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#### STONE AGE INSTITUTE PUBLICATION SERIES NUMBER 4

Series Editors Kathy Schick and Nicholas Toth

# THE HUMAN BRAIN EVOLVING:

## Paleoneurological Studies in Honor of Ralph L. Holloway



Editors

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#### FRONT COVER CAPTIONS

Center: Portrait of Ralph L. Holloway. Upper left: A modern human brain. Upper right: Ralph measuring landmarks on an endocast ca. 1976. Lower right: Homo habilis cranium KNM-ER-1813 from Koobi Fora, Kenya (photo by Holloway). Lower left: Ralph with an endocast of the Flores "hobbit" cranium.

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# **CHAPTER 5**

# THE FOSSIL HOMINIDS' BRAIN OF DMANISI: D 2280 AND D 2282

#### **DOMINIQUE GRIMAUD-HERVE AND DAVID LORDKIPANIDZE**

#### ABSTRACT

Since the discovery of the first mandible in 1991 at the site of Dmanisi, many other human fossil remains have been found at the site in association with archaeological artefacts and faunal remains dated between 1.81 and 1.77 My. Dmanisi is probably the oldest site outside of Africa, and was most likely an important migration route into Europe and Asia from Africa. Analysis of the two first hominid endocasts of D 2280 and D 2282 has been done. These endocats were compared with contemporaneous African fossil hominids (Homo habilis, Homo rudolfensis, Homo ergaster) and continental and insular Asiatic ones (Homo erectus). Dmanisi's endocasts are similar in size with the earliest specimens of Homo, while cerebral form, vascular middle meningeal pattern, cerebral morphology are more similar to Asiatic Homo erectus. Based on these similarities they can be assigned to the same taxon as early representatives of the genus Homo (Homo ergaster or even Homo habilis), suggesting Dmanisi played an essential role in the earliest settlement of eastern Asia.

#### **K**EYWORDS

Dmanisi, Brain, Human evolution, Cognitive capacities, Eurasia

#### INTRODUCTION

Discoveries of human fossil remains at Dmanisi are now well known, yielding five skulls, four mandibles and many postcranial elements and associated archaeological assemblages (Gabunia 1992, Gabounia & Vekua 1995, Gabounia et al., 1999, 2000, 2002; Vekua et al., 2002; Jashashvili, 2002; Rightmire et al. 2005; Lordkipanidze et al., 2006, 2007; Lumley et al. 2006). The faunal remains mostly consist of Villafranchian species assigned to the Late Villanian and Early Biharian, living in a mosaic environment of open steppe and gallery forests (Gabunia et al. 2000, 2001).

Most of the human remains have been discovered in layers V and VI, dated between 1.85 and 1.77 My (Gabunia et al., 2000, 2001; Lumley et al., 2002). Dmanisi is an important site for the understanding of early human migrations, since it is the oldest site outside of Africa, and it is in a geographically strategic position at the intersection of Africa, Europe, and Asia.

Skulls D 2280 and D 2282, an adult male and sub-adult female respectively (Lumley & Lordkipanitze, 2006 ; Lumley *et al.*, 2006), were scanned in superior view with a General Electric High Speed HAS scanner at the CHNO des Quinze-vingts in Paris under the care of Pr Cabanis with following acquisition parameters for both Georgian hominids: scanner energy 120 kV, 100 mA, 1.0 mm-thick slices; 25 cm field of view and 0.488 pixel size with a pixel matrix of 512\*512 for D 2280; 23 cm field of view and 0.449 pixel size with a pixel matrix of 512\*512 for D 2282. The sections were used to create three-dimensional computer models of both specimens using Mimics 8.1 software (Materialise N.V.). Stereolithographic reproduction from scanner data has been done.

#### MATERIAL

#### Fossil hominids'endocasts (Muséum national d'Histoire naturelle, Paris; Columbia University, New York)

OH 7, OH 13, OH 16, OH 24

KNM-ER 1813, KNM-ER 1470, KNM-ER 3733, KNM-ER 3883, KNM-WT 15000

Trinil 2, Sangiran 2, Sangiran 10, Sangiran 12, Sangiran 17, Sangiran 38

Ckn.D 1.PA.17. (Sin.II), Ckn.E 1.PA.16. (Sin.III), Ckn.L 1.PA.98. (Sin.X), Ckn.L 2.PA.99. (Sin.XI), Ckn.L 3.PA.100. (Sin.XII)

The above fossil material has been chosen to compare Dmanisi's hominids with contemporaneous fossil hominids from Africa: Olduvai (Tanzania) attributed to *Homo habilis*, East and West Rudolf (Kenya) attributed to *Homo habilis*, *Homo rudolfensis* and *Homo ergaster* and from insular Asia with more recent fossil from Sangiran and Trinil (Java) and from continental Asia in Zhoukoudian Lower Cave (China). Asiatic hominids are attributed to *Homo erectus*. The obtained results are also compared to the actual extinct human sample.

Endocasts from Olduvai (Tanzania) are not well preserved and those from East and West Turkana (Kenya) are in poor quality, so our data have been completed with results from Tobias (1987, 1991), Begun & Walker (1993), Holloway (1978, 1983), Holloway et al. (2004) and Saban (1984).

### Modern population (Muséum national d'Histoire naturelle de Paris)

n = 103 from Europe, continental and insular Asia, Africa, America and Oceania

595, 713,723, 726, 727, 728, 729, 730, 731; 732-3, 733, 748, 749, 754, 755, 764-1, 784, 788, 789, 794-3, 798-2, 800, 808, 1294-2, 1489, 1490, 1865, 3635, 3662, 3663, 3664, 3665, 3666, 3667, 3668, 3669, 3670, 3671, 3672, 3673, 3674, 3675, 3676, 3677, 3678, 3679, 3680, 3681, 3682, 3683, 3684, 3685, 3686, 3688, 3689, 3690, 3691, 3692, 3693, 3694, 3695, 3696, 3697, 3698, 3699, 3700, 3702, 3703, 3704, 3705, 3706, 3707, 3708, 3709, 3775, 3827, 3828, 4362, 4815, 5720, 5733, 9843, 9844, 9852, 9853, 9854, 10109, 10111, 10112, 10113, 10114, 12033, 19246, 21413, 24636, 24940, 24942, 25027, 25536, 25620, 27429, 30189, 30195.

#### **Methods**

Morphological description of encephalic relief and vascular imprints (venous sinuses and middle meningeal system) is realized on Dmanisi's endocasts. Comparison is done with human fossils from Africa and Asia. Cranial capacity has been estimated directly by immersion of endocasts in water, repeated three times, and the results averaged.

A traditional metrics study (linear and angular mea-

surements) (Table 1) was done in order to compare absolute and relative values between both Dmanisi's endocasts and African and Asiatic fossil hominids as well as a large extinct modern human reference sample. Principal components analysis was performed to synthesize information contained in 11 variables, selected in relation to the preservation of the Dmanisi endocasts. These measurements included width (WBE), average hemispheric length (LME), occipito-cerebellar projection (DOCE), both height (HGQE) and (HBRE), angular data (XBE, XLSE, XLIE) and sagittal chord of each cerebral lobe (CFR, CPA, COC). These 11 variables have been used on 47 specimens with 21 fossil hominids and 26 actual extinct human.

In the 3D geometric morphometrics study, particular care has been required to choose maximum common landmarks preserved on Dmanisi's endocasts and on the fossil human comparison sample from Africa and Asia. 3D coordinates of 28 anatomical landmarks were digitized on each endocast with a Microscribe 3DX digitizing arm (Table 2). Selection of 6 sagittal landmarks along interhemispheric fissure and 22 (11 X 2) parasagittal landmarks was done for this comparative analysis to determine the morphometrical affinities of Dmanisi's hominids. Landmarks coordinates have been fitted by Generalized Procrustes Analysis (O'Higgins 2000, Rohlf & Marcus 1993).

#### Preservation and brief description of encephalic and vascular imprints of Dmanisi's endocasts

The cranial cavity of D 2280 is perfectly preserved, producing a high quality endocast where all the relief and depressions are clearly visible. Unfortunately D 2282 is deformed with the inferior part of right hemisphere pushed inside and exhibits an altered internal surface. Many irregularities corresponding to sediment deposits disturbs full observation of the endocranial surface. Encephalic relief is visible only on the left side of the endocranium.

Both Dmanisi's endocasts have been described previously (Grimaud-Hervé *et al.* 2006). Most important morphological characters can be reminded here (Fig.1, Fig.2).

#### Vascularization

Concerning dura mater sinuses, superior sagittal sinus, visible on posterior part of D 2280, runs into the left lateral sinus and is well defined with noticeable relief approximately 8mm in diameter. On D 2282 the superior sagittal sinus is not noticeable on the sagittal or left lateral side. It is, though, discernable on the right with relief of 7.5mm. From this it is assumed that the superior sagittal sinus runs with the right lateral sinus on D 2282. Asymmetry is observed on these two fossil hominids, but without a preferential side being obvious. No spheno-parietal sinus is observed. Three sagittal arach-

### Table 1. Metric variables used in traditional multivariateanalysis 2D

#### Left lateral view

Maximal length (LME), average of right (LMDE) and left (LMGE) hemispheric length, measured from the most anterior point (endoglabella) to the most posterior (endoopisthocranion) of the endocast

Maximum height of maximum hemispheric length (HGQE), average of right (HGQDE) and right (HGQGE) heights

Maximum endobregma height of maximum hemispheric length (HBRE), average of right (HBRDE) and right (HBRGE) heights

Frontal chord (CFR), between the most anterior point of the frontal lobe and central fissure at the midsagittal plane

Parietal chord (CPA), between central fissure and perpendicular scissure at the midsagittal plane Occipital chord (COC) between perpendicular scissures and most depressive point of Herophile torcular at the midsagittal plane

Occipito-cerebellar projection (DOCE) measured by occipital projection perpendicular from Herophile torcular

Bregmatic angle (XBE) between maximal length and chord between most anterior point of the frontal pole and endobregma, average between right (XBDE) and left (XBGE) angle

Angle comprised between chord from perpendicular fissures at the midsagittal plane to endo-opisthocranion and chord from endo-opisthocranion to Herophile torcular (XLTE), average between right (XLTDE) and left (XLTGE) sides of the brain

Angle comprised between chord from perpendicular fissures at the midsagittal plane to endo-opisthocranion and maximal length of hemisphere (XLSE), average between right (XLSDE) and left (XLSGE) sides of the brain

Angle comprised between chord from endo-opisthocranion to Herophile torcular (XLIE), average between right (XLIDE) and left (XLIGE) sides of the brain

#### Upper view

Maximum width of the endocast (WBE), subdivided in right (WMDE) and left (WMGE) width

Maximum width on parietal lobes (WBE)

Maximum width on triangular part of third frontal gyrus (WCBE)

Right frontal surface (FRD)

Left frontal surface (FRG)

Right parieto-temporal surface (PTD)

Left parieto-temporal surface (PTG)

Right occipital surface (OCD)

Left occipital surface (OCG)

Right Hemispheric surface (HD) = FRD + PTD + OCD

Left hemispheric surface (HG) = FRG + PTG + OCG

Brain surface = HD + HG

### Table 2. Landmarks points digitalized in geometrical morphometrics 3D

#### Sagittal points

0	•
1	Base of encephalic rostrum between both left and
	right first frontal convolution in midsagittal plane
11	Intersection between left postcentral sulcus and
	interhemispheric fissure
14	Posterior interhemispheric point (= most
	depressed point of Herophile torcular)
15	Intersection between left and right perpendicular
	scissures and interhemispheric fissure

- 16 Intersection between precentral scissures and interhemispheric fissure
- 17 Middle point of frontal arch

#### Left parasagittal points

- 2 External edge of left encephalic rostrum
- 3 Orbital part of left third frontal convolution
- 4 Point of maximal curvature of triangular part of left third frontal convolution
- 5 Upper point of left sylvian valley (between opercular part of third left frontal convolution and left temporal lobe)
- 6 Most anterior point of left temporal pole
- 7 Left Euryon (corresponding to maximal endocranial width)
- 8 Point of maximal curvature of left supramarginal gyrus
- 9 Anterior point of left interparietal sulcus, means base of left first parietal convolution
- 10 Middle point of anterior edge of left first parietal convolution
- 12 Upper point between left temporal and left cerebellar lobes (= upper point of left temporocerebellar excavation)
- 13 Point of maximal curvature of left occipital pole

#### **Right parasagittal points**

- 18 External edge of right encephalic rostrum
- 19 Orbital part of right third frontal convolution
- 20 Point of maximal curvature of triangular part of right third frontal convolution
- 21 Upper point of right sylvian valley (between opercular part of right third frontal convolution and right temporal lobe
- 22 Most anterior point of right temporal pole
- 23 Right Euryon (corresponding to maximal endocranial width)
- 24 Point of maximal curvature of right supramarginal gyrus
- 25 Anterior point of right interparietal sulcus, means base of right first parietal
- 26 Middle point of anterior edge of right first parietal convolution
- 27 Upper point between right temporal and right cerebellar lobes (= upper point of right temporo-cerebellar excavation)
- 28 Point of maximal curvature of right occipital pole



Figure 1. D 2280 – Endocast in left and right lateral, superior, anterior and posterior views

noid granulations are noted in superior part of precentral convolutions on D 2282, one on the right and two on the left hemisphere.

The middle meningeal pattern is very poorly represented. On left hemisphere of D 2280 it is best preserved with individualization of two branches on the second temporal convolution. The anterior meningeal artery appears reduced and disappears at the third frontal convolution. The posterior ramus is more developed, and is subdivided in both directions into an oblique and lambdoidal branches. Neither ramifications nor anastomoses are observed on the Dmanisi's endocasts. On D 2282, just the superior middle meningeal branches are apparent on left hemisphere. The middle meningeal pattern exhibits plesiomorphies, but are poorly patterned with the absence of a spheno-parietal sinus in both Dmanisi's endocasts.

#### **Encephalic relief**

The longitudinal cerebral fissure is wide, resulting in a significant separation between the frontal lobes in both Dmanisi's endocasts. The longitudinal cerebral fissure displays a significant separation between the hemispheres until posterior hemispheric. The junction with perpendicular fissure constitutes a depression forward of endolambda. On the left hemisphere of D 2280 the lateral fissure is weakly impressed and inclined up and backward, becoming straightened at its extremity; it is also observed on the left side of D 2282. The lateral fissure is situated in the prolongation of the lateral valley, which is very wide, separating Broca's cap from the temporal pole. The junction between the central fissures is situated behind endobregma (35mm on D2280; too deformed on D 2282). Based on Holloway (1982) there is a left frontal petalia on D 2280 and a right right frontal petalia on D 2282, confirming the asymmetry observed on vascular pattern.

The precentral sulcus is weakly impressed, but detectable about 15mm in front of the central one, which is the breadth of precentral gyrus on both Dmanisi's hominids. A long and narrow encephalic rostrum is clearly individualized on D 2280 (this region is not preserved on D 2282) with the right and left first frontal convolution widely separated as noted before. The breadths of these convolutions appears equivalent. The anterior ramus of the central fissure is clearly impressed with individualized relief of the orbital part of the third frontal gyrus equal on both sides of D 2280. The left Broca's area shows the central fissure on D 2280 as well as the contralateral side in D 2282.

The postcentral sulcus is situated nearly 20mm behind the central one on D 2280. The postcentral gyrus is just little more developed than precentral. There was a smaller difference observed between these two struc-



Figure 2. D 2282 – Endocast in left and right lateral, superior, anterior and posterior views

tures in D 2282. The breadth of first parietal convolution decreases posteriorly (28 to 20mm on D 2280, 20 to 15mm on D 2282). The supramarginal lobule is well delimited on D 2280, more than it is in D 2282. The angular lobule surface is smaller with weaker relief on D 2280 contrary to what is observed in D 2282. The temporal lobes converge towards the brain with the temporal pole set back behind Broca's area on D 2280. The temporal poles are not preserved in D 2282. In addition, the occipital region in this hominid is too altered to provide any data. In D 2280, *sulcus lunatus* is in the posterior position commonly observed on genus *Homo*.

Left occipital lobe is in a set back position compared to the right on D 2280 with the reverse being the case in D 2282. Instead the occipital lobes of D 2282 are extensions of the temporal and parietal lobes without a clear boundary. The cerebellar lobes are situated under the occipital ones. These occipital and cerebellar posterior positions are the expression of weak cerebral rolling and opening of the basi-cranial angle, which are primitive conditions commonly observed in contemporaneous fossils hominids.

#### Morphological comparison

#### Vascular imprints

Any fossil endocast studied shows a spheno-parietal sinus which is scarce in the modern human sample. The superior sagittal sinus asymmetry corresponds with greater development of one hemisphere (Delmas & Chifflet 1950). When this posterior cerebral region is preserved, two patterns appear: In the first one, the superior sagittal sinus goes into the left transverse sinus which is generally larger than the right, like on OH 24 (Tobias, 1991), Sangiran 2 and 10 (Grimaud-Hervé and Saban 1996) and D 2280. In the second pattern the sagittal sinus goes into the right transverse sinus on D 2282, OH 13 and OH 16 (Tobias, 1991), ER 3883 and WT 15000 (Begun & Walker, 1993), Trinil 2, Sangiran 12 and 17, hominids from locus E and L of Zhoukoudian Lower Cave, and 80% of the modern sample (Grimaud-Hervé 1997, 2004). This latter group shows a more developed left hemisphere of significant length.

No relationship has been established between the meningeal system and the venous sinuses (Paturet 1964). The results of both parts are going to be treated independently. For the middle meningeal pattern, two groups appear. In the first one with the posterior branch

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Figure 3. Middle meningeal pattern



Figure 4. Endocranial transversal shape in anterior view

is very developed as exemplified in OH 7, D 2280 and Zhoukoudian Lower Cave hominids. In the second with the posterior branch is equivalent or reduced in prominence compared with the anterior middle meningeal branch such as is observed in ER 1813, ER 1470, ER 3883, WT 15000, Trinil and Sangiran hominids, and a great majority of the modern human sample (94%) (Fig.3). Although the differences between this sample and others are not significant, it appears that the morphology of the posterior branch of the middle meningeal artery is a plesiomorphic character.

#### Encephalic imprints

The encephalic rostrum, which is considered a plesiomorphic feature, has been observed on all studied fossil hominids where this region is preserved. It corresponds to the extension of the left and right first frontal convolutions next to the orbital roofs, which are separated by a wide, deep longitudinal cerebral fissure, particularly on the Dmanisi and Asiatic endocasts. Nevertheless, the outline varies according to region such that it is regularly concave on all African hominids, whereas it consists of two parts separated by an angle on Asiatic hominids and Dmanisi. This morphological character is very well individualized on that second group. A clear regression of the encephalic rostrum combined with a narrower interorbital space is observed on the modern sample. This may indicate a reduction in the importance of olfaction in the modern sample versus earlier fossils.

In the anterior view the same distinct group differences are observed. African *Homo ergaster*'s endocranial outline, in particular, is narrow and high, and is regularly convex from left to right in the orbital part of third frontal convolutions without an interruption in the transversal cerebral curvature. The outline of D 2280 is closer Asiatic *Homo erectus* with a wider and lower endocranial transversal shape. It is less marked in its convexity, and the thrd frontal convolution is interrupted in the medial region of the frontal lobes. The parietal lobes are interrupted by a vast depression corresponding to the middle frontal sulcus as it runs into the interparietal. The outline of this feature shows a slight twist similar to that observed on all fossil hominids of this group (Fig.4).

The frontal and parietal areas are smoothly limited on the African specimens compared with the more marked relief in Dmanisi, particularly D 2280 as well as the Asiatic hominids. The lateral valley is very broad in OH 24, ER 1813 and ER 1470 as well as *Homo ergaster*, while it is less broad in Asiatic *Homo erectus* and D 2280, meaning there has been greater development of the frontal and temporal lobes in these latter groups. In moderns the two areas so little if any separation in moderns, indicating a closer affinity of the Dmanisi and Asian fossils to moderns than African fossils. **However, all of the fossil hominids show the frontal lobes converging anteriorly, while they remain parallel in modern human sample.** 

The breadths of the pre- and postcentral convolu-

tions tend to correspond to particular evolutionary stages. It is notable that the postcentral gyrus is nearly always broader than the precentral in the endocasts sampled here. In the African hominids the postcentral convolution is equal to precentral one (OH7, OH13, OH16, OH24, KNM ER 1470, KNM ER 3883, KNM WT 15000), or slightly wider (KNM ER 3733). In Asiatic Homo erectus these two convolutions have either equivalent breadths, or the precentral gyrus is more developed, this phenomenon is more accentuated in the more recent Javanese fossil hominids from Ngandong and Sambungmacan. This indicates that there is an increase in motor areas between the early and later fossils. With regard to this morphological feature the Dmanisi endocasts are similar to KNM ER 3733. Thus, this derived feature is found on the two first representative hominids inside and outside of Africa.

In the lateral view it is noteworthy to note that the posterior encephalic shape differences between the African sample and the Asiatic hominids and D 2280. In the African sample the occipital lobes bulge only slightly beyond the cerebellum posteriorly, and are not delineated anteriorly from the parietal lobe. In the second group the occipital lobes are clearly projecting backwards, their anterior part situated above cerebellar lobes. This position corresponds to a rotation of the cerebellum under the cerebral mass, and the role of basicranial flexion in the position of the cerebrum through time.

In the superior view the D 2280 (D 2282 is too damaged) endocranial outline is very different from African *Homo ergaster*. In *H. ergaster* the anterior frontal region is strong in relation with the lateral cerebral convergence, showing slight cerebral development at this level. The D 2280 outline is globular, and is closer from the Asiatic *Homo erectus* shape with a noticeable widening of cerebral region from the lateral valley to the orbital part of third frontal convolutions.

#### **Results of Metrical Study**

#### **Cranial capacity**

The average of three tests corresponding to immersion of the endocast in water is presented in Table 1. These measurements present different values from those observed n the Dmanisi hominid endocranial capacities as measured using mustard seed (Gabounia *et al.* 2000, Lumley *et al.* 2006).

The cranial capacity values (Table 3) show a regular increase from more the ancient African and Dmanisi hominids to Asiatic *Homo erectus* and modern humans (Fig.5). The very small cranial capacity of D 2282 appears to be the result of damage. The measurement presented here is approximately 100ml less than previous measurements, placing this individual within the range of African *Homo habilis*, while D 2280 is towards to lower end of Asiatic *Homo erectus*. The encephalization quotient, recommended by some researchers (Armstrong

Fossil hominids	Direct method	References
D 2280	790	775 (Gabounia et al., 2000) 770 (Lumley M.A. de et al., 2005)
D 2282	(645)	650 (Gabounia et al., 2000) 625 (Lumley M.A. de et al., 2005)
D 2700		645 (Vekua et al. 2002), 600 (Lee, 2005)
D 3444		625 - 650 (Lordkipanidze et al. 2006)
OH 7	-	674 (Tobias 1975, 1991)
OH 13	618	673 (Tobias 1975, 1991)
OH 16	-	638 (Tobias1975, 1991)
OH 24	556	594 (Tobias 1975, 1991)
KNM-ER 1813	500	510 (Holloway, 1978)
KNM-ER 1470	760	752 (Holloway, 1978)
KNM-ER 3733	715	848 (Holloway, 1983)
KNM-ER 3883	785	804 (Holloway, 1983)
KNM-WT 15000	885	880 (Begun et Walker, 1993)
OH 12	656	
OH 9	1118	1067 (Holloway, 1975)
Bouri		995 (Asfaw et al., 2002)
Buia		800 (Abbate et al., 1998)
Sale		930-960 (Jaeger, 1975),
Sale		880 (Holloway,1981a)
Trinil 2	930	943 (Holloway, 1975)
Sangiran 2	840	815 (Holloway, 1975)
Sangiran 10	840	855 (Holloway, 1978)
Sangiran 12	-	1059 (Holloway, 1978)
Sangiran 17	960	1004 (Holloway, 1978)
Ckn.D 1.PA.17 - Sin II	995	
Ckn.E 1.PA.16 - Sin III	915	915 (Weidenreich, 1943)
Ckn.L 1.PA.98 - Sin X	1245	1225 (Weidenreich, 1943)
Ckn.L 2.PA.99 - Sin XI	1020	1015 (Weidenreich, 1943)
Ckn.L 3.PA.100 - Sin XII	1020	1030 (Weidenreich, 1943)
Homo sapiens (n=103)	$\mu = 1520$	Min=1190; Max=1940; VarCoef=11

Table 3. Cranial capacity in ml

1985, Bauchot et Stephan 1969, Hartwig-Scherer 1993, Holloway and Post 1982b, Jerison 1975, Mac Henry 1976, Martin 1990, 1995, 1996, Rightmire 1986, 2004, Ruff *et al.* 1997, Rosenberg *et al.* 2006, Tobias 2006), has not been calculated due to lack of data on stature.

#### **Univariate dimensions (Table 4)**

Univariate distributions are reported for both Dmanisi's endocasts, each hominid fossil group and for modern humans. **Concerning maximal hemispheric lengths, it is interesting to** note **important differences between both** ancient African hominids from East Turkana, ER 1470 and 1813. KNM ER 1813 is closer to the Olduvai specimens OH 16 and OH 24 than KNM ER 1470. However, both Dmanisi endocasts are similar to African *Homo ergaster* with distributions between 138.5 and 154 mm. As noted before (Grimaud-Hervé et al. 2006), Asiatic *Homo erectus* values are large when compared with Zhoukoudian Lower Cave hominids, which are near the modern human range. From *Homo habilis* to *Homo sapiens* the overall increase is 35.2%.

Maximal endocranial breadth (WME) is situated in the postero-inferior position on the second temporal gyrus in African and Asiatic fossils hominids, and is also found in the same poistion in the Dmanisi specimens, while it is positioned around the first temporal convolution in Homo sapiens. This endocranial measurement is scarcely joined with the endobiparietal maximal breadth (WBE), which is positioned around the supra marginal gyrus. WME and WBE are reduced in ER 1813 compared to ER 1470 (respectively 18.5mm and 25 mm). With the Dmanisi specimens D 2280 is closer to ER 1470 as well as smaller Asiatic hominids such as Ckn.D 1.PA.17 or Sangiran 2. D 2282 is closer to the Olduvai hominid values. The overall increase from Homo habilis to Homo sapiens for this measurement is between 38.7% and 33.8%.

Table 4. Univariate dimensions

	LME	WME	WBE	WPPE	WCBE	WPFE	HBBE	HGQE	HBRE	CFR	СРА	COC	XBE	DOCE	XLTE	XLSE	XLIE
D2280	145		105		88	98	95	57.75	57.25	101	50	48	46	11.75	151.75	74.75	77.25
D2282	140	100	96		80	84	75	42.25	40.25	94	44	45	38.75		114.5	56	58
H.habilis																	
Ν	4	5	5	5	2	2	2	4	4	3	3	2	1	3	1	1	1
Average	127.4	103.1	93.6	94.8	78.0	83.5	90.0	45.0	40.8	64.3	47.3	38.0	45.5	11.1	145.0	67.5	77.5
Var Coef	3.6	4.0	5.7	7.7	7.3	9.3	1.6	4.8	9.4	27.9	12.9	11.2		81.2			
ER1470	137.5	114.5	111	109	84	92	103	52.25	45.5	97	48	44	50.5	6.75	126.5	62	64.5
H.ergaster																	
Ν	3	3	3	2	2	1	3	3	3	3	3	3	3	3	3	3	3
Average	147.2	119.2	115.5	112.0	87.0	70.0	96.9	52.2	47.7	91.7	51.0	52.3	41.4	3.8	157.8	75.5	81.9
Var Coef	5.4	1.2	1.1	3.8	5.0		5.2	5.3	5.1	6.7	9.0	9.6	12.4	27.2	6.1	5.4	11.0
H.er.Java																	
Ν	4	5	5	5	4	4	3	5	5	4	5	5	4	5	5	5	5
Average	154.4	124.0	114.0	111.8	90.4	92.5	103.3	58.0	54.7	109.8	43.8	52.8	45,7)	11.5	124.9	60.8	64.1
Var Coef	4.1	4.2	4.6	4.8	4.9	11.5	3.0	3.6	1.8	2.0	14.2	6.7	4.4	19.9	6.1	6.3	9.2
H.er.China																	
Ν	5	5	5	5	3	3	5	5	5	5	5	4	5	4	4	4	4
Average	165.7	124.0	112.6	111.8	95.3	100.3	112.0	61.4	57.8	119.6	47.4	59.5	43.0	14.6	120.9	58.0	62.9
Var Coef	3.6	3.8	4.7	5.6	3.0	4.0	4.4	5.0	5.0	4.2	8.3	10.7	5.4	25.2	6.5	4.6	8.5
Extinct humans																	
Nb Spec.	105.0	105.0	105.0	104.0	105.0	105.0	104.0	104.0	104.0	104.0	105.0	105.0	27.0	103.0	26.0	26.0	26.0
Average	170.5	136.5	132.1	130.4	105.1	116.6	121.2	66.6	58.8	122.5	73.3	59.1	51.9	9.6	136.3	68.2	68.1
Var Coef	4.9	5.7	5.5	5.8	7.1	6.9	5.0	12.2	14.1	5.3	11.8	10.7	7.4	43.7	6.8	7.4	6.6
Maximum	187.3	152.0	150.0	147.5	127.0	138.0	136.0	88.8	85.0	137.5	88.0	77.0	59.8	20.0	151.3	75.3	76.0
Minimum	148.5	116.0	114.0	108.0	93.0	100.0	105.0	52.0	44.0	44.0	56.0	58.0	44.0	1.3	116.5	56.5	60.0



Figure 5. Cranial capacity



Figure 6. Occipito-cerebellar projection

With regard to the opercular part of third frontal convolutions the difference between ER 1813 and ER 1470 breadths (WPFE) is again similar to (78 and 92 mm) those of Dmanisi hominids (98 et 84 mm). ER 1813 and D 2282 are closer to OH 24 (82mm). D 2280, though, is closer Asiatic Homo erectus with regard to this feature, displaying an increase in the posterior frontal region not observed in African specimens. Growth between Homo habilis and extinct H. sapiens reaches more than 40%. The maximal breadth on the triangular part (WCBE) is close to the opercular part in African hominids, but is situated lower, becoming more central, in Homo sapiens. An important difference is noticed between ER 1813 and 1470 when compared to the Dmanisi hominids. In this measurement D 2280 is near Homo ergaster and Asiatic Homo erectus Sangiran-Trinil averages. Zhoukoudian Lower Cave are larger in comparison. An increase of 33% is noted between the more ancient fossil hominids of this study and Homo sapiens.

Total height (endobregma-endobasion = HBBE) measurement requires the preservation cerebral regions that are rarely preserved. D 2280 is similar to *Homo* ergaster's, but smaller than Asiatic *Homo* erectus (Javanese = 103.3mm, Chinese = 112mm). There is an increase of about 35% between *Homo* habilis and sapiens.

Partial height corresponding to the upper part of the

brain (HGQE) is used when the basal part of the brain is not preserved. This maximal point above endoglabellaendoopisthocranion is situated between endobregma and the central fissure. In general, this measurement is positioned more anteriorly in fossil hominids, but is positioned more posteriorly in more recent hominid groups. In Dmanisi D 2282 does not provide reliable data with regard to this measurement, while D 2280 does. D 2280 is closer to WT 15000 and Javanese *Homo erectus*, while the Zhoukoudian hominids (61.4mm) are closer to *Homo sapiens* (77.3mm). A major increase in height is observed in upper portions of the hemispheres (approximately 50%) from *Homo habilis* to *Hom sapiens*.

Concerning the occipito-cerebellar projection, there is a very clear distinction between the fossil hominids in this sample (Fig.6). In general, the regular sagittal curve of African specimens results in less overlap with the occipital obes when compared with Asian *H. erectus* specimens, which have protruding lobes. The occipital poles of African hominids from East and West Turkana only project slightly (average = 3.8mm). There is greater occipital projection in the nine Asian specimens value (average = 12.8mm). The occipital projection in D 2280 (D 2282 is too damaged) is similar to other *Homo erectus* (average = 11.8mm). Finally, the average in *Homo sapiens* is 9.65mm, but with greater variation near 50%.



Figure 7. Ratio of frontal chord (CFR) on F3 opercular part (WPFE) of the brain

Thus, Dmanisi D 2280 is clearly different from the African configuration, and is closer to that of *Homo erectus*, confirming similar configurations of this posterior region in Georgian and Asian endocasts.

In conclusion, the Dmanisi values of maximal hemispheric length are more similar to those of Homo ergaster than other specimens. Yet, with concern to maximal breadths D 2282 is closer to Homo habilis, while D 2280 is closer to Homo ergaster and gracile Asian Homo erectus. D 2280 exhibits significant frontal widening similar to Asiatic Homo erectus, a feature not observed in African specimens. This increase occurs more anteriorly in the triangular parts of third frontal convolutions. Finally, D 2280 is more similar to *Homo ergaster* with regard to total endocranial height, but is closer to Asiatic Homo erectus if only the upper region of the hemisphere is considered. Its occipito-cerebellar projection emphasizes the same pattern as Asiatic hominids. Thus, there is a significant distinction between African specimens one hand and the Dmanisi specimens, which tend to associated more with the Asiatic hominids, in particular with regard to the protrusion of the occipital lobes.

An analysis of the sagittal chord of each cerebral lobe (frontal = CFR, parietal = CPA and occipital = COC) displays an increase of 49% in the frontal and occipital lobes and 56% for the parietal lobes. The parietal sagittal chord is equal or superior to the occipital one in African specimens, *Homo sapiens* and the Dmanisi hominids. In Asiatic *Homo erectus* the occipital sagittal chord is always more developed which can be considered as an autapomorphy of this group.

With regard to the total sagittal curvature, the ob-

served ratios are quite stable with a more marked increase in the parietal region between African specimens and *Homo sapiens*. Asiatic *Homo erectus* displays a primitive character with less development in the medial sagittal portion of the brain. This is possibly due to the longer occipital representation observed in this group. This is particularity specific to Asiatic *Homo erectus*, and, thus, can be interpret as an autapomorphy.

The frontal sagittal chord compared to the maximum frontal breadth (Fig.7) is over 100 in fossil hominids and *Homo sapiens*, meaning that the breadth is more developed than length. This index is nearly the same between *Homo ergaster* and *H. sapiens*, while all Asiatic *Homo erectus* and Dmanisi possess a higher index, indicating reduced transversal development of the posterior frontal region. This new result confirms the morphological distinction of the fossil samples. The parietal sagittal chord compared to the maximal parietal lobe width is not significant. Instead the values merely distinguish fossil hominids from *Homo sapiens*, indicating an increase in parietal lobe development in this later group.

#### **Bivariate dimensions (Table 5)**

The ratio between maximal endocranial length and breadth shows the same repartitions between D 2282 and D 2280, which are distributed between African and Asiatic specimens. There is an apparent increase in length from ancient to more recent *Homo erectus*, but then this measurement remains stable throughout *Homo sapiens*. The breadth values are more similar between the groups, albeit the relative position of maximum breadth on the endocast varies (Fig.8).

	WME/ LME	WBE/ LME	HBBE/ LME	HBBE/ WBE	HGQE/ LME	HGQE/ WBE	CFR/ WPFE	XBE	XLTE	XLSE	XLIE
D2280			65.5	90.5	39.8	55.0	103.1	46	151.75	74.75	77.25
D2282	71.4		53.6	78.1	30.2	44.0	111.9	38.75	114.5	56	58
H.habilis											
N	4	4	2	2	4	4	1	1	1	1	1
Average	80.4	72.5	71.4	101.8	35.3	49.0	109.0	45.5	145.0	67.5	77.5
Var Coef	5.5	6.7	1.4	5.6	3.9	9.5					
ER1470	83.3	80.7	74.9	92.8	38.0	47.1	105.4	50.5	126.5	62.0	64.5
H.ergaster											
N	3	3	3	3	3	3	3	3	3	3	3
Average	81.2	78.7	65.9	83.9	35.5	45.2	101.5	41.4	157.8	75.5	81.9
Var Coef	6.4	6.6	4.8	5.9	6.1	5.7	11.1	12.4	6.1	5.4	11.0
H.er.Java											
Ν	4	4	3	3	4	5	4	4	5	5	5
Average	79.8	73.0	67.2	92.6	37.5	50.8	119.9	45.7	124.9	60.8	64.1
Var Coef	1.3	1.2	2.8	2.7	2.9	4.4	12.4	4.4	6.1	6.3	9.2
H.er.China											
Ν	5	5	5	5	5	5	3	5	4	4	4
Average	74.9	67.9	67.6	99.5	37.1	54.6	116.3	43.0	120.9	58.0	62.9
Var Coef	2.9	2.7	2.6	3.9	2.5	4.7	1.8	5.4	6.5	4.6	8.5
Extinct humans											
Nb Spec.	105	105	104	104	104	104	105	27	26	26	26
Average	80.2	77.7	71.3	71.3	39.2	50.4	105.4	51.9	136.3	68.2	68.1
Var Coef	7.5	701	6.2	6.2	13.3	10.8	6.8	7.4	6.8	7.4	6.6
Maximum	92.8	92.2	85.5	85.5	54.5	66.2	121.5	59.8	151.3	75.3	76.0
Minimum	66.1	64	61.5	61.5	29.1	40	85.6	44	116.5	56.5	60

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Table 5. Bivariate dimensions

The relationship between maximal endocranial length and height was determined using the total height of the endocast when available or the upper part of the hemisphere when the basal portion was missing. The results place Dmanisi in an intermediate position between African *Homo ergaster* and Asiatic *Homo erectus*. With regard to breadth the Dmanisi fossis lump with the African and Asian fossils. Bregmatic angle (between maximal length and the intersection with endobregma: XBE) is similar compared with the other fossils, while this measure is slightly wider in *Homo sapiens*, implying the development of frontal rounding and recurving inferiorly through time towards *H. sapiens*. Also, it appears that from this sample there is an increase in frontal convexity through time

The occipital angle was measured in lateral view (between endolambda – endoopisthocranion and endoopisthocranion-superior edge of transverse sinus = XLTE). This angle is opened in ER 1813 (145°), similar to that of *Homo ergaster* (157.8°) and D 2280 (151.8°). However, values from Asiatic *Homo erectus* are lower with the angle being more closed between the superior squama and nuchal plane of occipital bone, a feature unique to this group. The inferior angle (XLIE) is more opened than the superior one (XLSE) on all studied fossil hominids. This supports other morphological results where the weak superior angle accentuates the position of the occipital lobes relative to the extension of parietal and temporal lobes posteriorly. In *Homo sapiens*, these two angles are nearly equal implying an increase of the superior part of the lobe in relation to the occipital lobes, which are in a lower and more inferior position in comparison with the parietal lobes.

In conclusion, the index shows a symmetrical increase in the length, width and height of the brain through time. The short height of the superior part of the brain identifies fossil hominids as platyencephalic. In addition, the endocranial angles analysis shows a steady widening of the bregmatic angle compared to the occipital angle in African sample, albeit the reverse is true in Asiatic and Dmanisi hominids. All of the fossils have an inferior angle that is more open than the superior one, a condition not observed in *Homo sapiens*.



Figure 8. Ratio of the biparietal width (WBE) on the maximal length average (LME)

	SET	RH	LH
D 2280	(306,3)	(162,8)	143,5
Homo habilis (n)	260,8 (3)	131,5 (3)	129,3 (3)
ER 1470	313	153	160
Homo ergaster (n)	310,5 (n=2)	157,7 (n=2)	158,3 (n=3)
Homo erectus Java (n)	342.1 (n=2)	175,4 (n=2)	166,7 (n=3)
Homo erectus China (n)	372,3 (n=3)	187,8 (n=3)	184,5 (n=4)
100 <i>H.sap.</i> (Var Coef)	494,6 (7,7)	248,4 (8,3)	246,2 (7,6)

Table 6. Tab. 6 : Total endocranial surface (SET), right (RH) and left (LH) hemispheric areas

#### **Endocranial surfaces**

D 2282 is too damaged with regard to this assessment; however, the preservation of D 2280 is more amenable to such a description. Data on the frontal lobes of D 2280 position it between those from African *Homo ergaster* on one hand and Asiatic *Homo erectus* on the other. The left parieto-temporal area as well as the occipital ones are within the lower limit of variation observed in African *Homo ergaster*. An important difference is observed between the right and left parieto-temporal areas of D 2280, which displays deformation in the inferior part of the right lobe, meaning right hemispheric and total brain measurements from this specimen are only descriptive.

#### ASYMMETRY

Endocranial asymmetry was observed on the fossil and modern samples. It is assumed that each hemisphere is devoted to particular tasks with the left one being more oriented towards learning and analyzing, for example, articulate language organization, and the right one being more specialized towards emotion and relational aspects. However, we must keep in mind that the two cerebral hemispheres complement each other in any task execution as emphasized in Schmidt-Nielsen (1998), Bruner (2003), Stout et al. (2000, 2007, 2008), Sherwood et al. (2003, 2008), and Holloway et al. (2004).

Asymmetry in endocasts is often attributed to a particular petalial pattern (Holloway, 1982a). For example leftward asymmetry or right-handedness is assumed from right frontal (RF) - left occipital (LO) petalia. This petalial pattern is normally attributed to species within the genus *Homo* (LeMay, 1976; Holloway et al., 1982b; Gilissen 2001).

In our sample, any geographic or chronologic association appears in the endocranial outline analysis among the studied human fossils. D 2280 shows left frontal and right occipital petalia similar to ER 1813, Sangiran 2,

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	RFr	LFr	RPr	LPr	ROc	LOc
D 2280	58,7	58,5	(84)	67	20,1	18
Homo habilis (n)	47.2 (3)	46.5 (3)	64.7 (3)	64.7 (3)	19.7 (3)	21 (3)
ER 1470	56	55	76	81	21	24
H. ergaster (n)	54.5 (3)	54.8 (3)	80 (3)	78 (2)	23,2 (3)	23,7 (3)
H. erectus Java (n)	65,7 (3)	58,8 (4)	81,2 (3)	79,8 (3)	28,5 (4)	28,1 (5)
H. erectus China (n)	72,0 (3)	69,8 (4)	83,5 (3)	80,7 (4)	32,4 (4)	34,0 (5)
100 H. sapiens (Var Coef)	86.1 (12,1)	85.5 (11)	131.9 (10,2)	128.4 (8,8)	30.4 (18,2)	32.8 (19,2)

Table 7. Right and left frontal (RFr, LFr), Temporo-parietal (RTPa, LTPa) and occipital (Roc, Loc) lobes areas



Figure 9. PCA 2D (11 variables and 47 specimens)

10, 17 and Ckn.L.2.PA.99. A right frontal – Left ocipital petalia is observed in OH 13, OH 16, ER 1470, ER 3733, ER 3883, WT 15000, CKn.E.PA.16, Ckn.L.1.PA.98 and Ckn.L.3 PA.100 (Tables 6 & 7).

Results obtained from the *Homo sapiens* sample (n=100) are consistent with Gilissen's conclusion that a left occipital – right frontal petalia is common in modern humans (77%). It is a well-established fact now that the pattern of combined left-occipital and right-frontal petalias became more common in human evolution through time as asymmetrical lateral protrusions of the cerebral hemispheres became more common. Generally, brain asymmetries correspond with handedness. For example, left hemispheric dominance generally indicates right manual dexterity (Galaburda et al., 1978). However, recent studies do not support the association between this

petalial torque pattern and right-handedness (Good et al., 2001; Herve et al., 2006).

The conclusion of this analysis is that there is variability in observed asymmetry moving from early *Homo* through moderns, a feature confirmed by Holloway & De La Coste-Lareymondie (1982b), who stated that "this pattern is not consistently present in nonhuman primates or in hominid fossil brain endocasts until *Homo erectus*". Hemispheric asymmetry corresponding to lateralization phenomenon is essential in tracing evolutionary changes in brain organization and cognition. Comparison of the fossil hominid sample through metrical as well as morphological analyses demonstrates potential correlations with the behavioural stages of human evolution (Holloway, 1981b, 1982; Holloway et al., 2004; Chieze, 1983; Saban, 1984; Gilissen, 2001; Sherwood et al., 2008).

	LMDE	LMGE	HGQDE	HGQGE	HBRDE	HBRGE	WMDE	WMGE	XBDE	XBGE	DOCDE	DOCGE	XLTDE	XLTGE
D2280	146	144	58	57.5	57	57.5	66	57	46	46	11	12.5	151	152.5
D2282	140	140	41.5	43	39.5	41	48	52	39	38.5				114.5
H.habilis														
Ν	4	4	4	4	4	4	4	5	1	1	3	3	1	1
Average	127.8	127.1	45.8	44.3	41.6	39.9	52.8	49.6	48.0	43.0	11.5	10.7	148.0	142.0
Var Coef	3.6	3.6	5.7	3.9	11.1	7.7	7.2	3.4			87.3	75.2		
ER1470	137	138	52	52.5	45	46	52	59	50	51	5.5	8	129	124
H.ergaster														
Ν	3	3	1	3	1	3	3		1	3	1	3	1	3
Average	147.7	146.7	54.0	52.5	46.0	49.3	61.0		45.5	41.7	3.0	4.0	148.5	159.8
Var Coef	6.1	6.2		17.3		18.4				21.8		25.0		5.7
H.er.Java														
Ν	4	4	4	5	4	5	5	6	3	4	4	4	4	5
Average	154.8	154.1	57.5	58.4	55.1	54.2	62.6	61.4	44.0	46.4	12.6	10.3	125.0	124.4
Var Coef	4.3	3.9	4.1	3.1	1.1	2.4	6.2	2.5	2.3	4.8	18.4	21.3	8.5	7.7
H.er.China														
Ν	5	5	5	5	5	5	5	6	5	5	4	4	4	4
Average	165.4	166.0	59.8	63.0	56.2	59.4	61.7	62.3	42.5	43.4	14.8	14.4	119.3	122.5
Var Coef	3.4	3.9	5.1	4.9	5.8	4.2	2.4	6.1	6.3	5.0	16.3	34.2	3.4	9.7
Extinct humans														
Nb Spec.	105	105	104	104	104	104	105	105	27	27	103	103	26	26
Average	170.1	170.8	66.6	66.6	58.8	58.9	68.2	68.5	51.9	51.8	8.8	10.5	139.8	132.8
Var Coef	4.9	5.0	12.5	12.4	14.1	13.1	6.5	7.5	8.1	7.3	55.0	41.5	6.4	12.3
Maximum	187	189	90	87.5	85	76.5	79	88	61.5	60	21	21	161.5	156.5
Minimum	147	150	50	52	44	44	56	58	44	43	0	1	117.5	99.5

Table 8 : Asymmetry

#### Univariate metrics analysis

On all of the fossil and modern human samples (Table 8) the difference between left and right hemispheric length is always less than 4mm. There is not apparent trend for asymmetry to be directed more towards one side versus the other in African or Asiatic fossil hominids. A slight asymmetry is observed in D 2280. In modern humans (n=109), though, there is a slight trend toward eftward asymmetry (54.1%) (170.8mm, VarCoef=5mm) (13.8% equivalent and 32.1% right with 170.1mm, VarCoef=4.9).

Right maximal hemispheric width is slightly larger on all African fossil hominids, D 2280 and Javanese *Homo erectus* from Trinil and Sangiran. However, no real trend appears in Zhoukoudian Lower Cave sample or in moden humans (n=105; left width=68.5mm, VarCoef=7.5; right width=68.2, VarCoef=6.5)

Concerning the superior hemisphere height at endobregma or endovertex level, all African fossil hominids from Olduvai and the Turkana region, Asiatic *Homo erectus* from Sangiran and Trinil, both Georgian fossil hominids, and the modern humans sample do not show any particular trend. Only Zhoukoudian Lower Cave hominids exhibit a more elevated height (towards the left). However, the meaning of this last this result should be considered with caution, since the result is drawn from only five individuals.

No asymmetric trend has been observed concerning bregmatic angle opening on left or right hemisphere in fossil or modern samples. The right occipital angle opening is greater in KNM ER 1813 and 1470 as well as in modern humans (139.8° VarCoef=6.4, left=132.8°, VarCoef=12.3). However, the other endocasts studied here are distributed equitably between left and right asyemmetries. Similar results were observed for the superior and inferior parts of the occipital angle.

No particular trend appears concerning the occipito-cerebellar distance in modern humans, which instead shows tremendous variability. In the fossil hominid sample, the repartition is equivalent between both groups, confirming either a left or right petalia distribution without any chronologic or geographic association. No asymmetry appears in the well preserved frontal and occipital lobes surfaces of D 2280.

#### Cerebral relief and vascular imprints

The study of the variation of encephalic relief and vascular imprints provides useful data on asymmetries through time. The endocranial surfaces of Olduvai and Turkana (East and West) are incompletely preserved. According to Begun and Walker (1993) relief of the left frontal is more developed in KNM ER 1813, but less so in KNM WT 15000 and KNM ER 1470. KNM ER 3733 and 3883 are too damaged for comparison. All Asiatic *Homo erectus* specimens from Sangiran, Trinil (Java) and from Zhoukoudian Lower Cave (China) have less relief in left frontal lobes. In moderns 72% exhibit left frontal relief against 16% for with more developed relief on the right frontal lobe (12% are equal).

D 2280 preserves some relief, displaying equivalent left and right frontal relief, except for the *pars triangularis* of third frontal convolution which seems bulge more on the right hemisphere. Both of these surfaces are clearly delimited from *pars orbitalis* and *pars opercularis*. The opercular part of second parietal gyrus produces an eminence on both hemispheres of D 2280 similar to that seen in modern humans. This area is a little more developed in the left parietal lobes of Asiatic *Homo erectus*. The supramarginal gyrus and angular gyrus are more accentuated with clearer limits on left temporo-parietal lobes of Asiatic *Homo erectus*, 45% of modern humans (37% on the left, 18% equivalent), and in D 2280. It is more developed on right hemisphere in OH13; however, the endocranial surface preservation of other fossils from Olduvai do not allow for any comparison. No difference was noted by Begun and Walker (1993) for this cortical region for WT 15000.

In modern human right-handers it is common to observe a larger right frontal lobe associated with a left one showing a more developed third frontal convolution (in particular the orbital and triangular parts) and left dominance of the supramarginal gyrus, which is included in Wernicke's area (LeMay, 1976). However, according to Gannon et al. (1998) and Sherwood et al. (2003) great apes exhibit humanlike asymmetry in Broca's area homologue and planum temporale, which is more localized to the supramarginal gyrus. Thus, there is debate about whether the humanlike asymmetry patterns expressed in non-human primates autapomorphic or plesiomorphic characters that could be expected to be resent in our early ancestors (Sherwood et al., 2008).

With concern to vascularization no relationship has been established between the meningeal system and the venous sinuses (Paturet 1964). No major trend has been observed between fossil hominids, which correlates with the results for frontal and occipital petalias. This is unlike modern humans, which exhibit a sagittal sinus going to the right transverse sinus on 77% (21% on the left and 2% indetermined), and have a more developed left hemisphere. The poor preservation on the right surface of D 2280 doesn't allow for any comparison between the middle meningeal pattern in both hemispheres. This vascular system seems more developed on the left side of the brain of Javanese Homo erectus, but is symmetrical in Chinese hominids. This left predominance reaches 43% (13% right). in modern humans, while 45% are symmetrical. Based on the fossil hominid sample vascular asymmetry seems to be considered autapomorphic character of modern humans, albeit we are uncertain what the correlation may be to cognitive abilities. In conclusion, there is no general trend with regard to vascularization in fossil himinids. The results show a rightward dominance for the frontal and temporo-parietal lobes, and a leftward dominance for the occipital lobes is associated with more developed cerebral relief on left side of the brain.

#### **Principal components analysis**

Correlation matrices suggest a strong relationship between the above data, except DOCE which corresponds to occipito-cerebellar projection (measures in lateral and superior views) (Table 9). The factorial weights table of each variable on each principal component demonstrates that all retained dimensions are correlated with the first principal component. It is the size effect that implies that small hominid endocasts are placed in positive values and larger ones in negative values. The result is that fossil hominids from Africa and Asia are in the right part of the graph, while more recent humans from the upper Palaeolithic to moderns are in the left part (Table10).

Principal component analysis applied to the endocast coordinates shows a polarized axis where the two first components reach 81% (Fig. 9). The first one (65.9% of total variance) is related to anterior cerebral region development, while increasing of the frontal and parietal chords is associated with elevation of the central region of the brain between the precentral and postcentral sulci (corresponding to HGQE, HBRE and XBE) on one hand and supramarginal gyrus development (corresponding to WBE) on the other. So the first axis clearly separates fossil hominids into two groups, African and Asiatic ones with short, low and narrow general dimensions and short frontal and parietal sagittal chords from modern humans.

The second component (15.2% of total variance) shows closing of the inferior part of the occipital angle, which is related to the occipito-cerebellar projection (DOCE), position of cerebral lobes and posterior cerebral rotation. In fossil hominids, the more open inferior occipital angle is observed in African endocasts with D 2280, which shows the most plesiomorphic pattern for this feature. The Asiatic sample, Javanese and Chinese, exhibits a slight narowing of the angle, but a higher occipito-cerebellar projection. D 2280 could be an Asiatic variation, since its absolute value for occipito-cerebellar projection is clearly outside that of the African sample. DOCE, which is only slightly smaller in PC1, is very large in the second component. However, this relative position of Dmanisi is the result of 11 variables. Its XLIE value is closer to African specimens. Endocasts situated on the negative axis show small a occipito-cerebellar projection (African hominids) than those ones with positive values in the superior where there is a notable backwards projection (Asiatic hominids).

The first axis of variation separates fossil hominids from modern humans. Three groups are clearly delimited on the graph. Endocasts in the inferior right quarter are the smallest in the three general dimensions (length, width, heights). The frontal angle is more narrow in this group, illustrating the low value of general cerebral bending. This group exhibits most opened angle in the inferior part of the occipital region, emphasizing a plesiomorphic configuration. The Asiatic sample, subdivided into Javanese as more archaic, and Chinese as more modern, demonstrates closeness in the inferior occipital angle and projection of occipito-cerebellar region. The pattern of increasing values from the African group to modern humans with concern to general dimensions, opening of frontal angle and closeness of the inferior occipital is clearly emphasized on this analysis.



Figure 10. PCA 3D with shape changes along PC1 and PC2

	DOCE	HGQE	HBRE	LME	WBE	CFR	СРА	COC	XBE	XLSE	XLIE
DOCE	1										
HGQE	0,32	1,00									
HBRE	0,36	0,92	1,00								
LME	0,63	0,68	0,55	1,00							
WBE	0,17	0,83	0,68	0,68	1,00						
CFR	0,53	0,87	0,78	0,85	0,74	1,00					
СРА	0,12	0,65	0,56	0,53	0,66	0,47	1,00				
COC	0,53	0,63	0,49	0,73	0,58	0,66	0,25	1,00			
XBE	0,01	0,73	0,60	0,23	0,60	0,48	0,48	0,40	1,00		
XLSE	-0,65	0,12	0,10	-0,27	0,20	-0,16	0,29	-0,19	0,19	1,00	
XLIE	-0,81	-0,31	-0,22	-0,66	-0,20	-0,51	-0,06	-0,59	-0,17	0,68	1

Table 9. Correlation matrix (11 variables and 47 specimens)

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Variable	CP 1	<b>CP 2</b>	CP 3	CP 4	CP 5
LME	-0.47	0.36	-0.41	-0.11	0.32
WBE	-0.41	-0.29	0.02	-0.60	0.04
HGQE	-0.38	-0.18	0.31	0.19	-0.16
HBRE	-0.28	-0.17	0.39	0.42	-0.06
DOCE	-0.09	0.24	-0.05	0.21	-0.13
CFR	-0.45	0.15	0.28	0.15	0.47
CPA	-0.30	-0.46	-0.66	-0.41	-0.22
COC	-0.24	0.23	0.12	0.33	-0.55
XBE	-0.10	-0.13	0.17	0.03	-0.36
XLSE	0.01	-0.37	0.04	-0.20	0.08
XLIE	0.15	-0.47	0.11	-0.15	0.38
Sdt.Deviat	27.41	13.17	8.66	7.03	5.92
Pr Variance	0.66	0.15	0.07	0.04	0.03
Cum Prop	0.66	0.81	0.88	0.92	0.95

Table 10. Factorial weights of variables on principal components

#### MORPHOMETRIC AFFINITIES OF DMANISI BRAINS

Particular care has been taken to choose the most landmarks preserved on the Dmanisi endocasts and other fossils. Procrustes superposition was peformed on 14 sagittal and left parasagittal landmarks digitalized in three dimensions (x,y,z) on 20 fossils specimens (Tale 2). This selection covers the majority of the left hemispheric surface, and is the result of the preservation state of D 2280. The D 2280 endocast was compared with African and Asiatic fossil hominids, and to upper Palaeolithic H. sapiens by principal components analysis. The two first components account for 49.5% of the total variance. The first component (27.5%) clearly separates two groups. All of the modern humans are on the positive side of the axis (Fig.10), while almost all of the ancient fossil hominids are placed on the negative side, including the Dmanisi specimen. Negative values correspond with elongated and low endocast shapes due to the lower position of the medial part of the brain, maximal endocranial width in a lower and more posterior position, and, finally, frontal and occipital extremities placed in prolongation of the maximal length. All these morphological features are considered as plesiomorphic.

On the positive side of the axis the shortness of the brain is underlined by the lower position of the anterior frontal part, which is rounding downward and backward, and the occipital and cerebellar lobes, which round downward and frontward. As a result these two cerebral regions are brought closer. Clear elevation of the posterior frontal and anterior parietal regions is noticed in more rounded endocasts. These phenomena are associated with the more anterior and superior position of the maximal endocranial width at the base of the parietal lobes. Thus, on the graph all modern humans are clearly situated on the positive side, and all the fossil hominids, African and Asiatic, are mixed together on the negative side of the axis.

Individualization in the two groups appears on the second component (22%). Asiatic hominids are placed in the negative part of axis, Africans in the positive part. Dmanisi hominids are intermediate between both fossil plots, while modern humans are intermixed with the fossils. The outline of the endocranial shape emphasizes a longer hemisphere with similar elevation in African hominids compared to Asiatic ones. Maximal endocranial width is situated superiorly in the second group. In superior and lateral views the different outlines of the first parietal convolution between African and Asiatic hominids is apparent. In African endocasts this is regularly convex between the sagittal plane and the maximal endocranial width contrary to Asiatic hominids which show an interruption in the curvature with a depression towards the level of the interparietal sulcus. Dmanisi joins the Asiatic sample in possessing a large and depressed sulcus. Dmanisi's position on the graph is intermediate between African and Asiatic groups, perhaps indicating the acquisition of derived characters similar to those observed in Asiatic Homo erectus.

#### Function

Clear regression of the encephalic rostrum, associated with a narrower interorbital space, is observed between the hominid fossil sample and modern humans. This difference can perhaps be functionally interpreted as an indication of a decreasing emphasis on olfaction. According to Sherwood et al. (2008), brain size enlargement in human evolution might have led to a greater degree of functional neocorticalization with this structure taking on more direct influence of other brain regions, allowing for greater voluntary control over actions, contributing to human-specific behavioural abilities, such as the modality and stimulus dependence of language. Broca's area, located in the third frontal gyrus, is a key component of the cortical circuitry in language production. It is more developed on the left hemisphere in 95% of humans as demonstrated by functional imaging or cortical stimulation studies (Parrot, 1981; Habib et al., 2000; Sherwood et al., 2003). For Arbib (2005) the role of Broca's area is more important that expected. Recent brain imaging data suggest important non-linguistic functions relevant to language development in the inferior frontal gyrus, revisiting the role of Broca's area in language, which has surely played as crucial a role in the evolution of human speech as gestural communication has in nonhuman primates. According to Lieberman (2007), "the starting points for human speech and language were perhaps walking and running". Earlier humans would be an intermediate stage in the evolution of language, indicating that this process was gradual and not an abrupt phenomenon. Of course, some form of speech, or different form of communication must have been in place in archaic hominids, allowing for culture and knowledge transmission through generations. Nevertheless, since the frontal lobes are involved in functions such as abstraction, planning and articulate language, their expansion and development are of great importance.

Expansion of the parietal lobes in modern humans (Grimaud-Hervé, 1997; Bruner 2004) is associated with enlargement of the temporal lobes. Both have key functions with regard to language comprehension, verbal memory and face recognition. Parietal cortex expansion is also important in human evolution, affecting visuospatial and sensory integration, multimodal processing and social communication (Holloway 1995). Important in the evolution of manual dexterity, the extension of posterior parietal cortex is presumed to have aided changes related to object manipulation, motor planning and, therefore, stone tool production (Stout & Chaminade, 2007). But we have to keep in mind that many asymmetries are expressed in nonhuman primates, and that plesiomorphic characters represent the substrate for a pre-adaptation to hemispheric specialization in human evolution. In this context, Aboititz et al. (2006) have emphasized the existence of a cortical sensory-motor auditory-vocal circuit, which was probably present in monkeys, and which served as the precursor for the cortical language circuits in the human brain (Broca's and Wernicke's areas). This idea is supported by recent neuroimaging studies in the monkey (Semenferedi and Damasio, 2000; Gil-da-Costa et al., 2006). Of course, study of the fossil record is limited to endocranial geometry and morphological description, which correspond only to macroscopic pattern. Unfortunately, any information that could be available on the architecture of the cerebral tissues and their associated functions is lost in the fossil record.

Using techniques as MRI (Magnetic Resonance Imaging) or FDG-PET (FluoroDeoxyGlucose Positron Emission Tomography), descriptions of activated cerebral areas during particular duties is possible, and allows one to establish the relationships between function and brain structure. Functional imaging research on modern humans cannot directly infer the cognitive capacities of extinct Homo species, but does permit speculation with regard to the development of evolutionary significant behaviours. The results of experimental toolmaking (Oldowan and Acheulean) by expert subjects (Schmidt-Nielsen, 1998; Stout et al., 2000, 2008) emphasizes the importance of visuomotor coordination, postural deportment, proprioception and hierarchical action organization. Increased activation of the ventral premotor and inferior parietal elements of the parietofrontal praxis circuits in both hemispheres and of the right hemisphere homologue of Broca's area suggest coevolutionary hypotheses linking the emergence of language, toolmaking, functional lateralization and association cortex expansion in human evolution (Falk, 1992, 2005; Gibson and Ingold, 1993; Holloway 1981b; Holloway et al., 2004; Tobias, 1991).

Actions involved in the toolmaking task are reflected in the activation of the left inferior parietal lobe, while knowledge of tools and tool-use are reflected in activation of the left posterior temporal cortex. According to Stout et al. (2008), results of functional imaging research with modern humans cannot directly reveal the cognitive capacities or neural organization of extinct hominin species but can clarify the relative demands of specific, evolutionarily significant behaviours. As expected in this study, expertise was associated with increased inferior parietal lobe activation during Oldowan toolmaking, but contrary to this expectation, this activation was strongly bilateral. Regions adjoining human anterior interparietal sulcus are also involved in the storage of visuospatial properties associated with tool manipulation. Thus, bilateral activation revealed in Stout et al. (2008) shows that expert performance is supported by an enhanced knowledge of the action properties of the tool and the body system, rather than semantic knowledge about appropriate patterns of tool use. The authors conclude that the task of Oldowan toolmaking is inherently bimanual with distinct but complementary roles for the two hands which confirm that hypotheses linking language capacities and tool-use typically focused on left hemisphere have to be discussed. The right hemisphere seems to play an important role in language processing (Bookheimer 2002), and contributes to elements of perception and action on larger spatio-temporal scales. Particular tasks require cortical association structures (Gilissen, 2001; Aboitiz and Garcia 1997; Amuntz et al., 1999; Wu et al., 2006). The archaeological record of technological change in understanding human cognitive evolution has to be reassessed, since it may be likely that ancient hominids and modern humans could have been

capable of utilizing similar tool making techniques. For example, archaic tools, which are not indicative of their cognitive abilitis, can be found with modern humans (Carbonell et al., 1995; Shea, 1997; Lévêque et al., 1993; d'Errico et al., 1998; Mellars, 1996; Roebroeks and van Kolfscoten, 1995). These neurological results obtained from magnetic resonance imaging of expert archaeologists perhaps provide an explanation for the absence of asymmetrical frontal and temporo-parietal lobes in African fossil hominids associated with Oldowan culture. In addition, a slight left predominance has been found in Asiatic fossil hominids, which is related to Wernicke's area of auditory comprehension.

#### CONCLUSION

Results of Dmanisi's brain study seem to link D 2282 with the African fossil hominid sample (cranial capacity, univariate and bivariate dimensions). These measurements place D 2282 closer to *Homo habilis*, suggesting it possesses many plesiomorphic morphological features commonly observed in *H. habilis* as well as *Homo ergaster*. A lateralization phenomenon is observed in the orientation of longitudinal superior sinus on African and Asiatic hominids, but no chronological or geographical groups have been noticed. This asymmetry is observed primarily in the most ancient fossil hominids of our studied sample. This sinuses lateralization corresponds with the observed petalial patterns noted on all of the specimens here.

The middle meningeal system of Dmanisi's hominids is very poor with scarce ramifications and no anastomoses unlike those observed on most ancient African hominids. Asiatic Homo erectus meningeal system is more developed with more ramified branches. The Dmanisi endocranial morphological features as compared to African fossil hominids from Olduvai, East and West Turkana, and to Asiatic ones from Trinil and Sangiran in Java and Zhoukoudian in China, allows one to emphasize some of the similarities which can be interpreted as plesiomorphies. This is the case of the systematic encephalic rostrum present on all specimens, which corresponds to the first and second convolutions that invaginate between the orbital roof and are determined by the size of the interorbital space. This morphological character is related to olfaction, and is well developed in all early fossil hominids.

Frontal and parietal relief are scarcely individualized in the African sample, and are more marked with less diffuse limits in D 2280 and Asiatic *Homo erectus*. The Sylvian valley, which is particularly broad in the African sample, is narrower on Dmanisi and Asiatic hominids with clear development of frontal and temporal lobes which lie more closely together because of closing of Sylvian valley. In most ancient Asiatic *Homo erectus* the precentral gyrus breadth is often wider (or equivalent to the postcentral). This trend is accentuated on more recent Asiatic *Homo erectus* such as Ngandong for example. Most ancient African hominids exhibit equality of the breadth of the pre- and post-central convolutions. ER 3733 (on which this character can be observed) exhibits a slightly broader post central gyrus. The same observation is also true of both Dmanisi's hominids as well as modern humans.

Convergence of results obtained from morphological, univariate and bivariate analysis, and morphometrical 2 and 3D analyses contribute to a synthetic approach concerning the phyletic position of the Dmanisi hominids. Size factors distinguished African hominids and Dmanisi from Asiatic sample. Those excluding size emphasize the morphological features that are traditionally difficult to quantify. These show an unquestionable closeness between D 2280 (D 2282 is too damaged to be integrated into this analysis) and Asiatic hominids, which are distinct from the African sample as well as modern humans.

The primary results, based on the small fossil sample, possibly suggests that the first African representatives from the genus *Homo* (*Homo habilis* or *Homo ergaster*) could have evolve into archaic *Homo sapiens*, which could be the ancestor of anatomically modern *Homo sapiens* in Africa. In addition, these African fossils may also provide a link to the Dmanisi fossils, which share strong affinities with Asian *Homo erectus*, as well. One of these fossils hominids (D 2280) exhibits derived characters similar to those observed in Asiatic *Homo erectus*, implying that the Dmanisi fossils lie near the origin of the Asian fossils.

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