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A. Balzeau



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ARE THICKENED CRANIAL BONES AND EQUAL PARTICIPATION OF THE THREE STRUCTURAL BONE LAYERS AUTAPOMORPHIC TRAITS OF *HOMO ERECTUS*?

L'ÉPAISSEUR CRÂNIENNE ET SA CONSTITUTION INTERNE : AUTAPOMORPHIES DE L'ESPÈCE *HOMO ERECTUS* ?

Antoine BALZEAU¹

ABSTRACT

Numerous studies have proposed different lists of morphological features to define the species of *Homo erectus*; among these, some are considered to be autapomorphic. The intention of this study is to discuss two of these possible autapomorphic traits: thickened cranial bones and equal participation of the three structural bone layers (inner and outer tables, diploe) in this thickening. This study brings new information concerning cranial vault thickness and structural composition in the mid-sagittal plane of some Asian *Homo erectus*. The Ngandong and Sambungmacan fossils, as well as the Zhoukoudian and Sangiran individuals, have cranial vault thickness values within the range of variation observed in our *Homo sapiens* comparative sample. Moreover, even if the frontal and sagittal keels in *Homo erectus* constitute a relief on the external cranial vault surface, they do not necessarily correspond to a real thickening of the underlying bone. The diploic layer principally contributes to their internal composition. Similarly, the diploe constitutes the greatest part of the total vault thickness along the mid-sagittal plane, particularly in the frontal and occipital *tori*, in the analysed fossils of this extinct species. Finally, our results show that *Homo erectus* individuals have cortical tables as well as diploe variation and distribution patterns similar to anatomically modern *Homo sapiens*. Therefore, the two tested autapomorphic traits for *Homo erectus* can no longer be considered as valid.

Keywords: *Homo erectus*, cranial vault thickness, CVT, bone structure, inner and outer tables, diploe, autapomorphy, CT.

RÉSUMÉ

L'épaisseur importante de la voûte crânienne et l'hyperossification de la table compacte externe, deux caractères considérés comme autapomorphiques pour l'espèce Homo erectus, sont étudiés. La variation de l'épaisseur et sa constitution interne ont été analysées le long du plan sagittal médian chez des représentants de l'espèce Homo erectus. Les fossiles de Ngandong, Sambungmacan, Sangiran et Zhoukoudian étudiés ont dans l'ensemble des valeurs d'épaisseur crânienne qui se situent dans la variabilité de notre échantillon d'Hommes anatomiquement modernes. De plus, les fossiles attribués à Homo erectus et Homo sapiens partagent le même schéma de distribution de l'épaisseur crânienne et des tables osseuses le long du plan sagittal médian. Si la carène sagittale chez Homo erectus constitue un relief osseux externe, elle ne correspond pas nécessairement à un réel épaissement de l'os sous-jacent, ni à celui de la table compacte externe comme admis jusque là. Le diploé en compose la majeure partie comme cela est observé sur les torus frontal et occipital transverse. Les caractères testés ne sont donc pas des autapomorphies de l'espèce Homo erectus.

Mots-clés : *Homo erectus, épaisseur de la voûte crânienne, structure osseuse, tables interne et externe, diploé, autapomorphie, CT.*

1. UMR 5198, USM 204, CNRS, Équipe de Paléontologie Humaine, Département de Préhistoire du Muséum National d'Histoire Naturelle, 17 place du Trocadéro, 75016 Paris, France, e-mail : abalzeau@mnhn.fr

INTRODUCTION

Homo erectus is one of the oldest hominid species discovered and has been widely studied, particularly with respect to its origin, out-of-Africa and dispersion modalities (e.g. Antón *et al.* 2002b; Dennel 2003) and its status in relation to anatomically modern *Homo sapiens* (e.g. Thorne, Wolpoff 1981; Stringer *et al.* 1984; Wolpoff *et al.* 1984, 2000; Stringer, Andrews 1988; Hublin, Tillier 1991; Frayer *et al.* 1993; Lieberman 1995; Détroit 2002; White *et al.* 2003; Etlér 2004). Moreover, different geographical and chronological morphs have been proposed among Asian fossils based on cranial morphological variations (e.g. Weidenreich 1943, 1951; Antón 2002; Antón *et al.* 2002a; Kidder, Durband 2004; Balzeau, Grimaud-Hervé 2006). Discussions concerning *Homo erectus* definition have particularly focussed on the Asian fossils, which were discovered first. Numerous papers have proposed different lists of morphological features, and some of them are considered as autapomorphic (derived characteristic unique to a given taxon) for *Homo erectus* (e.g. Le Gros Clark 1940, 1964; Mayr 1944, 1950; Arambourg 1957; Howells 1966, 1980; Jacob 1971, 1976a, b; Howell 1978; Hublin 1978, 1986, 1989; Andrews 1984; Stringer 1984; Wood 1984; Clarke 1990; Kennedy 1991; Bräuer, Mbua 1992; Leigh 1992; Dean 1993; Brown 1994; Wu, Poirier 1995; Wood, Collard 1999; Wood, Richmond 2000; Zeitoun 2000; Delson *et al.* 2001; Antón 2002, 2003). Among these autapomorphic features are thickened cranial bones and equal participation of the three structural bone layers in this thickening.

Cranial bone thickness has been widely qualified for *Homo erectus* but rarely quantified. About this aspect, Weidenreich (1943, p. 161) wrote: "It is well known that the skull caps of fossil hominids appear considerably thicker than those of modern man. But as yet, so far I was able to ascertain, no one has provided actual figures or deemed the entire phenomenon worth special consideration". Nevertheless, thickened cranial bones have been considered as a diagnostic feature for *Homo erectus* by many authors (e.g. Weidenreich 1943; Le Gros Clark 1964; Hublin 1978; Andrews 1984; Wood 1984). Previous studies have obtained various results and interpretations for this feature (Kennedy 1991; Kennedy *et al.* 1991; Bräuer, Mbua 1992; Brown 1994; Gauld 1996; Antón 1997), whereas cranial vault thickness (CVT) has often been used to discuss individual taxonomic attribution (e.g. Kennedy *et al.* 1991; Delson *et al.* 2001; Baba *et al.* 2003; Manzi *et al.* 2003). Concerning the internal bone

composition, Weidenreich (1943, p. 163) first commented: "In *Sinanthropus*, all three constituents of the bone take equal part in the thickening, the two tables slightly more than the diploe". Since then, this feature has often been regarded as an autapomorphic feature of *Homo erectus* (e.g. Hublin 1986, 1989, 1991; Gauld 1989; Kennedy 1991; Bartsiokas 2002; Bräuer *et al.* 2003).

The purpose of this study is first to examine the particularities of the cranial bone thickness and internal composition in some Asian *Homo erectus* fossils, and compare those with anatomically modern *Homo sapiens* material. Then, based on this new data, we will discuss the validity of the proposed autapomorphic status of these traits for *Homo erectus*.

MATERIALS AND METHODS

Materials

The *Homo erectus* samples include fossil individuals from Ngandong (Ngandong 2, 7 and 12) and Sambungmacan sites (Sambungmacan 1 and 3). These fossils were collected along the Solo river, Java, Indonesia (Oppenoorth 1932; Jacob 1973; Sartono 1976, 1979; Jacob *et al.* 1978; Márquez *et al.* 2001). The results concerning their absolute age are debated, some could be less than 50 ka old (Swisher *et al.* 1996). Concerning their individual age, Ngandong 2 is generally recognized as an immature individual, Ngandong 7, Ngandong 12 and Sambungmacan 1 as adult individuals (e.g. Antón 1999). Sambungmacan 3 was first described as a young female (Delson *et al.* 2001; Antón *et al.* 2002a). Based on the study of endocranial and internal cranial features, an immature status cannot be excluded for this individual (Balzeau 2005). The bone thickness data of the Ngandong and Sambungmacan fossils were obtained on the original fossils using computed tomography (CT) scans. Additional data were collected on Sangiran hominids by direct measurement of the original fossils Sangiran 10, 18a, 19a and 38 and by means of CT scanning for a Sangiran 17 parietal fragment. These individuals were all collected in the Bapang (Kabuh) formation in the Sangiran dome area, Java, Indonesia and are probably around 1 million years old (e.g. Swisher 1997; Langbroek, Roebroeks 2000; Bettis *et al.* 2004). Finally, data for the Zhoukoudian fossils are based on the monograph of Weidenreich (1943). Comparative samples include anatomically modern *Homo sapiens* adult individuals from European Upper Palaeolithic sites (Cro Magnon 1, 2, 3

and Pataud 1) and the North African Epi-Palaeolithic sites of Afalou Bou Rhummel and Tatoralt (Afalou 2, 12, 13, 28, 30, 34 and Tatoralt XI C1, XII C1, XV C2, XV C4, XV C5, XVII C1). These individuals are known to be robust (Lahr 1994; Lahr, Wright 1996; Balzeau, Badawi-Fayad 2005) and are not considered representative for the whole variation in *Homo sapiens*.

All the fossils were CT scanned with a General Electric High Speed HAS scanner at the CHNO des Quinze-vingts in Paris. Acquisition parameters varied according to individual mineralization states and size of the fossils (Badawi-Fayad *et al.* 2005). Settings ranged between: 100-120 kV, 90-250 mA, 0.3-1.0 mm-thick slices, reconstruction increment 0.4-0.5, 23-25 cm field of view, and 0.45-0.59 pixel size with a pixel matrix of 512*512. The CT data sets were visualized and analyzed using Merge eFilm 1.8.1 and Materialise Mimics 7.1 software. The CT data sets do not show any noticeable artifacts, even though some fossil skulls show different degrees of mineralization. Moreover, the Hounsfield values for each of the studied fossils are within the range covered by the scanner, resulting in the absence of overflow artifacts.

Methods

From a methodological point of view, many aspects have to be considered in order to perform an analysis of the cranial vault thickness and internal composition. At first, attention must be paid to the reproducibility measurement. The determination of cranial landmarks varies between observers. The most easily recognizable landmarks are situated on sutural intersections. However, individual developmental stages may influence their localization when fontanelles are opened or when sutures are obliterated. Less confidence can be placed in type II or III landmarks (*sensu* Bookstein 1991; O'Higgins 2000) in terms of homology than in type I landmarks. This is important when only a few measurements are sampled and compared which are solely based on landmarks obtained by construction (*e.g.* frontal or parietal eminences, centre of a bone in a pre-defined plane, a maximal curvature or extension). This sort of landmark may cause large inter-individual variability in the thickness values and may vary in terms of morphological significance between hominid species. In addition, anatomical landmarks on the cranial external surface do not necessarily have a counterpart on the internal surface. Cranial vault thickness is quantifiable

through observation of various orientations: perpendicular to the external or internal cranial surface or in the maximal or minimal extensions. Values vary noticeably depending on this orientation, particularly at the cranial superstructures. Furthermore, thickness values may vary according to the cranial external structures and position and development of the endocranial structures (*e.g.* *tori* and keels, internal frontal and occipital crests, venous and meningeal impressions or even pathological and traumatic after-effects). Finally, the conservation state of the fossils and their diagenetical and taphonomic history must be considered since these factors can influence original internal composition and thickness of the cranial vault.

We have developed a specific analytical protocol to overcome these limitations by using the mid-sagittal plane to quantify CVT and internal bone composition (*fig. 1*). Indeed, this plane is clearly reproducible in both *Homo erectus* and *Homo sapiens* individuals. In addition, the definition of this plane is not influenced by the variations of size and morphology of the different bones of the cranial vault between these two species.

We have used CT data to obtain a large number of measurements concerning CVT and internal composition. CT data correspond to a successive set of slices defining the whole fossil. Each image crosses the bony structures in various orientations. Thickness quantification can be done where the acquisition is perpendicular to the cranial surface and thickness. The mid-sagittal plane is the only one in the whole data set, which extends perpendicularly to the cranial thickness in its full extension. On each individual's corresponding slice, the boundary between outer, diploic and inner table, as well as with the surrounding air, was identified by manual segmentation (SMM: *Seuillage Manuel Multiple* or *Multiple Manual Thresholding*). This procedure consists of measuring the median value (or half maximum height, HMH) from the CT value of the two elements, of which the interface should be defined (Spoor *et al.* 1993; Schwartz *et al.* 1998). The manual segmentation has to be made each time the attenuation coefficient of one of the elements varies along the interface. It allows for accurate identification of the interface between two structures, despite local fluctuation in CT numbers (Balzeau 2005). This segmentation protocol enabled isolation of the exact area corresponding to the bone extension in order to quantify CVT, on the one hand, and the exact extension of the inner table, of the diploe and of the outer table, on the other hand. In some instances the internal bone layers could not be isolated because they were not preserved

due to diagenetic transformations. This is the case for the entire mid-sagittal plane of Sambungmacan 1 (Balzeau *et al.* 2002), and for some smaller sections for the other Asian fossils. The spatial resolution limitations of the HMH methodology are known to overestimate thickness values when very thin distances are measured (see *e.g.* Spoor *et al.* 1993). However, the elements quantified in this study do not reach this limit (*e.g.* internal constituents were always more than 1 mm thick when it was possible to quantify them). There are no overflow artifacts in the analyzed datasets and we have used a specific protocol to precisely isolate the different components of the images. The only limitation to this study is due to the spatial resolution of the datasets and to the partial volume averaging artifact, which is inherent to CT. We estimate that errors in measurements do not exceed ± 0.25 mm, and are smaller in most cases. In addition, the spatial resolution of the CT datasets was similar for all the studied individuals, resulting in a comparable precision for the measurements. Four principal landmarks are defined on the external cranial surface: the sagittal glabella (noted as Gs), the sagittal bregma (Bs), the sagittal lambda (Ls) and the sagittal external occipital protuberance (Os). The term sagittal is used here to disassociate these landmarks from the classical anatomical landmarks. They do not exactly correspond to the type I landmark definition as they are defined on a 2D plane. However, they remain easily recognizable and reproducible. The following step is to use the internal projection perpendicularly to the endocranial surface of these landmarks to delimitate

four endocranial chords from the sagittal glabella to the foramen magnum. Then, these chords are divided in equal segments and thickness is measured at each interval. Gs-Bs and Bs-Ls are divided in 20, Ls-Os in 15 and Os-foramen magnum in 5. Thickness is quantified perpendicularly to the endocranial surface. Indeed, the internal cranial surface presents less topographic variations than the external cranial surface. In effect, measurements obtained perpendicular to the external surface vary widely as a result of topography changes (*e.g.* between glabella and the supraorbital sulcus). Thickness values may be influenced by the sutures extension at bregma and lambda or for the parietal bones. Even if some measurements are minimized in these areas, none of the studied individuals show an opened suture, which could have resulted in a null thickness value. Outer and inner table and diploe thickness are quantified at the parietal bones junction only in the individuals with completely fused sagittal suture. These variations were not available for the Ngandong and Sambungmacan hominids. Moreover, whenever possible, the analysed plane is chosen to include the internal frontal crest. The internal occipital crest is included in this plane for all the analysed *Homo erectus*, because of its pronounced development in these fossil hominids. It is also the case for most of the comparative sample, even if this morphological area is less pronounced and sometimes partially outside the mid-sagittal plane. Finally, while a comparison between several individuals based on a unique metric measurement is not meaningful, our protocol permits us to present a comparative analysis

| | Combined vault thickness (mm) | Combined vault thickness/endocranial chord | Vault thickness surface (mm ²) |
|---------------------------------------|-------------------------------|--------------------------------------------|--------------------------------------------|
| <i>Homo erectus</i> | | | |
| Ngandong 7 | 620 | 2.20 | 2867 |
| Ngandong 12 | 644 | 2.28 | 3020 |
| Sambungmacan 1 | 589 | 2.07 | 2900 |
| Sambungmacan 3 | 647 | 2.34 | 2952 |
| <i>Anatomically modern H. sapiens</i> | | | |
| Mean value | 637 | 1.92 | 3398 |
| standard deviation | 84.7 | 0.28 | 413.2 |
| Range | 502-778 | 1.5-2.4 | 2676-4038 |

Table 1—Absolute and relative data of the thickness of the cranial vault for Ngandong and Sambungmacan fossils and anatomically modern *Homo sapiens* ($N = 12$, mean values, standard deviation and range of variation for the Afalou Bou Rhumel and Taforalt individuals).

Tabl. 1 - Données absolues et relatives d'épaisseur crânienne chez les fossiles de Ngandong et Sambungmacan et les Hommes anatomiquement modernes d'Afalou Bou Rhumel et de Taforalt ($N = 12$, valeurs moyennes, écarts-types et variations maximales).

of the vault thickness and structural layers distribution on 60 landmarks on the whole mid-sagittal plane (fig. 1). Our whole thickness dataset is affected by the development of the frontal and occipital *tori* as well as by those of the bregmatic eminence or keels. As these features are considered characteristic for *Homo erectus*, their inclusion in our study afforded a better approach when comparing morphologies of *Homo erectus* with those of anatomically modern *Homo sapiens*.

Table I gives cranial vault thickness metrical data, based on the analytical protocol described above. The first column gives the combined vault thickness for the 60 landmarks along the mid-sagittal plane. The ratio of combined thickness over endocranial chord corresponds to an estimation of the mean cranial thickness in the mid-sagittal plane and is independent of the skull size. The endocranial chord is quantified directly on the mid-sagittal plane on the CT dataset. The mid-sagittal vault thickness surface (from the glabella to the foramen magnum in the mid-sagittal plane) is obtained by multiplying each landmark thickness value by the endocranial distance, which separates it from the adjoining landmark. This variable depends on the fact that each inter-landmark space is of rectangular shape. However, it has the same definition for each individual and enables better quantification of the skull size. Finally, a direct measurement of the cross-sectional bone area in the mid-sagittal CT slice was not possible, because of variations in the conservation state of the fossils and of the important influence of the suture closure state on this measurement. Because of small sample size, we do not propose any statistical approach for the variation of the CVT. Moreover, inner table, diploe and outer table thicknesses are complex datasets, with values lacking for the fossils, which does not permit a statistical analysis or a Geometric Morphometrics approach.

RESULTS

Cranial vault thickness

With regard to the thickness distribution along the analysed plane, the Afalou Bou Rhummel and Tatoralt skulls (N = 12) present well-developed superstructures (fig. 1). The Cro Magnon (N = 3) and Pataud (N = 1) individuals yielded absolute thickness values around or smaller than the Afalou Bou Rhummel-Tatoralt mean and are generally in the lower part of the measured range. However, all these individuals share the same pattern of

cranial vault thickness distribution along the mid-sagittal plane (Balzeau 2005). In comparison with previous studies (e.g. Todd 1924; Martin 1928; Twiesselmann 1941; Weidenreich 1943; Kennedy 1991; Ross *et al.* 1998; Lynnerup 2001), Afalou Bou Rhummel and Tatoralt cranial thickness values are outside the variation of these actual populations but are within the range of variation observed in fossil samples (e.g. Brown 1994). Because of the good state of preservation and a larger number of individuals, we use the Afalou Bou Rhummel and Tatoralt individuals as a comparative sample for the forthcoming analyses of the *Homo erectus* characteristics.

Table I gives a comparison of the cranial vault thickness data between Ngandong and Sambungmacan *Homo erectus* (N = 4) and our anatomically modern *Homo sapiens* sample (N = 12). Results for Sambungmacan 1 include estimation for a few measurements for the frontal bone anterior part. The values of the combined thickness of *Homo erectus* fossils (between 589 and 647 mm) are close to the mean value of the comparison material (637 mm); and the mean value for the *Homo erectus* fossils is significantly less than the mean value for the anatomically modern *Homo sapiens* ($t = -2.2748$, $P < 0.05$). The ratio combined thickness/endocranial chord of *Homo erectus* (2.07-2.34) is well within the range of the comparison material (1.5-2.4); and the mean values for the *Homo erectus* fossils and for the anatomically modern *Homo sapiens* are not significantly different ($t = 1.0485$, $P = 0.312$). Finally, the Ngandong and Sambungmacan *Homo erectus* values for vault thickness surface (2867-3020 mm²) are within the lower range of variation of the comparison material (2676-4038 mm²); and the mean value for the *Homo erectus* fossils is significantly less than the mean value for the anatomically modern *Homo sapiens* ($t = -98.042$, $P < 0.01$). It is clear that neither absolute nor relative metrical data of the Ngandong and Sambungmacan *Homo erectus* specimens exceed the variation of the anatomically modern *Homo sapiens* sample.

Figure 2 presents the comparison of the cranial vault thickness distribution between Ngandong and Sambungmacan *Homo erectus* and anatomically modern *Homo sapiens* from Afalou Bou Rhummel and Tatoralt along the mid-sagittal plane. Ngandong 2, an immature specimen, has a less pronounced frontal superstructure, whereas its frontal squama has thickness values within the adult variation. Sambungmacan 3, an immature/subadult individual, also has less developed superstructures than adults. Some Ngandong 7 thickness values are affected

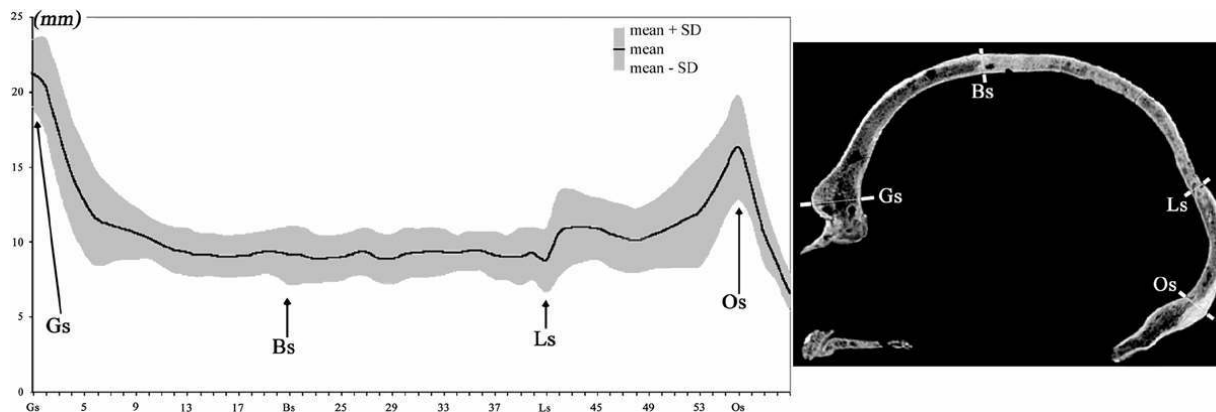


Fig. 1—Variation in the thickness of the cranial vault (mean \pm 1 S.D., in mm) along the mid-sagittal plane for the anatomically modern Homo sapiens from Afalou Bou Rhummel and Taforalt and illustration of the analysed plane. The cranial thickness is quantified from the sagittal glabella (Gs) to the foramen magnum.

The graphic representation of the data corresponds to the successive landmarks from left to right.

Fig. 1 - Variations de l'épaisseur crânienne (en millimètres, valeur moyenne – trait noir – et plus ou moins l'écart-type – zone grisée –) le long du plan sagittal médian chez les Hommes anatomiquement modernes d'Afalou Bou Rhummel et de Taforalt et illustration du plan d'analyse. L'épaisseur crânienne est mesurée à partir de la glabelle sagittale (notée Gs) jusqu'au foramen magnum. La représentation graphique des données obtenues correspond à l'acquisition pour les 60 points repères du plan sagittal médian, de la gauche (Gs) vers la droite (le foramen magnum).

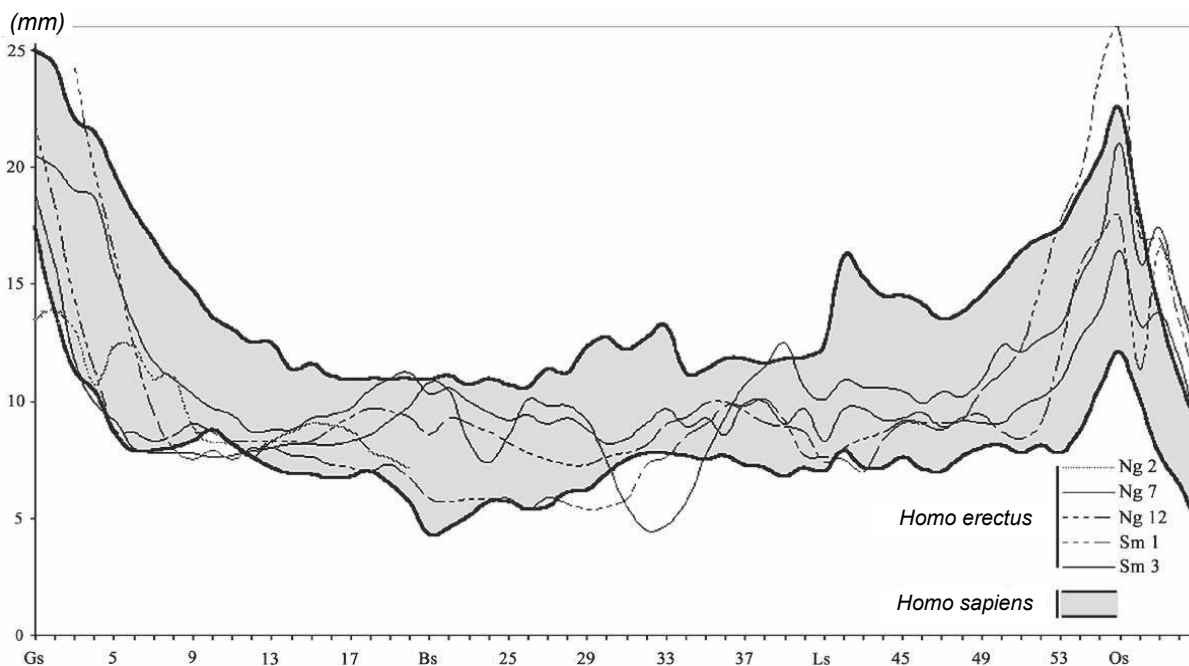


Fig. 2—Variations in the thickness of the cranial vault (in mm) along the mid-sagittal plane for Ngandong and Sambungmacan fossils (individual results) and the maximal extension for the anatomically modern fossil Homo sapiens from Afalou Bou Rhummel and Taforalt (dark lines and grey area).

Fig. 2 - Variations de l'épaisseur crânienne (en millimètres) le long du plan sagittal médian pour les fossiles de Ngandong et Sambungmacan (variations individuelles, représentées par les courbes grises et noires, pleines et pointillées) et variation maximale observée chez les Hommes anatomiquement modernes d'Afalou Bou Rhummel et de Taforalt (comprise entre les deux traits noirs gras et figurée par la zone grisée).

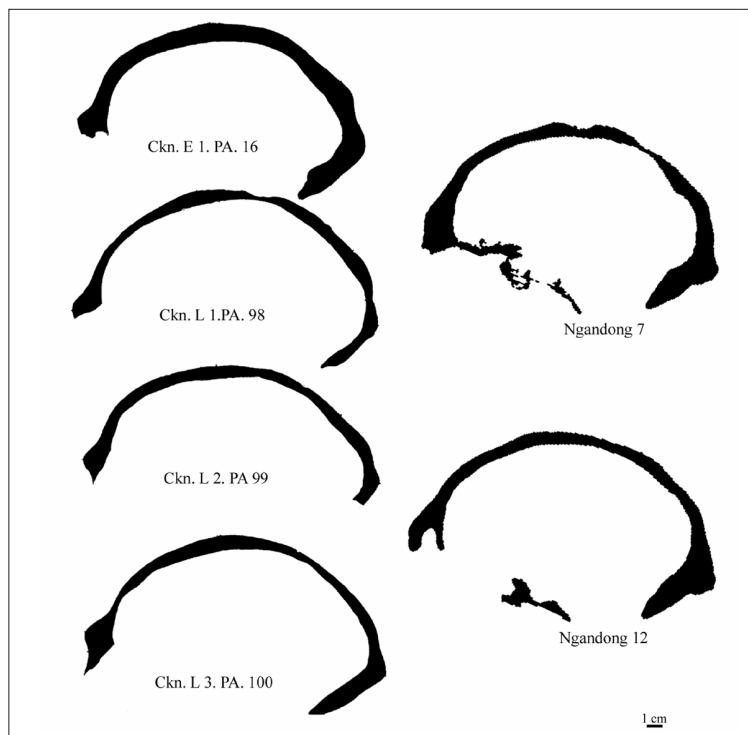


Fig. 3—Outlines of the cranial vault in the mid-sagittal plane for the Zhoukoudian fossils (after Weidenreich 1943) and the Ngandong 7 and 12 individuals.

Fig. 3 - Contours de la voûte crânienne dans le plan sagittal médian pour les fossiles de Zhoukoudian (d'après Weidenreich 1943) et comparaison avec ceux de Ngandong 7 et Ngandong 12 (obtenus par les méthodes d'imagerie).

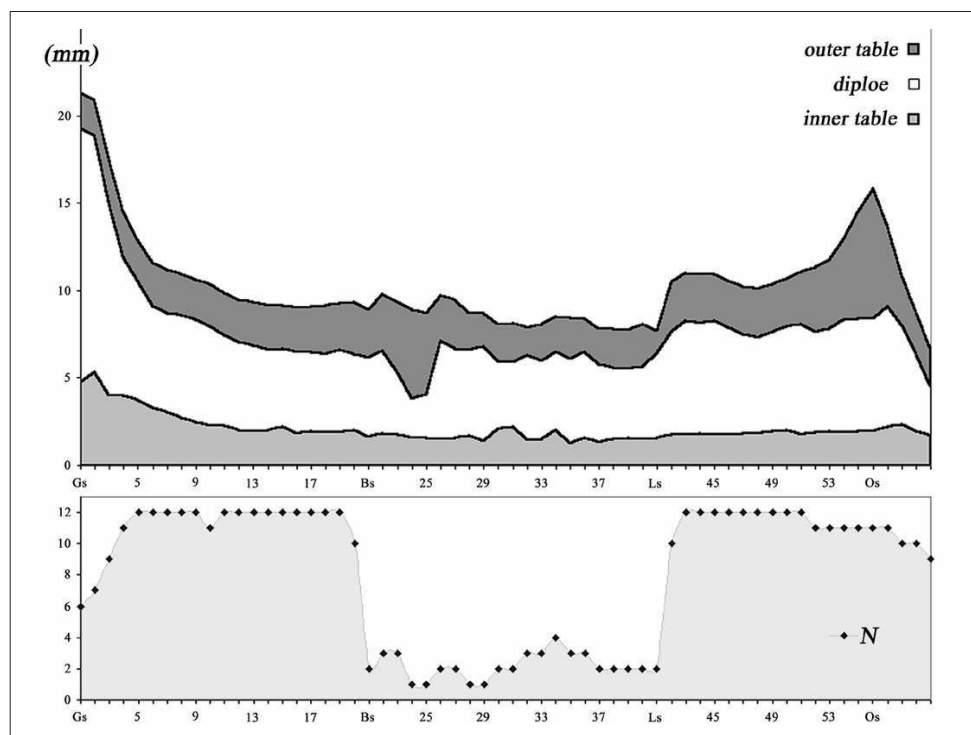


Fig. 4—Variation in the mean of the thickness of the inner table, diploe and outer table (in mm) along the mid-sagittal plane for the anatomically modern fossil *Homo sapiens* of Afalou Bou Rhummel and Taforalt and number of individual (*N*) for each landmark data. *N* is lower at the sutural intersections (bregma and lambda) and along the sagittal junction of the parietal bones (because of the sagittal suture presence). The different internal layers are not individualised where the sutures are not totally closed.

Fig. 4 - Variation moyenne de l'épaisseur (en mm) de la table interne (représentée en gris clair), du diploé (en blanc) et de la table externe (en gris foncé) le long du plan sagittal médian chez les Hommes anatomiquement modernes d'Afalou Bou Rhummel et de Taforalt et nombre d'individus (*N*) pour chaque point repère ou l'épaisseur des constituants internes est quantifiée. *N* est plus faible aux intersections de sutures (bregma et lambda) et à la jonction des os pariétaux dans le plan d'analyse en raison de la présence de la suture sagittale. Les tables denses et le diploé n'ont pu être mesurés lorsqu'ils n'étaient pas individualisés en raison de la présence de sutures avec une synostose incomplète.

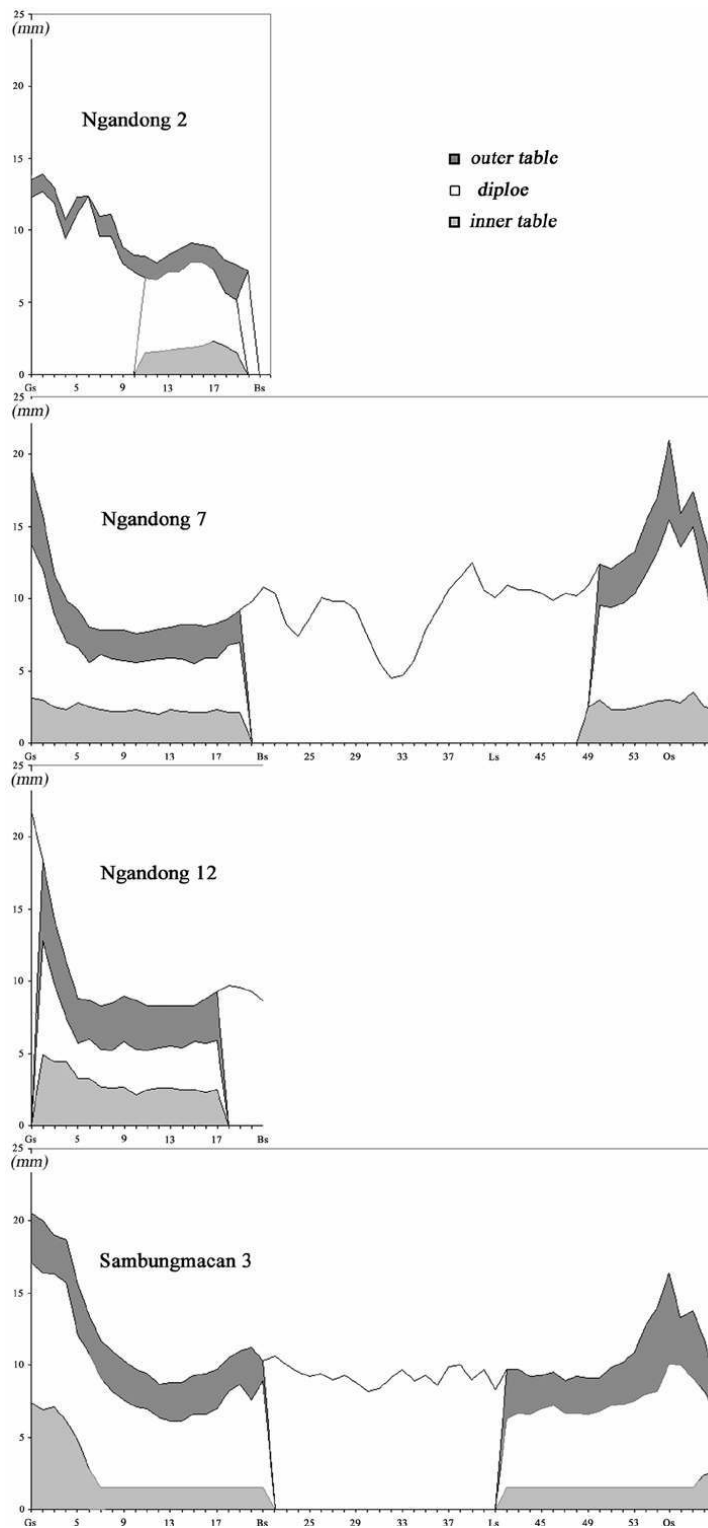


Fig. 5—Variation in the thickness of the inner table, diploe and outer table (in mm) along the mid-sagittal plane for Ngandong and Sambungmacan fossils.

Fig. 5 - Variation de l'épaisseur (en millimètres) de la table interne (représentée en gris clair), du diploé (en blanc) et de la table externe (en gris foncé) chez Ngandong 2 (qui est un os frontal isolé), Ngandong 7 (pour l'os frontal et l'os occipital, les tables osseuses ne sont pas dissociées pour cet individu à la jonction des os pariétaux), Ngandong 12 (pour l'os frontal, les tables osseuses ne sont pas conservées sur le reste du plan sagittal médian) et Sambungmacan 3 (pour l'os frontal et l'os occipital).

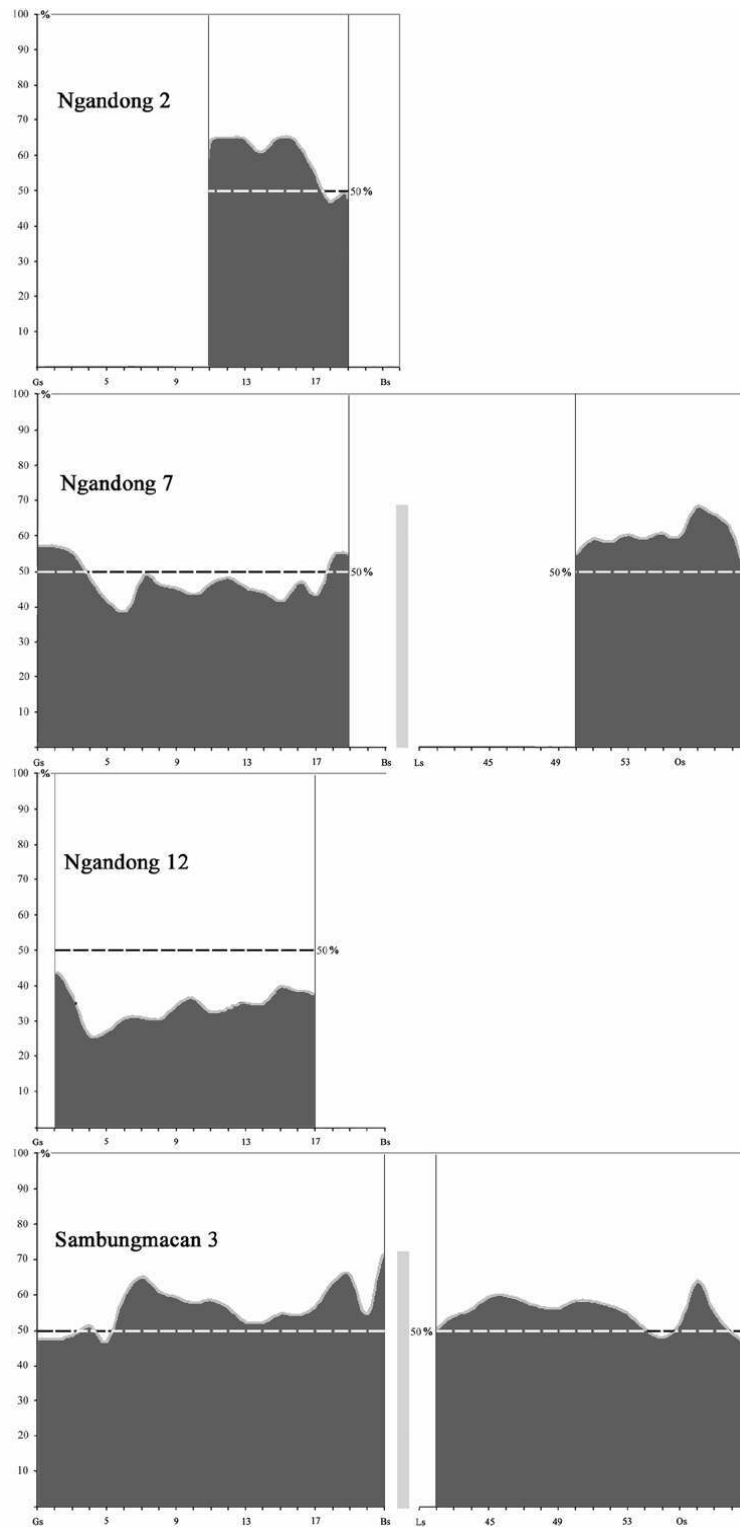


Fig. 6—Diploic participation in the thickness of the total vault (in %, represented in dark grey) for Ngandong and Sambungmacan fossils on the frontal bone and the occipital bone in the mid-sagittal plane. The dotted line represents 50% of the thickness of the total vault.

Fig. 6 - Proportion (en %) de l'épaisseur du diploé (représentée en gris foncé) par rapport à l'épaisseur crânienne totale (qui correspond à la valeur 100 %) pour l'os frontal (partie gauche du graphique) et l'os occipital (partie droite du graphique) chez Ngandong 2, Ngandong 7, Ngandong 12 et Sambungmacan 3. La ligne pointillée représente 50 % de l'épaisseur crânienne totale.

by pathological alteration consequences (Balzeau *et al.* 2003). Indeed, this individual's curve shows two regions of great thinning for the parietal bones (*fig. 2*). Generally, the curves of the *Homo erectus* specimens are well included in those of the anatomically modern *Homo sapiens*. Only 3 of the 60 values in the superior extension of Ngandong 12 exceed the range of variation of the comparison material in the occipital torus area. The other Ngandong and Sambungmacan *Homo erectus* individuals yielded values along the extension of the analysed plane within the range of variation of the comparison material. The nuchal squama of the *Homo erectus* individuals is thicker than those of anatomically modern *Homo sapiens*. The internal occipital crest is very robust in these *Homo erectus* fossils, much more so than in *Homo sapiens*. This region is the only one on the entire mid-sagittal plane where cranial thickness values differ between Ngandong and Sambungmacan *Homo erectus* and *Homo sapiens*. Finally, for the upper part of the vault, the Ngandong and Sambungmacan *Homo erectus* individuals share the same pattern of cranial vault thickness distribution as the anatomically modern *Homo sapiens* (*fig. 2*).

Additional data were quantified on original fossils from the Sangiran site. Thickness was evaluated at the middle of the frontal bone, the vertex and the bregma directly on the fossils. These data provide further information concerning Asian *Homo erectus* variability for cranial thickness. Sangiran 38 has a thickness of 8 mm at the middle of the frontal bone. The mean values for the Ngandong and Sambungmacan fossils are between 8 and 8.5 mm for the surrounding landmarks in this area (*fig. 2*). Value at the bregma is 9 mm for Sangiran 38 and 10.5 mm for Sangiran 10, whereas Ngandong and Sambungmacan fossils have a mean value of 9 mm and an extension between 6 and 11 mm (*fig. 2*). Values at the vertex allow us to consider the parietal mid-sagittal junction thickness. At this point, the thickness of Sangiran 38 is 10.5 mm, that of Sangiran 10 is between 8.5 and 10.5 mm and that of the Ngandong-Sambungmacan parietal bones (*fig. 2*) ranges between 8 and 11 mm. A complete comparative study is necessary to validate these observations. However, these observations suggest that Sangiran 10 and 38 have cranial thickness values within the range of variation of the Ngandong and Sambungmacan fossils in the mid-sagittal plane.

Finally, as a CT scan appears to be problematic for the Zhoukoudian fossils, we propose a graphic comparison of the mid-sagittal outlines between these individuals and the Ngandong hominids (*fig. 3*). The Ngandong 7 and

12 illustrations were obtained by using their mid-sagittal CT slice in order to be comparable with the data reported by Weidenreich (1943). Frontal and occipital superstructures are developed and cranial thickness appears important for the Zhoukoudian fossils. Based on this representation, Ckn.E1.PA.16 would have the highest thickness values. Nevertheless, this individual seems to lie within the range of variation previously observed in the Ngandong and Sambungmacan samples. Generally, the cranial vault thickness of the Zhoukoudian and Ngandong individuals shares a similar distribution and range of variation along the mid-sagittal plane.

Internal composition of the cranial bones

Figure 4 illustrates the mean values of the thickness of the inner table, diploe and outer table of the anatomically modern *Homo sapiens* from Afalou Bou Rummel and Taforalt. The values for each layer may vary to a great extent, but all individuals share a similar distribution pattern along the analysed plane (Balzeau 2005). The Cro Magnon and Pataud individuals are well within this range of variation (Balzeau 2005).

In our Ngandong and Sambungmacan *Homo erectus* sample, the variability is quite small and does not seem to be affected by the individual developmental age (*fig. 5*). On the frontal bone, the inner table is thicker in the glabellar region depending on the internal frontal crest development. It is thinner posteriorly and is regular in thickness on the frontal posterior half. In this area, values are quite small and within the range of variation of the comparison material. Similarly, the diploe is thicker anteriorly, thinner in the medial part of the frontal bone and thicker close to the sagittal bregma. The diploe is thicker in Sambungmacan 3 and Ngandong 2 than in Ngandong 7 and 12. The Ngandong and Sambungmacan *Homo erectus* values are within the range of variation of the comparison material (*fig. 4, 5*). The outer table is thinner anteriorly than in the posterior half of the frontal bone. Ngandong 2 has the lowest values, Ngandong 12 the highest. The Ngandong and Sambungmacan *Homo erectus* thickness values are close to the mean of the comparison material. On the occipital bone, Ngandong 7 and Sambungmacan 3 share a common pattern for the thicknesses of the inner table, of the diploe and of the outer table. Values are always within the range of variation of the anatomically modern *Homo sapiens* (*fig. 4, 5*). Sambungmacan 3 presents a slightly thicker outer table, whereas Ngandong 7 has the more developed diploic layer. Ngandong 7 has the greatest

cumulated thickness. For these two fossils, the diploe is thick with an expansion in the occipital torus area. The outer table has a homogeneous thickness in the anterior half of the occipital bone. It is slightly thicker near the sagittal external occipital protuberance and posteriorly. Nevertheless, the diploe constitutes the greatest part of the total thickness (fig. 5, 6). So, the Ngandong and Sambungmacan *Homo erectus* variations follow the same pattern as the comparison material even if the outer table is thinner than the mean in the anatomically modern *Homo sapiens* (fig. 4, 5).

A Sangiran 17 left parietal fragment (with dimensions of 60.4 by 16.8 by 28 mm) was analysed by CT. We have delimited a smaller rectangular shape area situated in the region of the parietal eminence in order to quantify the internal composition. It measures 16.6*9.9 mm with a maximal thickness of 13.7 mm. This region shows perfect conservation in the internal layers and is perpendicularly orientated to the CT data acquisition. Size restriction permits us to consider only a region where inner and outer tables are parallel, thus preventing overestimation of the cranial thickness. The diploe constitutes 67.4% of the thickness of this area, the inner table 15.2% and the outer table 17.4%.

Finally, photos of Sangiran 18a (fig. 7) and 19a (fig. 8) show the original distributions of the cortical and diploic layers at some breaks. These illustrations are not directly comparable with previously presented profiles of thickness layers, but do allow appreciation of the relative participation of the thickness of the internal cranial constituents. Sangiran 18a is a frontal bone fragment corresponding to the glabellar region and to the squama anterior and mid-sagittal parts. The original internal composition is preserved despite diagenetic processes. The lateral view illustrates the clear predominance of the diploic layer in the frontal superstructure region (fig. 7). Sangiran 19a is an occipital right part fragment including a part of the lambdoid suture. The maximal cranial thickness is less than 1.5 cm at the level of the break (fig. 8d). The inner and outer tables are very thin, whereas the diploe constitutes the great majority of the total thickness in this area, which corresponds to the lateral extension of the occipital torus.

DISCUSSION

The anatomically modern *Homo sapiens* individuals from European Upper Palaeolithic sites (Cro Magnon 1,

2, 3 and Pataud 1) and the North African Epi-Palaeolithic sites of Afalou Bou Rummel and Taforalt are known to be robust (e.g. Lahr 1994; Lahr, Wright 1996; Balzeau, Badawi-Fayad 2005) and are not considered representative for the whole variation in *Homo sapiens*. Nevertheless, these points do not influence the results of the hypothesis testing conducted here. Indeed, the purpose is to test whether *Homo erectus* individuals have thickened cranial bones and equal participation of the three structural bone layers in this thickening.

Cranial vault thickness

On the frontal bone, the Ngandong and Sambungmacan *Homo erectus* and anatomically modern *Homo sapiens* individuals have similar values of bone thickness and share a similar pattern of thickness distribution in the mid-sagittal plane (fig. 2).

The frontal, coronal and sagittal keels, as well as the bregmatic eminence, are often considered to be related to the characteristic cranial hyperossification of *Homo erectus* (e.g. Weidenreich 1943; Le Gros Clark 1964; Santa Luca 1980; Andrews 1984; Stringer 1984; Hublin 1986; Kennedy 1991; Antón 2003). Kennedy (1991) remarked: "The ectocranial keels may be characterized as discrete linear areas of thickened bone, not associated with muscle attachments, situated along suture lines and radiating from bregma". However, it is not clear whether keels are supposed to be an external cranial surface relief, a thickened bone area, or both. By observation of the external cranial surface, the frontal and sagittal keels constitute a wide and antero-posteriorly continuous relief on the Zhoukoudian fossils. These structures are less developed on the Sangiran individuals, while they have a more individualised bregmatic eminence. The Ngandong and Sambungmacan fossils show diffuse reliefs with a great individual variability.

Our CT data analysis enables us to consider local variations of topography and thickening of the cranial vault in the mid-sagittal plane (fig. 2). Therefore, we have information about the expression of the frontal and sagittal keels as well as the bregmatic eminence in terms of cranial vault outlines and thickness variations. The bregmatic eminence on Ngandong 7 corresponds to an expansion of the cranial vault thickness. The external outline varies, whereas the internal outline has a regular curvature in the corresponding region. Ngandong 12 has a wide and slightly developed relief prolonged by a sagittal keel. The latter constitutes a small thickness variation. The external

cranial outline is slightly raised on a large antero-posterior extension. The Sambungmacan 3 bregmatic eminence is a thickening situated in the frontal keel prolongation. This relief is laterally stretched and may correspond to the beginning of the coronal keel formation. The thickness variation is regular and concerns both the internal and external outlines. On Sambungmacan 1, the relief visible on the external vault surface does not correspond to a localized vault thickening, but to the shape of the bones. The anatomically modern *Homo sapiens* samples present a large variability for the thickness distribution in this area. However, some individuals show a prebregmatic thickening similar to the Asian fossils. This means that the keels or the bregmatic eminence defined by external vault surface observations do not always correspond to a real vault thickening in *Homo erectus*. They may only represent a variation of the shape of the external outline. Moreover, some anatomically modern *Homo sapiens* individuals present external surface reliefs (cf. Kennedy 1991; Lahr 1994) and vault thickening. Based on this evidence, the peribregmatic keels and eminence cannot be considered as an autapomorphic trait of *Homo erectus*.

Our thickness data illustrate that Ngandong and Sambungmacan *Homo erectus* and anatomically modern *Homo sapiens* share a similar morphology for the occipital plane. There is a thickening in the anterior part of this bone. This feature is more evident in the comparison material (fig. 1). Posterior to the lambda, external and internal outlines first diverge, while the external outline continues with regular curvature, the internal outline later converges back to the external. Concerning the occipital torus, thickness values do not separate Ngandong and Sambungmacan *Homo erectus* and anatomically modern *Homo sapiens*. The nuchal plane is the only area where the bone thickness differs between Ngandong-Sambungmacan *Homo erectus* and anatomically modern *Homo sapiens*. These differences are perhaps due to the disassociation between inion and endinion, which is considered to be a *Homo erectus* autapomorphic feature (e.g. Jacob 1976a; Andrews 1984; Stringer 1984). However, Kennedy (1991) showed that it is not a *Homo erectus* autapomorphy, but a primitive feature shared by fossil hominids and apes. Moreover according to this author, inion and endinion relative positions show a great variability in both anatomically modern *Homo sapiens* and *Homo erectus* with an overlapping of their respective characteristics. We have used the sagittal external occipital protuberance instead of the inion. Indeed, this point was easier to define on the mid-sagittal plane. On the

endocranial surface, the endinion is a landmark defined by construction and is localized at a venous junction. The position of this landmark depends on the width and trajectory of the venous sinuses. In our analysis the region of interest corresponds to the internal occipital crest relief in the mid-sagittal plane. Few landmarks posterior to the occipital torus were used, because of the variable state of preservation of the studied material. Therefore, we cannot precisely determine the relative position of the endinion to the inion. Nevertheless, our results show that Ngandong and Sambungmacan *Homo erectus* present thickness values for the nuchal plane, which exceed the variability of the comparison material. This is due to the important development of the internal occipital crest in Ngandong and Sambungmacan *Homo erectus*. This corresponds to the wide space separating the two cerebellar lobes in this species, whereas these lobes are closer in anatomically modern *Homo sapiens*. In relation to the development of the internal occipital crest, the nuchal plane would be the only region of the mid-sagittal plane, where Asian fossils have a thicker vault than the anatomically modern *Homo sapiens*.

Generally, the fossils from Ngandong and Sambungmacan (fig. 2), as well as from the Sangiran and Zhoukoudian sites (fig. 3), have absolute vault thickness values within the variability of our comparative sample composed of anatomically modern *Homo sapiens*.

Internal composition of the cranial bones

Weidenreich (1943, 1951) first proposed for *Homo erectus* a nearly equal participation of the three constituents of bone with a slight emphasis on the inner and outer tables. As noted by Kennedy (1991), the figure used for illustration by Weidenreich (1943: fig. 20) shows that the diploe forms the greatest portion of total skull thickness on a fragment of parietal. Hublin (1986, 1989, 1991) attributes a generalized thickening of the *Homo erectus* mainly to cortical bone expansion. Hublin (1991) states that : « la plupart des caractères 'autapomorphes' d'*Homo erectus*' peuvent être mis en relation avec une augmentation de la masse osseuse compacte et ses conséquences géométriques. Nous incluons dans ces manifestations d'hyper-ossification : l'épaississement des tables interne et externe des os, ... ». However, these conclusions result from an analysis of the distribution of the structural layers in modern *Homo sapiens*. Thus, this feature has often been considered as autapomorphic

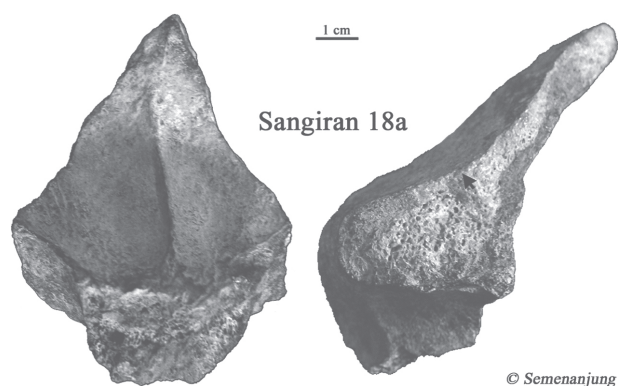


Fig. 7—Endocranial and left lateral views of the Sangiran 18a frontal fragment (photographs F. Détroit, Semenanjung). Dark arrows show the cortical table extension.

Fig. 7 - Vues endocrânienne et latérale gauche du fragment d'os frontal Sangiran 18a (photographies F. Détroit, Semenanjung). Les flèches noires montrent l'extension de la table externe.

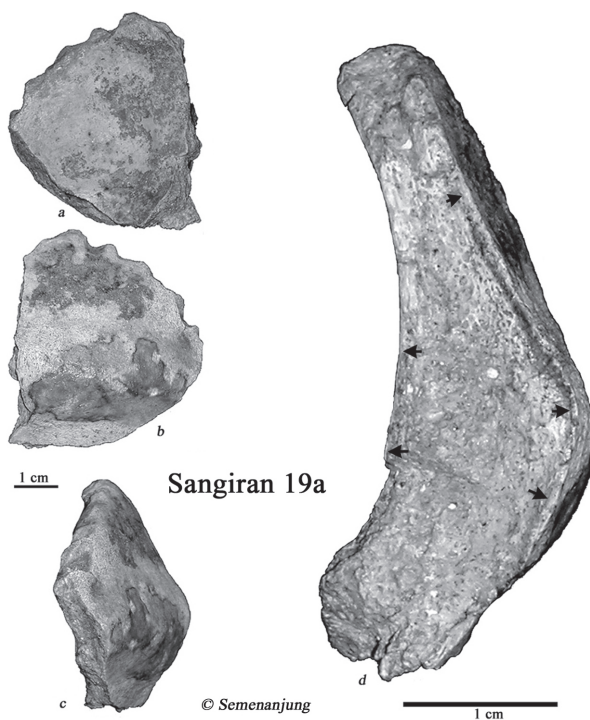


Fig. 8—Endo (a), exocranial (b), right (c) and left (d) lateral views of the Sangiran 19a occipital fragment (photographs F. Détroit, Semenanjung). Dark arrows show the cortical table extension.

Fig. 8 - Vue endocrânienne (a), exocrânienne (b), latérales droite (c) et gauche (d) du fragment d'os occipital Sangiran 19a. (photographies F. Détroit, Semenanjung). Les flèches noires montrent l'extension des tables denses.

for *Homo erectus*, but this has rarely been tested. Our results enable discussion of the structural composition of the vault along the mid-sagittal plane and comparison of *Homo erectus* and anatomically modern *Homo sapiens*.

On the Ngandong and Sambungmacan *Homo erectus* individuals, except for one, the diploe constitutes the greatest part of the frontal bone thickness (fig. 6, as well as on Sangiran 18a, fig. 7). Moreover, these *Homo erectus* fossils share a similar pattern of relative composition for the cortical tables and the diploe with anatomically modern *Homo sapiens* (fig. 4, 5). In the peribregmatic region, the Ngandong 7 vault thickening is due to the expansion of the diploic layer, whereas the thickness of the cortical tables does not vary (fig. 5). The Ngandong 12 prebregmatic eminence shows an increased participation of both the outer table and the diploe (fig. 5). For Sambungmacan 3, only the diploe thickness varies in this region (fig. 5). The outer table is thicker anteriorly to the bregma, because of the presence of the unfused sutures. The frontal and sagittal keels, as well as the bregmatic eminence, are not characterised by an important and unique participation of the outer table, in contrast to Hublin (1986). The diploe makes a significant contribution to the thickness (fig. 6). Moreover, the state of the suture synostosis affects the formation and development of these keels as the cortical tables recover the diploe in the sutural areas. On the occipital plane, *Homo erectus* fossils and anatomically modern *Homo sapiens* share a similar and relatively constant distribution of the three structural layers. The diploe constitutes the greatest part of the total thickness (fig. 6, 8). Similarly, the *Homo erectus* occipital superstructures do not present a different internal composition to the comparative sample (fig. 4, 5). The outer table is not the principal constituent of the thickness in this region, even in the occipital torus area (fig. 6).

This study presents new data about CVT and internal composition in some Ngandong and Sambungmacan fossils by mean of CT data analysis; and complementary information was available for some Zhoukoudian and Sangiran individuals. However, further work is needed to better quantify the variation for these features in Asian *Homo erectus*. In addition, similar analyses have to be carried out on older hominids, on African *Homo* (from the first representatives of the genus *Homo*, considering *Homo ergaster/erectus*, to *Homo heidelbergensis/rhodesiensis*) and Georgian fossils in order to discuss the polarity of the newly observed traits.

CONCLUSIONS

We have developed a specific protocol in order to avoid difficulties resulting from cranial landmarks or measurement definitions as well as limitations in interpretations when only one or a few thickness data are used. CVT and internal composition were quantified along the mid-sagittal plane for a total of 60 landmarks.

The thickness of the frontal and probably the squamous parts of the occipital bones seem to fit into the variability of *Homo erectus* adults at a very early stage of individual development as seen in Ngandong 2, and, to a lesser degree, in Sambungmacan 3. The frontal superstructure thickness would reach the adult variability later. For the internal composition, variations seem to be limited during growth and development. The inner and outer tables as well as the diploic layer are probably dissociated precociously in *Homo erectus* ontogeny (as shown by the Mojokerto fossil; Balzeau *et al.* 2005). Our results suggest that relative growth of these layers depends more on individual variability than on a general pattern with a predominance of one (or two or all) of the internal constituents of the cranial bone.

If the frontal and sagittal keels in Ngandong and Sambungmacan *Homo erectus* constitute a relief on the external cranial vault surface, they do not necessarily correspond to a real thickening of the underlying bone. Moreover, the diploic layer principally makes up their internal composition. Similarly, the diploe comprises the largest part of the total thickness of the frontal and occipital torus in this extinct species. The definitions of the latter superstructures and keels have to be revised as they are not due to a unique expansion of the outer table. The only particularity in cranial vault thickness for *Homo erectus* concerns the nuchal plane. Because of the important development of the internal occipital crest, total thickness for this area exceeds that of anatomically modern fossil *Homo sapiens*. However, this supports Kennedy's point of view (1991) that thickening of the inferior cranium is a primitive trait.

Important cranial vault thickness is considered as an autapomorphic trait for *Homo erectus* (e.g. Weidenreich 1943; Le Gros Clark 1964; Hublin 1978; Andrews 1984; Wood 1984; Rightmire 1990; Kennedy 1991; Kennedy *et al.* 1991; Gauld 1996; Zeitoun 2000; Delson *et al.* 2001; Antón 2003). Our results permit discussion of the validity of this autapomorphy. The Ngandong and Sambungmacan fossils, as well as the Zhoukoudian and Sangiran individuals, have cranial vault thickness values

within the variability observed in our comparative sample. Therefore, the tested autapomorphy concerning the vault thickness in *Homo erectus* is not confirmed.

Since Weidenreich's first proposition (1943), it has been generally accepted that *Homo erectus* differs from *Homo sapiens* in its internal cranial vault composition. This extinct species is defined as presenting an equal participation of the three structural layers and an important thickening of the outer table in the superstructure areas (e.g. Hublin 1986, 1989, 1991; Gauld 1989; Kennedy 1991; Bartsiokas 2002; Bräuer *et al.* 2003). Our results show that some Ngandong, Sambungmacan and Sangiran *Homo erectus* have cortical tables and diploe variation and distribution patterns similar to anatomically modern *Homo sapiens*. Moreover, the diploe generally constitutes about or more than 50% of the total vault thickness along the mid-sagittal plane for these *Homo erectus* individuals (fig. 6). Therefore, the tested autapomorphy concerning the internal cranial vault composition in *Homo erectus* is also not confirmed.

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