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CHARACTERISTICS AND VARIATION OF THE TEMPORAL BONE PNEUMATIZATION IN ASIAN *HOMO ERECTUS*

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Abstract: The temporal bone is used frequently to identify taxonomic affinities of genus *Homo* fossils based on external morphological features. In the meantime, the temporal bone pneumatization has rarely been examined, particularly in Asian *Homo erectus*. We put forward a comparative morphological and quantitative analysis in Asian *Homo erectus* from the sites of Ngandong, Sambungmacan, and Zhoukoudian, and of Neandertals and anatomically modern *Homo sapiens* in order to document the variability of temporal bone pneumatization during hominid evolution. The Zhoukoudian fossils have a unique pattern for the temporal bone pneumatization, whereas Ngandong and Sambungmacan fossils as well as the Neandertals are closer to the modern human pattern. Our results support the hypothesis that this pneumatization expansion is related to available space and to the temporal bone morphology. Finally, the phyletic implication of this pneumatization is very limited in the analysed taxa as the variation is large within the same species.

Keywords: *Homo erectus*, Ngandong-Sambungmacan, Zhoukoudian, pneumatization, temporal bone, CT.

Introduction

The temporal bone is used frequently to identify taxonomic affinities as it contains several features that differentiate Asian *Homo erectus* individuals from anatomically modern *Homo sapiens* and from Neandertals (e.g. Le Gros Clark 1964; Andrews 1984; Stringer 1984; Hublin 1986; Kennedy 1991; Elyaqine 1995; Zeitoun 2000; Harvati 2003; Villmoare 2005). These features concern principally the external surface of the temporal bone, and the semicircular canals (e.g. Spoor, Zonneveld 1994, 1998; Hublin *et al.* 1996; Spoor *et al.* 2003). Moreover, concerning Asian *Homo erectus*, the Zhoukoudian fossils differ from the Indonesian individuals in metric and morphologic patterns (e.g. Weidenreich 1943, 1951; Santa Luca 1980; Antón 2002, 2003; Détroit 2002; Kidder, Durband 2004; Terhune *et al.* 2007). In the meantime, there are no comparative studies on the temporal bone pneumatization in these species or in the different chronological groups of Asian *Homo erectus*. The purpose of this study is to describe the disposition and the extension of the pneumatization of the temporal bone in fossils belonging to Neandertals, anatomically modern *Homo sapiens* and particularly in Asian *Homo erectus*; in order to document the variation of temporal bone pneumatization during hominid evolution.

Material and method

The Asian *Homo erectus* sample is composed of Ngandong 1, 7 and 12, Sambungmacan 1 and 3 and these fossils CT data. A comparison is proposed with the Zhoukoudian fossils based on the Weidenreich monograph data (1943). Comparative samples include classic European Neandertals (La Chapelle-aux-Saints 1, La Ferrassie 1, La Quina H5 and H27, Spy 1 and 10) and anatomically modern *Homo sapiens* (Cro Magnon 1 and 2 and Pataud 1). Comparative morphological and

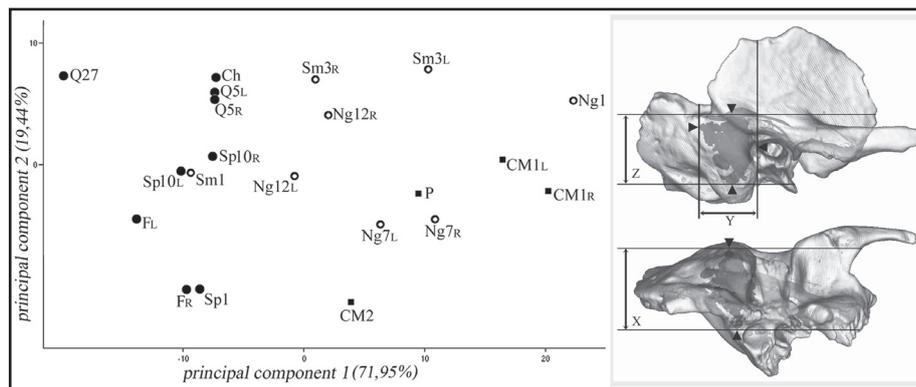


Figure 1: First and second principal components of the PCA of the 3D extension of the temporal bone pneumatization and illustration of the quantified dimensions of the pneumatization on La Quina H27; variables correspond to the maximal distance where cells extend (between the black triangles) according to defined orientations (resulting in the distances represented by the black arrows): X is the maximal extension of the pneumatization in a coronal orientation, Y its maximal antero-postero extension in a para-sagittal orientation, Z its maximal extension in a vertical orientation, crv the cube-root of the volume. Symbols have the following correspondence: empty circles: Asian *Homo erectus* (Ng1, 7, 12: Ngandong 1, 7 and 12; Sm3, 3: Sambungmacan 1 and 3; R: right temporal, L: left temporal), black circles: Neandertals (Ch: La Chapelle-aux-Saints 1; F: La Ferrassie 1; Q5, 27: La Quina H5 and H27; Sp1, 10: Spy 1 and 10), black squares: anatomically modern *Homo sapiens* (CM1, 2: Cro Magnon 1 and 2; P: Pataud 1).

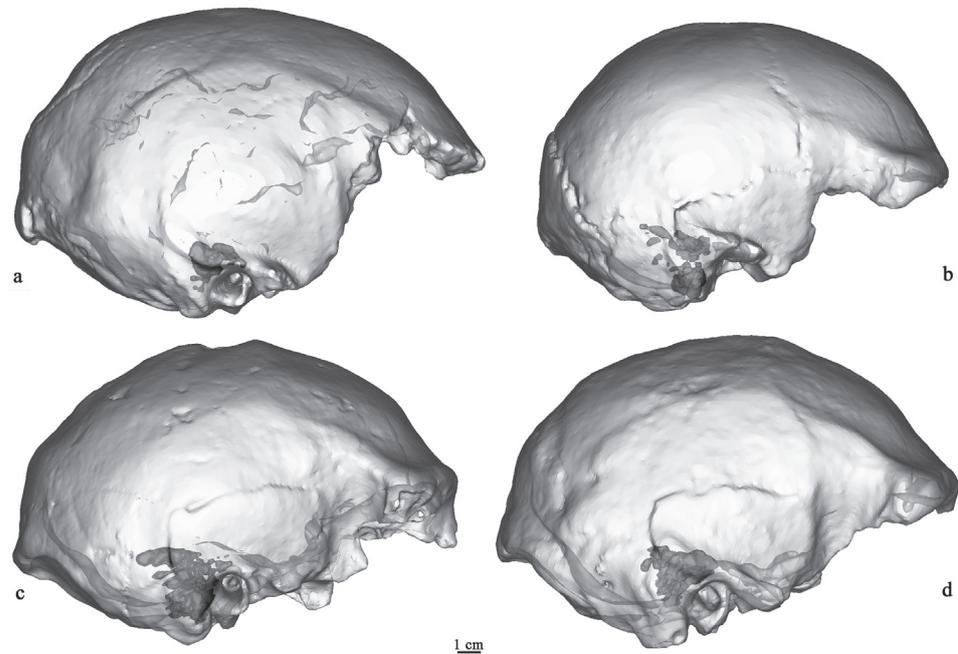


Figure 2: Right lateral views of the 3D reconstructions of the skull and of the temporal bone pneumatization of Sambungmacan 1 (a), Sambungmacan 3 (b), Ngandong 7 (c) and Ngandong 12 (d).

quantitative analyses were conducted on CT data. The fossils were CT scanned with a General Electric High Speed HAS scanner at the “CHNO des Quinze-vingts” in Paris (except Spy 1 and Spy 10, *cf.* Semal *et al.* 2005). Acquisition parameters vary according to individual mineralisation state, and size of the fossil (Badawi-Fayad *et al.* 2005). Setting range between: 100-120 kV, 90-250 mA, 0.3-1 mm thick slices, field of view of 12-25 cm and 0.23-0.59 pixel size with a pixel matrix of 512*512. The CT data sets were visualized and analysed using Materialise Mimics 7.1 and ArteCore (<https://www.nespos.org>) software. The CT data sets do not show any noticeable artefacts even though the fossil skulls under study may be heavily mineralized. Following previous experiences (*e.g.* Balzeau 2005; Balzeau *et al.* 2002, 2003, 2005; Balzeau, Grimaud-Hervé 2006), we used the CT data to extract information concerning pneumatization and to quantify its extension inside the temporal bone. The reconstruction in 3D of the pneumatization was based on data

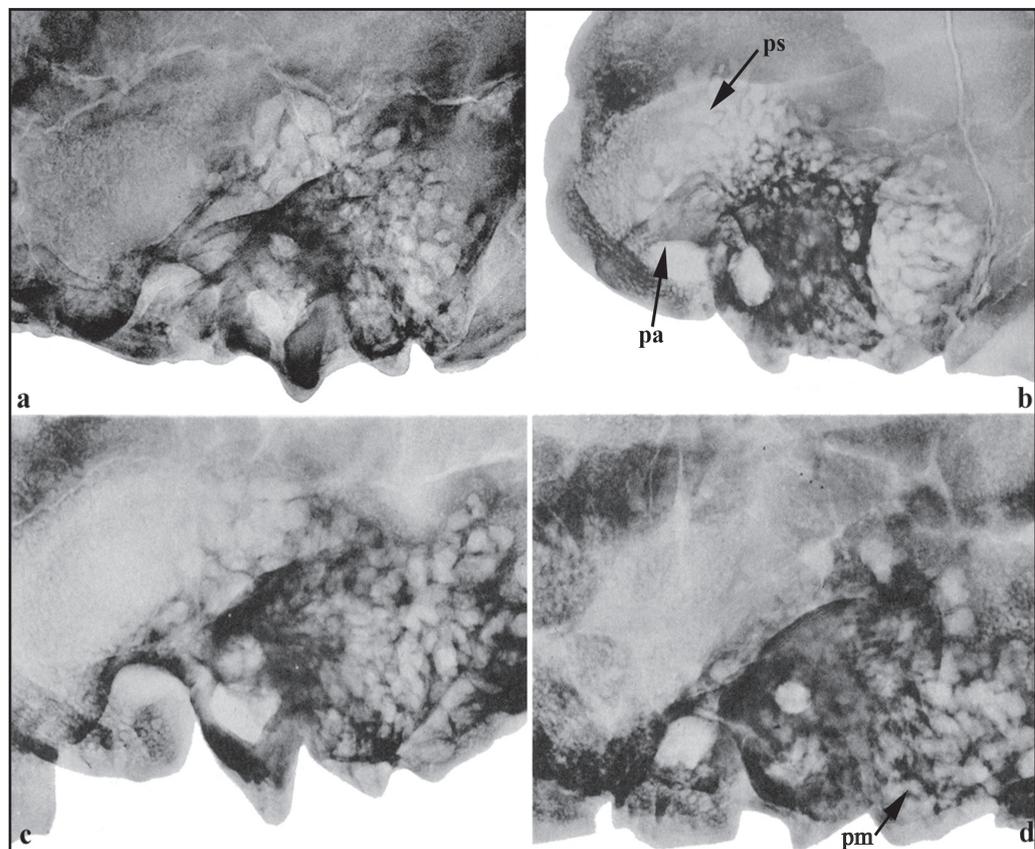


Figure 3: Radiographs of the left temporal bone of Ckn.E 1.PA.16 (a), Ckn.H 3.PA.68 (b), Ckn.L 2.PA.99 (c) and Ckn.L 3.PA.100 (d) (from Weidenreich 1943). Black arrows: pa: pneumatization of the articular tubercle, ps: pneumatization of the squamous temporal, pm: pneumatization of the mastoid process.

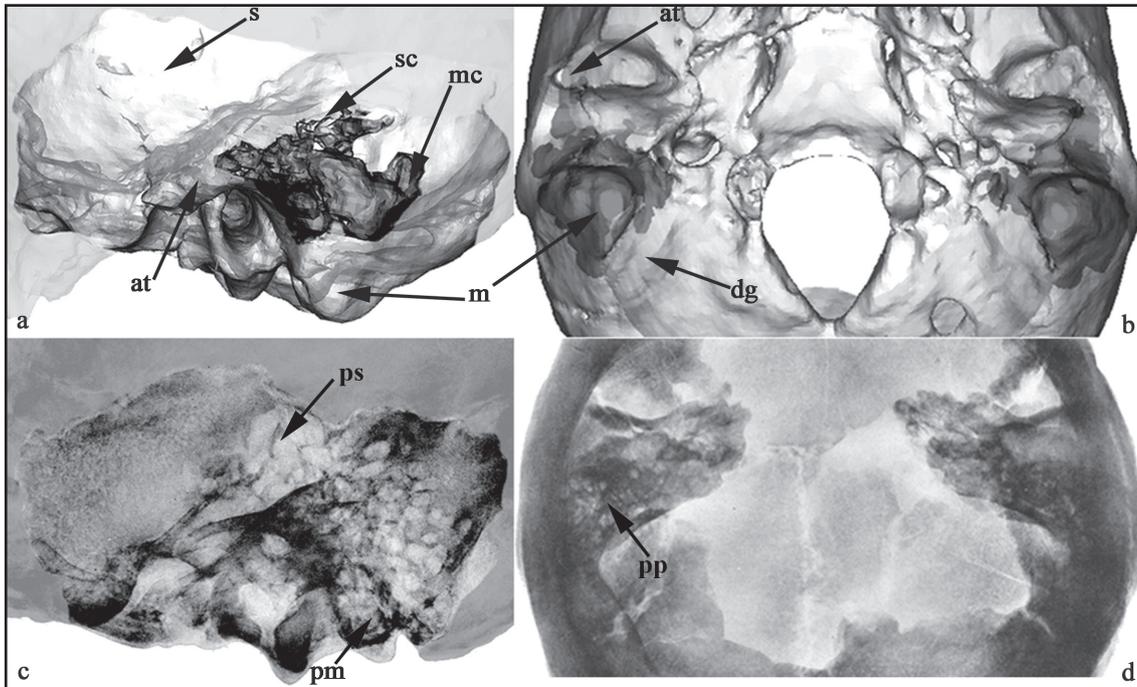


Figure 4: Pneumatization of the temporal bones of Ngandong 7 (a and b, 3D reconstructions based on CT data) and Ckn.E 1.PA.16 (c and d, images based on radiographic data, from Weidenreich 1943) in lateral (a and c, both are left temporal bones) and inferior (b and d) views. Black arrows: at: articular tubercle, dg: digastric groove, m: mastoid process, mc: mastoid crest, sc: supramastoid crest, s: squamous temporal, pm: pneumatization of the mastoid process, pp: pneumatization of the petrous part, ps: pneumatization of the squamous temporal.

obtained by using segmentation protocol adapted to fossil hominids morphological study. On each CT slice, the boundary between the bone and the air (the cells) was identified by manual segmentation. This protocol consists in using multiple threshold values in function of the variation of the temporal bone mineralization and permits to obtain the precise outlines of the whole cells and then precise 3D reconstructions. Dimensions of the pneumatization were quantified based on the 3D reconstructions (Figure 1): X (maximal extension of the pneumatization in a coronal orientation), Y (maximal antero-postero extension in a para-sagittal orientation) and Z (maximal extension in a vertical orientation) variables correspond to the maximal distance where cells extend according to each orientation when the skull is in anatomic position. The volume of the pneumatization is the total volume of the whole of the cells for each temporal bone. The cube-root of the volume was used (noted crv) because other measures are linear during the metrical analysis. Bilateral data were accessed when the state of conservation permitted the performing of the pneumatization reconstruction. This metric data were analysed by principal component analysis (PCA) using Past 1.40 software (Hammer *et al.* 2001). PCA is a procedure permitting to calculate hypothetical variables which account for as much of the variance in the multi-dimensional data as possible (Harper 1999). PCA permits the reducing of the number of variables but also to illustrate the possible correlations between the original variables. PCA analyses were performed both on the original dimensions of the pneumatization and on the log-transformed values of the same variables. Moreover, log-shape

ratio method (Mosimann 1970) is not applicable to our metric data consisting of three linear distances and a volume. Finally, we did not standardize the pneumatization dimensions according to the temporal bone dimensions. Indeed, this bone metric variation between the analysed species would have induced bias in the analysis of the temporal bone pneumatization distribution.

	crv	X	Y	Z
PC 1	0.04582	-0.08756	0.8636	0.4943
PC 2	-0.3407	-0.9371	-0.03969	-0.06506

Table 1: Loadings of the variables on the first and second components of the PCA of the 3D extension of the temporal bone pneumatization (crv is the cube-root of the volume of the pneumatization, X corresponds to the maximal extension of the pneumatization in a coronal plane, Y to the maximal antero-postero extension in a para-sagittal plane, Z to the maximal vertical extension; Figure 1).

Results

A principal component analysis (PCA) is put forward with the pneumatization 3D extension variables and its volume (Table 1 and Figure 1). The two first PCA axes explain 91.39% of the total variation. Y and Z are positively and highly expressed by the first PCA axis (respectively loadings of 0.8636 and 0.4943, Table 1). X and crv load negatively on the second PCA axis (respectively loadings of -0.9371 and -0.3407, Table 1). As a result, the individuals with high values for these variables are situated on the bottom-right of this plane (Fig. 1). A similar distribution of the individuals was observed on the plane defined by the two first axes of a principal component analysis conducted on the log-transformed values of the same set of variables. The different taxa are partially separated along the first axis: the Neandertals are on the left, the

anatomically modern *Homo sapiens* on the right and the Asian *Homo erectus* have an intermediate position but overlap with the other groups. The distinction along the first axis is principally due to differences in size whereas the disposition of the cells does not seem to present taxonomic characteristics. The second axis does not differentiate between these groups. However, X and crv load principally on this second PCA axis (Table 1), illustrating a relation between these two variables. The antero-posterior extension of the pneumatization (Y) does not appear to covariate with the volume in this analysis. So, the volume of the pneumatization seems to be principally related to the lateral development (characterized here by the X variable), and to a lesser degree by the vertical development (Z), of the cells composing the temporal bone pneumatization.

Cro Magnon 1 and 2 and Pataud 1 share a similar pattern of pneumatization distribution. These individuals do not have pneumatization in the temporal squamous part. They have few cells in the articular tubercle whereas pneumatization does not propagate in the zygomatic process. Some cells follow the supramastoid crest as far as close to the parietal notch. The petrous part has a reduced pneumatization. Numerous cells extend into the mastoid process; they have random dimensions but always constitute a large volume. In Neandertals, the development of the pneumatization shows some individual variability, but maintains a similar pattern of distribution (Balzeau, Radovčić 2008). Pneumatization of the superior part of the squamous temporal is absent. There are no pneumatic cells in the articular tubercle and they are numerous in the petromastoid area. Their size varies from small to large whereas their high concentration can make them connect together.

Ngandong 7, Ngandong 12 and Sambungmacan 3 tend to be highly symmetrical for the temporal bone pneumatization (Fig. 1 and 2). Moreover, these fossils show a great homogeneity concerning the position and extension of the pneumatization. None of them shows expansion of the pneumatization into the squamous temporal. It extends slightly in the articular tubercle only in Ngandong 7. Pneumatization is principally localized in the superior regions of the mastoid process and petrous part in Ngandong 7 and 12 and Sambungmacan 1. Some cavities extend into the inferior part of the mastoid process only in Sambungmacan 3. From a lateral view, in no individual does the pneumatization continue posteriorly to the mastoid crest and only in Sambungmacan 1 above the supramastoid crest. The cells vary widely in size, from small to very large extension. Thus, pneumatization is mainly restricted to the area included inferiorly to the supramastoid crest and anteriorly to the mastoid crest in these Ngandong and Sambungmacan *Homo erectus* individuals in lateral view (Fig. 2).

The pattern presented by the Zhoukoudian fossils (Fig. 3) is different from what we observed in the Ngandong and Sambungmacan sample (Fig. 4). In these Chinese specimens, pneumatization extends anteriorly into the articular tubercle in Ckn.H 3.PA.68 and Ckn.L 2.PA.99. Cells may widely propagate in the squamous temporal as shown by Ckn.H 3.PA.68. Numerous cells invade the mastoid process in all the studied individuals. From an inferior view, the antero-posterior extension of the pneumatization in Ckn.E 1.PA.16 does not appear as clearly as in a lateral view because of the superposition of the osseous structures. However, its lateral extension appears to be large in the petrous part and possibly in the petrous apex, much more than in the Ngandong and Sambungmacan *Homo erectus* individuals. Finally, pneumatization extends posteriorly to the mastoid process and the digastric groove, particularly in Ckn.E 1.PA.16 and Ckn.L 3.PA.100. Pneumatic cells have variable dimensions and appear to be larger anteriorly, posteriorly and superiorly to the temporal bone. So, the Zhoukoudian fossils present a large propagation of pneumatization with an inter-individual variation. It appears that cells may propagate in the whole temporal bone in these fossil individuals (Fig 3 and 4).

Discussion

Concerning modern humans, pneumatization of the temporal bone presents a large variability. Its development is generally limited to the mastoid, perilyabyrinthine and petrous regions, whereas expansion in the squamous is rare and not extensive (e.g. Turner and Porter 1922; Allam 1969; Wolfowitz 1974; Schuller 1976; Schuller-Ellis 1979; Virapongse *et al.* 1985; Sherwood 1995). Many functional implications to the development of the temporal bone air cells have been proposed (e.g. reception of sounds, resonance, insulation, air reservoir action, acoustic dissipation, protection for external violence or minimizing of the skull mass, Virapongse *et al.* 1985). This pneumatization could have a genetic contribution (e.g. Cheate 1923; Diamant 1940). Nevertheless, a great part of the medical literature deals with pathological conditions (e.g. Bayramoğlu *et al.* 1997; Sato 1997; Görür *et al.* 2006). Temporal bone pneumatization has also been studied in non-human primate species (e.g. Sherwood 1995, 1999; Hill 2007) or at the transition from early hominids (*Australopithecus* and *Paranthropus*) to early *Homo* (e.g. Zonneveld, Wind 1985; Grine, Strait 1994; Sherwood *et al.* 2002). Pneumatization is invariant and symmetrical in apes and extends throughout the whole temporal bone. *Australopithecus afarensis*, *A. africanus*, *A. anamensis* and *A. ramidus*, as well as *Paranthropus*, (Kimbel, Johanson 1984; White *et al.* 1994; Ward *et al.* 1999; Sherwood *et al.* 2002) share the ape-like pattern of pneumatization expansion. According to this last author, there is a reduction in pneumatization with the appearance of the genus *Homo*.

Our observations bring new information about the variation of the temporal bone pneumatization in some members of the genus *Homo*. The Neandertals and *Homo erectus* individuals, where bilateral data were available, tend to be highly symmetrical for the temporal bone pneumatization. Moreover, the Neandertals individuals and the *Homo erectus* fossils from Ngandong and Sambungmacan share a similar pattern for the temporal bone pneumatization with modern humans, whereas the Zhoukoudian fossils exhibit a unique pattern that differs from apes and genus *Homo* patterns (Fig. 4). The Zhoukoudian fossils present a large propagation of pneumatization with an inter-individual variation, as cells may propagate

in the whole temporal bone. Some other morphological variations are visible among the Asian *Homo erectus*. The Zhoukoudian individuals are characterized by a relatively wide midvault and narrow occipital bone compared with the Ngandong-Sambungmacan individuals (cf. Antón 2002; Kidder, Durband 2004). So, the basicranial configuration of the Zhoukoudian fossils corresponds to a large biauricular width in relation to the lateral extension of the superior part of the vault, whereas the Ngandong-Sambungmacan fossils have a relatively lower biauricular width-biasterrionic width ratio. In the meantime, whereas Zhoukoudian and Ngandong-Sambungmacan *Homo erectus* share a similar pattern in what concerns cranial vault thickness distribution (Balzeau 2006), these fossils present differences concerning endocranial morphology (Holloway 1980; Grimaud-Hervé 1997; Balzeau *et al.* 2002; Balzeau 2005): the Ngandong and Sambungmacan hominids show a more developed endocranial width in comparison with its length than the Zhoukoudian individuals. In the same way, the temporo-parietal unit shows a development of its surface in relation to the whole cerebral lobes between Zhoukoudian and Ngandong-Sambungmacan *Homo erectus*. The variation in metric and morphological patterns observed for the skull between the Zhoukoudian and Ngandong-Sambungmacan fossils may be related to this endocranial morphological variation. The lateral development of the parietal and temporal lobes, as well as the individualization of the cerebral parietal eminences, influenced the conformation of the lateral and basal parts of the vault. This development led to a set of different constraints on the endocranial surface of the temporal bone and particularly to a vertical straightening of the temporal bone squama between Zhoukoudian and Ngandong-Sambungmacan *Homo erectus* (e.g. Weidenreich 1951; Santa Luca 1980; Grimaud-Hervé 1982; Kennedy 1991).

The Zhoukoudian fossils have very developed pneumatization, contrary to the Ngandong and Sambungmacan fossils. These variations in pneumatization development between *Homo erectus* samples from Zhoukoudian and Ngandong-Sambungmacan may be explained by the relative cerebral expansion and modifications of cranial base morphology between these two groups (Balzeau, Grimaud-Hervé 2006). These changes did not permit the extension of the cells anteriorly to the mastoid process and in the squamous temporal in the Ngandong and Sambungmacan fossils. The opposite was observed in the Zhoukoudian fossils. Consequently, the Zhoukoudian *Homo erectus* have a unique pattern for the temporal bone pneumatization, whereas contemporaneous and younger Asian and European fossils are closer to the modern human pattern. The temporal bone pneumatization does not have an active role in determining cranial base morphology, whereas these cells propagate according to the available space in the bony structures and constraints undergone (Balzeau, Grimaud-Hervé 2006).

Conclusions

The phyletic implication of the temporal bone pneumatization seems to be limited in the studied taxa as the variation is large within the same species. Ngandong/Sambungmacan and Zhoukoudian individuals present very different patterns of temporal bone pneumatization. Whereas the Zhoukoudian fossils have very developed pneumatization, it is not the case with the Ngandong and Sambungmacan fossils. The relative development of the corresponding cerebral regions in the Ngandong and Sambungmacan hominids is correlated with a vertical straightening of the temporal bone squama and a relative reduction of the base width (*sensu* Kidder, Durband 2004). These changes did not permit the extension of the cells in the squamous temporal and beyond the mastoid and petrous areas in the Ngandong and Sambungmacan *Homo erectus*. Our results comfort the view (Sherwood *et al.* 2002) that this pneumatization development is related to correlated morphology and relative disposition of the bones and cerebral lobes in this region (Balzeau, Grimaud-Hervé 2006). Even if the evolution of the temporal bone pneumatization in the genus *Homo* appears more complex than previously described, further work is needed to understand the temporal bone pneumatization variation in the genus *Homo*. Similar analyses have to be done on the other chronological groups of Asian *Homo erectus* but also on the African (from the first representatives of the genus *Homo*, considering *Homo ergaster/erectus*, to *Homo heidelbergensis/rhodesiensis*) and Georgian fossils.

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