, and a smoother outline. However, the presence of a speno-parietal sinus on the endocranial surface is not easily detectable, and many analyses have been biased by an unclear variability.

The mark of Breschet's sinus is a rather rare character; it is poorly expressed in Asian *Homo erectus* and has an extremely low incidence in modern humans, but a

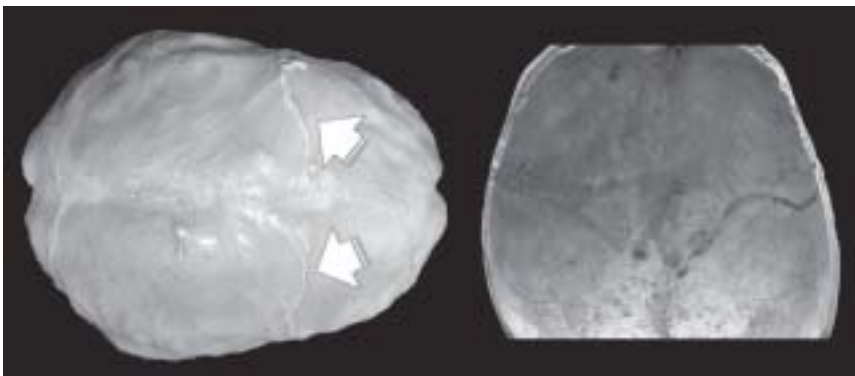


Fig. 6 - The trace of a bilateral speno-parietal sinus originating from a lateral lacuna, on the endocast of the Feldhofer calotte (left) and on a modern endocranial surface (right).

high frequency in Neandertals (Gracia, 1991; Saban, 1995; Grimaud-Hervé, 1997). The common presence in Neandertal specimens has even been proposed as an autapomorphic trait. It is clear that cladistically it is not possible to define a character on the basis of a high frequency; thus, it would be better not to use this feature in phylogenetic inferences. Nevertheless the distribution of this feature in Neandertal populations could be useful as a marker of genetic isolation, more than for functional (adaptive or physiological) hypotheses. The prevalence in the modern populations - ranging from 5 to 20% - is higher in males than in females, but without a clear relation with size (Bruner *et al.*, 2003).

It must be stressed that, as previously described for the MMS, these characters should better be defined as “epigenetic”. The genetic background probably acts indirectly, leading to some volumetric development that secondarily affects the vessels morphology together with a marked environmental variables. Affinities between specimens or taxa for some of these features should therefore be interpreted as a common structural and functional environment. Sinuses become wider and deeper along craniosynostotic sutures, but shallower in artificially deformed skulls. In the latter situation, compensatory processes take place far away from the deformation, and the frequency of OMS rises to almost 71% (O’Laughlin, 1996). In some cases the internal jugular outflow can be almost entirely redirected to the vertebral plexus, through a communication with the cranial base (Andeweg, 1996), or partially shifted to the emissary veins and foramina.

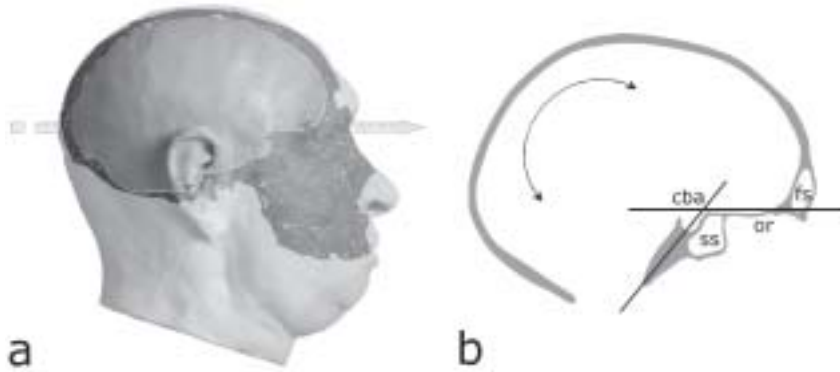
Presently, no relationships have been found between the meningeal and venous patterns (Bruner *et al.*, 2003).

Generally, the venous drainage does not seem to present any adaptive variation within the different *Homo* species. The only characters showing a particular prevalence are those regarded as non-adaptive genetic markers, namely the speno-parietal sinus and the occipito-marginal system. The patterns at the confluence of sinuses, with all the extreme variability presented, could be merely a secondary product of cerebral asymmetries (Romagna-Manoia, 1911; Grimaud-Hervé, 1997). Except for their possible role as interbreeding (kinship) indices and except for analyses in which these traits are investigated *per se* in a within-species context, they presently should not provide any functional approach to the evolution of the genus *Homo*.

### Functions, processes and brain evolution

As previously stressed, cranial growth is strictly related to brain development both in size and shape changes (Enlow, 1990). At the same time, the endocranial structures can direct and balance the endocranial pressure following principles based on forces and tensions. All the meningeal layers (including the *falx cerebri*, the *falx cerebelli* and the *tentorium cerebelli*) act as a network of biomechanical supports providing a sensitive control of the developmental dynamics (Moss & Young, 1960; Jeffrey, 2002). The brain and endocranium constitute a complex feedback system in which every structure is ontogenetically linked to the whole system, with fine genetic regulation associated with marked physiological plasticity.

Considering the entire cranial system, the development of a specific district will clearly affect the balance of the structural network. In many extinct hominids the functional cerebral axis - namely according to the *in vivo* position of the head - could have been aligned with the maximum cerebral length (Fig. 7a). It should be tested how and how much the development of the parietal volume in the modern population induced a re-orientation of the entire structure with a separation between the geometrical axis (fronto-occipital) and the new functional one (fronto-parietal). The vertical development of the whole cranium probably has a determinant role on the basicranial flexion (Bruner *et al.*, 2003). Furthermore, a parietal enlargement should influence the morphogenesis of the cranial base architecture, that represents the interface between neurocranium and splanchnocranium directly or by means of the paranasal sinuses (Fig. 7b). Presently, a large and complex literature on this issue is



**Fig. 7 - a) the skull (dark shade) and the endocrast (light shade) of Saccopastore 1 are superimposed on the facial reconstruction of the same specimen based on forensic anthropology techniques (morphing by Kennis & Kennis). The functional axis of the brain should be oriented according to its maximum fronto-occipital length. b) Mid-sagittal neurocranial section of a modern cranium showing the relationship between parietal development, cranial base angle (cba), orbital plates (or), sphenoidal sinus (ss), and frontal sinus (fs).**

still not sufficient to characterise these processes (e.g. Lieberman, 1998; Strait, 1999; Lieberman *et al.*, 2000; McCarthy, 2001), in which causes and consequences are tightly entangled.

The external and multidimensional context in which brain evolution has taken place must also be recognised. As previously stressed, the human brain receives an exceptional quota of the total energy, and its evolution necessarily involves a marked rearrangement not only of anatomy and morphology, but also of life-style, ecology, economy and behaviour. A caloric restriction induced on biological tissues improves their lifespan, and the result of such an energy reallocation could well be related to the particular human longevity (Hofman, 1984; Dani, 1998), with all the consequences for the demographic, social and cultural systems (Hawkes *et al.*, 1998). Furthermore, the process of encephalisation may have been linked to a general decrease of the gastrointestinal structures, with a rearrangement of diet and ecological parameters (Aiello & Wheeler, 1995). Ontogenetically, a major evolutionary role in brain evolution could have been played by heterochronic processes (Holloway, 1995), through a shifting of the whole developmental system and reorganisation of the entire life-cycle. In this context, it may be useless to try to find some evolutionary relationship or some causal explanation, and it would be safer to employ a global approach to understand the underlying mechanisms and the biological dynamics.

### **Neurobiology and brain functional anatomy**

The real analytical background of a paleoneurological approach is represented by the experimental advances and database of the neurosciences. Neontological studies provide the best complementary information to compare paleontological data with *in vivo* systems, allowing inferences about functional processes based on the morphological domain. As in paleontology, imaging and biomedical engineering currently represent an incredible source of information. Using techniques like Magnetic Resonance Imaging (MRI) or Positron Emission Tomography (PET) it is possible to quantify and describe morphology and physiology with extreme resolution and details, allowing direct analyses not biased by post-mortem and dissection consequences.



The “uniqueness” of the human brain has been one of the main goals of the neurosciences, but until recent applications there has been no agreement about the quantification of the problem. A direct comparison of neocortical layers in human and non-human primates has shown that the human neocortex is actually larger than predicted for a primate with a comparable brain-size (Rilling & Insel, 1999). Furthermore, the prefrontal cortex is even more convoluted than the relative primate pattern, and during hominid evolution the development of the neocortical white matter outpaced the development of the neocortical grey matter, suggesting an increase of connectivity more than neural reproduction. A similar pattern has been proposed for the temporal areas, with a departure from the ape trajectory and an increase of connections (Rilling & Seligman, 2002). At the same time, after decades of the recognised common molecular homology between *Homo* and the chimpanzee, it has now been found that the small differences between these two species are probably regulatory and located in the cerebral tissues (Enard *et al.*, 2002). In the context of functional craniology, physiological homeostasis and the biomechanical approach based on the D’Arcy Thompson perspective, a tension-based theory of brain morphogenesis has been proposed to explain the cerebral compact wiring, in which mechanical tensions along axons, dendrites and glial structures can be used to interpret species-specific folding patterns (Van Essen, 1997). Thus morphology, brain imaging and molecular databases represent a full package available for the formulation of models in the neurosciences.

The frontal lobes have been related to the main human potentialities like creative thinking, artistic imaging, working memory, planning and decision making, language control and emotions. Therefore, it was assumed that during human evolution the frontal lobes had been particularly developed to allow the expression of human qualities. On the contrary, it seems that humans do not show more enlarged frontal areas than expected by the ape pattern (Semendeferi *et al.*, 1997; Semendeferi & Damasio, 2000). Some differences may occur in the limbic frontal cortex, linked to emotional reactions and social behaviour, but they are limited to unclear size variability and not to tissue organisation (Semendeferi *et al.*, 1998). Thus, the frontal lobes cannot have had a determinant role during human evolution, following the pattern of encephalisation without shifting from a plesiomorphic trajectory.

In contrast, the parietal areas seem to have been a major determinant in human evolution, in relation to the visuospatial integrative processes they control (Holloway, 2000). The right parieto-temporal system is directly activated during spatial discrimination and visuospatial analysis (Faillenot *et al.*, 1999), as well as in detection and integration of sound movement (Griffiths *et al.*, 1998). Females have relatively more developed grey matter in these areas (Nopoulos *et al.*, 2000). The left fronto-parietal structures (especially the supramarginal gyrus) are involved in spatial orienting and “motor attention” (Griffin *et al.*, 2001; Rusworth *et al.*, 2001). Both superior parietal lobules are activated by contralateral finger movements during spatial selection and visuomotor tasks (Shibata & Ioannides, 2001). The spatial processing potentialities are related to the visual area of the parietal cortex (Serenio *et al.*, 2001), involving the control of eye movement (Rusworth *et al.*, 2001). There is probably a direct involvement of the parietal lobes and their subregions even in cognitive tasks and association systems (Culham & Kanwisher, 2001).

A separation between the parietal and temporal lobes is often ambiguous, and it is not easy to identify a clear anatomical boundary between these two districts. In non-human primates, spatial behaviour, generally related to parietal systems, induces the activation of the superior temporal areas in both hemispheres, while in modern humans it involves only the right structures of the same complex (Karnath, 2001; Karnath *et al.*, 2001). The left counterparts in modern humans represent a large portion of Wernicke’s area, leading to hypotheses about the possible coevolution of different hemispheric specialisations. Humans seem to have a larger temporal lobe and insula with respect to the allometric hominoid pattern (Semendeferi & Damasio, 2000). However, a slight asymmetry of the left temporal planum can be detected in

chimps as a probable plesiomorphic character, suggesting a basal anatomical substrate for the evolution of language (Gannon *et al.*, 1998).

Particular attention must be paid to recent studies of cerebellar functions. The cerebellar lobes have always been interpreted as the centre of motor functions and coordination, but it is now clear that the cerebellum plays a role in cognition, behaviour and emotions (Rapaport *et al.*, 2000). The cerebellum includes a large number of neurons with respect to its size, and it is connected via the thalamus to the dorsolateral prefrontal cortex, medial frontal cortex, parietal and temporal areas, anterior cingulate and posterior hypothalamus. It is therefore possible to hypothesise a cognitive role based on the integration of cortical structures. By means of this extreme connectivity, the cerebellar lobes act during the timing, ordering and precision execution of motor programs (Roland, 1993), as well as in working memory and cognitive tasks (Desmond *et al.*, 1997), olfactory naming and recognition processes (Qureshy *et al.*, 2000), perception, cognition and timing (Gao *et al.*, 1996), and somatosensory discrimination of shape (Roland *et al.*, 1989; Seitz *et al.*, 1991; Bodegert *et al.*, 2001). During cognitive tasks an increase in left frontal and right cerebellar activity has been recorded, with an integrative coordination between search and selection of responses (Desmond *et al.*, 1998). Even in episodic memory the right lateral cerebellum shows the development of a complex cortico-cerebellar network (Andreasen *et al.*, 1999). In comparison with hominoid variability, humans show smaller cerebellar lobes than predicted by the allometric ape pattern (Semendeferi & Damasio, 2000). Furthermore, even though modern human males have larger brains than females, the cerebellar structures do not present size differences between the sexes (Nopoulos *et al.*, 2000). Nevertheless, cerebellar functions have not yet been completely investigated, although a key role in the integration, organisation and coordination of cortical processes seems reasonable (Rapaport *et al.*, 2000).

It must be stressed that paleontological and neontological studies seem to agree in most of the assumptions and hypotheses tested. Longitudinal and cross-sectional information intersect and are complementary for the exploration of small differences produced by complex evolutionary systems. In a circular indetermination theorem, between newly discovered fossils and techniques, the human brain analyses itself.

### **Computed tomography and paleontology**

The more a fossil specimen is substantial and well preserved, the more its morphology is often poorly available for inspection. The geological matrix that includes it can be difficult to remove without damaging the specimen. Moreover the same matrix generally fills the empty spaces inside the bones. Even if some inner structures are well preserved and free from inclusions, the importance and conservation of fossils do not allow invasive inspections. Similar constraints limit the availability of the fossil itself to the “flow of information”, that is a data exchange between institutions, museology and didactics. The endocranial cavity is particularly sensitive to these limits, being often filled with geological matrices and scarcely available to a detailed inspection. Paleoneurology has been therefore particularly advantaged by the computed tomography facilities, that have rapidly increases the available database (Tobias, 2001).

Since X-rays have been used in medicine, paleontologists have tried to apply radiology to the study of fossils, with a successful development of a useful database (i.e. Skinner & Sperber, 1982; Kricun *et al.*, 1999). Limits of this technology concern the resulting overlapping of the anatomical structures, a certain amount of parallax error, the stillness and bidimensionality of the images. In the early 1970s the development of Computed Tomography (CT) represented the most powerful support to biomedical imaging, and the most complete application of radiographic techniques (Spoor *et al.*, 2000a).

During a CT scan, the X-ray beam turns around the object with a planar 360° rotation. On the opposite side of the emission, the signal passing through the object is recorded by a detector. The result is a single slice where the density of each point is

derived by the integration of all the signals produced by the emission cycle. The radiographic product is then not the entire object, but a single slice of it, without overlapping and parallax distortion. What is exactly recorded is the attenuation coefficient of single volumetric units to X-rays, that depends upon parameters such as density and composition of the structures. These volumetric units (voxels) have a surface on the beam plane that depends upon the resolution adopted, and a depth depending upon the thickness of the beam used. Resolution is related to the power of the machine itself and inversely proportional to the Field of View (FOV) scanned, that is the area affected by the emission. Slice thickness is generally set to 1 mm, but it can be lowered by virtual interpolation of data, overlapping of successive slices, or using industrial  $\mu$ CT that can reach an extremely low thickness. Sequential machines scan the object by successive and parallel slices, that can be contiguous, embricated or separated by intervals. For each slice the object is moved one step forward, allowing the scan of the subsequent section. Recently, more advanced machines use helicoidal or spiral scanning, with the beam rotating constantly around the object moving continuously through the emission. This technique allows higher resolutions, quicker scanning, and a lower risk of the object moving from its initial position. However, the volumes between the spiral tracks are inferred by interpolation, and this procedure may then be inappropriate if minor differences have to be recorded.

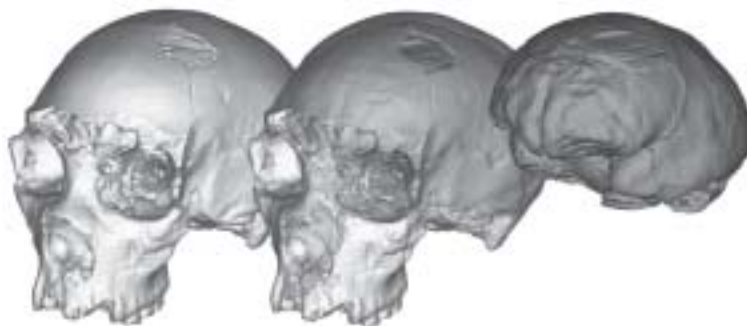
The attenuation coefficient of each voxel is coded into a grey scale value (CT-numbers), and graphically reported on the screen or printed on a hard-copy. The conventional scale used in computed tomography is the Hounsfield scale, named by the developer of the CT technique. The scale ranges from -1000 Hounsfield Units (HU) for air, to 0 HU for water to a maximum of 3096 HU for harder structures. It is often useful to translate the same values into a scale ranging from 0 to 4096. Beyond this threshold the scale can be saturated and the result is an overflow of the signal. Older machines used to set the scale back to zero over 4096 units, with a sudden fall of chromatism to low values (black overflow). Alternatively, the scale can be fixed to the maximum value independently of the excess of density, with a (suspected!) constant maximum signal (white overflow). However, recent machines can extend the range beyond the conventional 4096 units.

Applications to paleontology require some additional solutions and tricks, due to the particular nature of the scanned objects (Spoor *et al.*, 2000a, 2000b). Overflow is generally present and widespread in mineralised structures, and a recalibration of the scale with aluminium may be required. Large volumes can attenuate the entire beam producing a lack of signals and artefacts, needing an increase of the tube load or of the slice thickness. The different selection of high and low energy components of the beam due to the mineralisation of fossils can produce beam hardening, that is a larger output prevalence of the high energy frequencies. To avoid a lowering of CT-numbers and dark artefacts the scale can be recalibrated or the specimen can be included in Plexiglas or water bags.

The scan plane must be previously chosen so as to optimise the localisation and characterisation of the structures analysed, with the Frankfurt horizontal and the otoradiological planes being the most commonly used references.

A serial group of slices can be assembled sequentially to reconstruct different scan planes (*multiplanar reformatting*) or the entire 3D volume scanned. Computed imaging allows a full set of operations that make morphology completely available for virtual manipulation, such as isolation of structures, biomedical engineering and surgery or heterologous reconstruction. The virtual operations work directly on differences and selection of attenuation coefficients and thresholds, grouping or excluding pixels (*segmentation*) and assembling volumes by iterative procedures (Fig. 8).

After computed manipulation, virtual volumes obtained from real structures can be moulded back to physical ones, producing *stereolithographic models* (Zur Nedden *et al.*, 1994; Hjalgrim *et al.*, 1995). A laser beam is used to polymerise artificial resins slice by slice, following procedures developed for engineering rapid prototyping and providing high-resolution casts available for scientific and teaching purposes.



**Fig. 8 - Virtual reconstruction of the Saccopastore 1 skull by computed tomography, segmentation of the endocranial volumes after the removal of the geological matrix included in the endocranial cavity, and isolation of the endocast.**

Applications to paleontology were introduced early in the 1980s (Tate & Cann, 1982; Conroy & Vannier, 1984; Wind, 1984, 1989; Vannier *et al.*, 1985; Vannier & Conroy, 1989a, 1989b; Zonneveld *et al.*, 1989), but the development of informatics and electronics made this technique fully available and competitive only in the following decade (Zollikofer *et al.*, 1995, 1998; Recheis *et al.*, 1999a; Spoor *et al.*, 2000b). Clearly, a first target is the elimination of inner and outer stone matrix that can permeate fossils, and the analysis of the preservation status of the specimen. The fossil is virtually extracted from its matrix, and different physical components are then characterised and localised by thresholding the whole volume slice by slice. The *attenuation spectrum* refers to the distribution of the pixel population along the Hounsfield range, that allows the identification of peaks and the characterisation of the density pattern, that is the number of different physical components and their degree of overlapping and separability. If the specimen shows some degree of taphonomic distortion, its virtual replica can be tentatively unwarped.

After the fossil has been “cleaned”, its inner structures can be segmented and reconstructed, allowing analysis of the whole cranial anatomy (Seidler *et al.*, 1997; Thompson & Illerhaus, 1998; Bookstein *et al.*, 1999; Maureille & Bar, 1999; Manzi *et al.*, 2001; Bruner & Manzi, 2002), bone thickness and dental enamel (Spoor *et al.*, 1993; Weber & Kim, 1999), bony labyrinth (Spoor *et al.*, 1994; Spoor & Zonneveld, 1995; Spoor *et al.*, 2003), maxillary sinuses (Rae & Koppe, 2000) and, of course, endocranial capacity and brain morphology (Conroy *et al.*, 1998, 1990, 2000a, 2000b; Recheis *et al.*, 1999b; Broadfield *et al.*, 2001; Bruner *et al.*, 2002; Prossinger *et al.*, 2003).

Both virtual imaging and stereolithographic models can be used in teaching and museology, with applications ranging from the production of moulds and casts to the *morphing* techniques used to reconstruct soft tissues from bony remains. In summary, computed imaging produces a tool to make the whole morphology available, and to preserve the original specimens.

### **Some methodological remarks**

The “smoothed” and heterogeneous morphology of the brain makes it very difficult to localise and characterise many structures and features. Traces are often hardly recognisable, and the anatomical references are not represented by landmarks but rather through areas with no clear boundaries. The detection of some traits is even dependent upon the different orientation of the casts, the shading factor, or the possibility to touch the specimen. The only reference plane is the midsagittal one, that is rather biased by cerebral asymmetries. The petalias - being individual-specific - could make it difficult to compare single specimens, or to compute “average

morphotypes". Considering the paleanthropological context, it must also be taken into account that the variability within the genus *Homo* is rather limited for many endocranial diameters, and that conversely the fossil record is often too small to allow a full statistical approach. Some future efforts should be devoted to a better characterisation of the cerebral morphology. The brain has a smooth and "fuzzy" surface, that is difficult to code and score into measures or discrete characters. A large amount of self-training and experience still represents an important part of the analyses. Therefore, the quantification of the cerebral variability should develop more detailed procedures aimed at increasing the resolution of the differences between individuals, populations, and species, using techniques ranging from the analytical tools of the complexity, to the fuzzy approaches.

Nevertheless, a large amount of information can be tested on the available database and, paradoxically, the limiting factor is still the scarce information on the variability in the modern human populations. Characters as the middle meningeal vessels, the venous sinuses, the arachnoid granulations, or the hypostotic/hyperostotic endocranial traits, are poorly investigated, with scarce data on their origin, development, and distribution (see Bruner *et al.*, 2003). Other features, as the processes involved in the cranial base flexion or the interaction between the brain and bone surfaces, are widely debated and still controversial. Clearly, one of the main purposes of the paleoneurological comparative target should be represented by the development of a large database to fill this lack of basic information.

What should be constantly considered is that the endocranial reconstructions are models - either physical or virtual - with specific resolution limits related to techniques or problems concerning the state of preservation of the specimens. Therefore we must be cautious when inferring brain morphology from endocranial analyses, which mainly describe the partial variability of endocranial features and not the original cerebral structures themselves. Anyway, the paleoneurological analysis of the endocranial morphology still represents the major source of direct knowledge on the evolution of the cerebral structures. The large amount of information available from a fossil endocast will be fully exploited only by considering their functional meaning and the structural processes involved.

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*I would like to dedicate this work to Massimo Cresta, who showed me a way to look at the humankind with the eyes of the mind, with the respect of the History, and with the pleasure of the dreamers.*

## ABSTRACT

**Tracce fossili del pensiero umano: la paleoneurologia e l'evoluzione del genere *Homo***

**Riassunto** - La paleoneurologia rappresenta lo studio dell'evoluzione delle strutture cerebrali tramite l'analisi morfologica e anatomica dei volumi e delle caratteristiche

endocraniche. La ricostruzione dei calchi endocranici degli ominidi fossili permette lo sviluppo di inferenze sull'anatomia funzionale, sulla fisiologia, e sulla filogenesi. La dimensione e la forma dell'encefalo devono essere considerati in un contesto strutturale nel quale le relazioni tra le varie componenti sono il risultato di un sistema integrato biomeccanico e funzionale. In questa rassegna vengono sintetizzati i recenti progressi sullo studio delle strutture cerebrali nell'evoluzione umana, considerando le conoscenze attuali sulle asimmetrie, sul sistema vascolare meningeo medio, sui seni venosi, e su altre strutture correlate. Un'attenzione particolare viene rivolta allo sviluppo delle neuroscienze, che permettono lo sviluppo di ipotesi neuro-funzionali. La tomografia computerizzata e l'elaborazione di immagine hanno rappresentato il maggior contributo allo sviluppo delle analisi paleoneurologiche. Tuttavia, la morfologia endocranica non rappresenta univocamente le originali anatomie cerebrali, e i risultati morfologici devono essere opportunamente interpretati. La paleoneurologia resta comunque l'unico strumento disponibile per analizzare direttamente l'evoluzione dell'encefalo umano.

**Parole chiave** - Calchi endocranici, evoluzione cerebrale, genere *Homo*.

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