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Variation and Characteristics of the Cranial Vault Thickness in the Krapina and Western European Neandertals

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Abstract

The Krapina collection constitutes the largest sample of Neandertal individuals. However, comparisons of these fossils with other Western European Neandertals have been limited because of the fragmentary condition of the Krapina specimens and because gracility and small dimensions of the cranial remains were attributed to phylogeny and to geological age or to a sex/age bias in the composition of the sample. This study focuses on cranial vault thickness to document new evidence on its variation in the Neandertals. The results demonstrate the similarities between Krapina and the Western European Neandertals in thickness of the cranial vault along the mid-sagittal plane. Finally, Neandertals have characteristics that distinguish them from anatomically modern Homo sapiens *fossils.*

INTRODUCTION

The Krapina collection represents the largest sample of Neandertal individuals, with as many as 70 fossil individuals (*1*). However, there are no associated post-cranial bones or complete crania (*2*) and recent studies have particularly focused on the dental remains (e.g., *3, 4*) or on the more complete cranial remains (e.g., *5*, *6*). Moreover, the age distribution and the skeletal composition of the Krapina collection are interpreted by some authors as illustrating a demographic crisis *(7)* or an ancestral condition for survivorship characteristics (*1*, *8*). Finally, comparisons of the Krapina fossils with other Western European Neandertals have been limited because of the fragmentary condition of the Krapina specimens, and because gracility and small dimensions of the cranial remains were attributed to phylogeny and to geological age or to a sex/age bias in the composition of the sample (*6*).

Neandertals are generally considered as exhibiting thickened cranial bones (e.g., *9–13)*. Moreover, cranial vault thickness based on measurements obtained from few and isolated locations has often been used to discuss individual characteristics or individual taxonomic attribution (e.g., *14–22*). But as yet, it is not clear to which extend Neandertals have thick bone (*11, 23*, *24*); and what can be the characteristics of the Neandertals for this feature compared with anatomically modern *Homo sapiens* or with other fossil hominid species. It was for example previously proposed that Neandertals have the same pattern of increased vault thickness than *Homo erectus* (*11*).

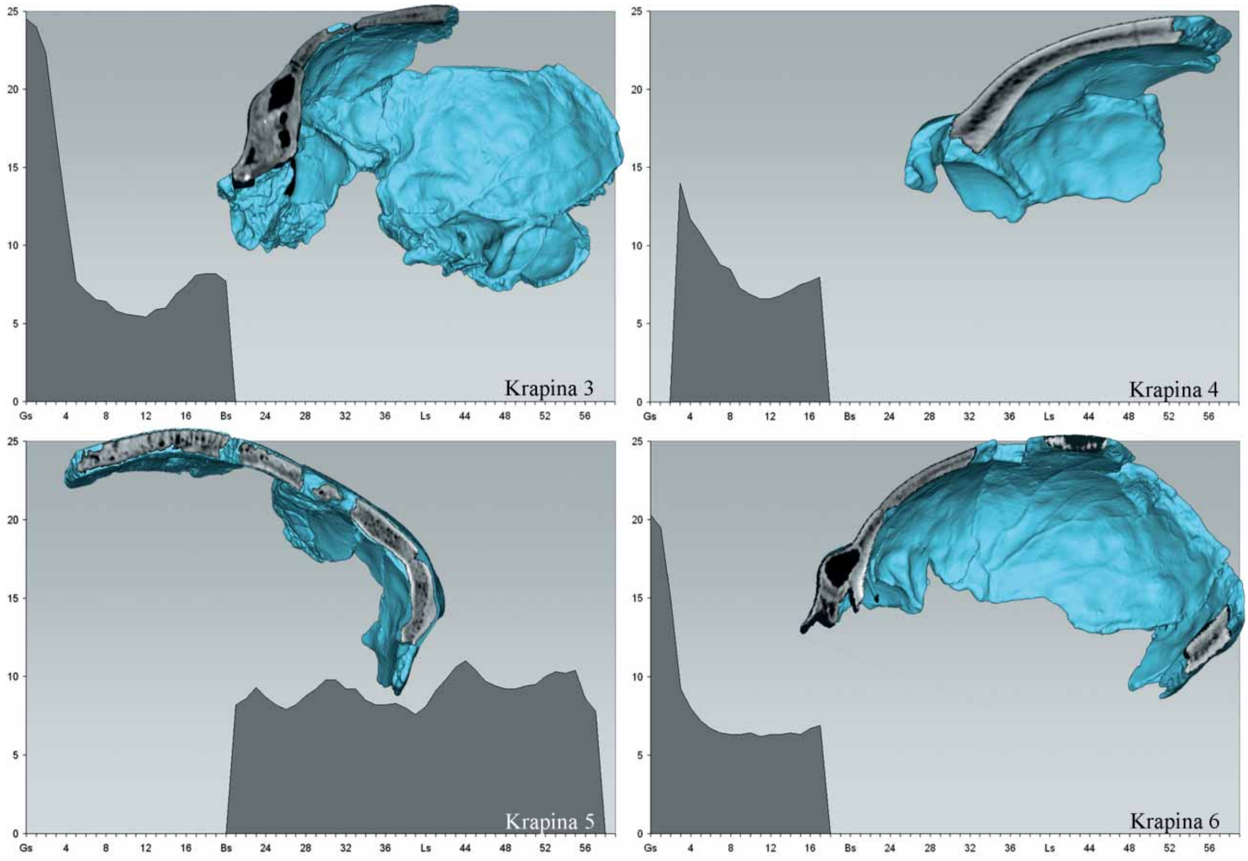

Figure 1. *Variation in the thickness of the cranial vault (in mm) along the mid-sagittal plane for Krapina 3, Krapina 4, Krapina 5 and Krapina 6, illustrating their mid-sagittal plane and partial 3D reconstruction in left lateral view. The cranial thickness is quantified from the sagittal glabella (Gs) to the foramen magnum, and the graphical representation of the data corresponds to the successive landmarks from left to right.*

This study presents new evidence about the characteristics of the Krapina fossils compared to Western European Neandertals, as well as about the possible unique features of Neandertal cranial vault thickness.

MATERIALS

The material includes four adult specimens from Krapina (*25*, *26*) [Krapina 3, Krapina 4, Krapina 5 and Krapina 6 (Figure 1)]. A second sample includes »classic« Neandertal specimens from Western Europe, comprising five adult individuals: La Chapelle aux Saints 1, La Ferrassie 1, La Quina H5, Spy 1 and Spy 10. Comparative samples include anatomically modern, adult *Homo sapiens* individuals from European Upper Palaeolithic sites (Cro Magnon 1, 2, 3, Pataud 1 and Rochereil), European Mesolithic site (Téviec 8, Téviec 9 and Téviec 16) and north African Epi-Palaeolithic sites of Afalou Bou Rhummel and Taforalt (Afalou 2, 12, 13, 28, 30, 34 and Taforalt XI C1, XII C1, XV C2, XV C4, XV C5, XVII C1). These individuals are known to be robust (*27–29)* and are not considered representative for the complete variation in *Homo sapiens*. However, this sample is used to compare features with a possible size/robustness related component with fossil hominids.

Comparative quantitative analyses of the cranial vault thickness (CVT) were conducted using computed tomography (CT) data. The fossils were CT scanned in different institutions. Acquisition parameters varied according to individual mineralization states and size of the fossil. The Krapina sample was CT scanned with a Siemens Sensation 16 at University of Zagreb Hospital, Bolnica Sestara Milosrdnica, Department of Radiology. Settings ranged between 120 kV, 74–100 mA, 0.6–1.0 mm thick slices, with a reconstruction interval of 0.5 mm, 18–23 cm field of view, and 0.35–0.45 mm pixel size with a pixel matrix of 512*512. Spy 1 and Spy 10 were CT scanned with a Siemens Somaton 64 at the ULB ERASME in Brussels. Settings were 0.6 mm-thick slices, with a reconstruction interval of 0.3 mm, 23.8 cm field of view, and 0.465 mm pixel size with a pixel matrix of 512*512 (*30)*. The Croatian and Belgian fossils were CT scanned during the Neandertal Tools project (TNT, https://www.nespos.org/; [31–32]). La Chapelle aux Saints 1, La Ferrassie 1 and La Quina H5, as well as the anatomically modern *Homo sapiens* fossils were CT scanned with a General Electric High Speed HAS scanner at the CHNO des Quinze-vingts in Paris. Settings were 120 kV, 250 mA, 0.625 mm-thick slices, with a reconstruction interval of 0.45 mm, 23 cm field of view, and 0.45 mm pixel size with a pixel matrix of 512*512 (*33*). The CT data sets were visualized and analyzed using ArteCore 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 artefacts.

METHODS

From a methodological point of view, many aspects have to be considered to perform an analysis of the cranial vault thickness (CVT). At first, attention must be paid to the reproducibility measurement, since determination of cranial landmarks varies between observers. The most easily recognisable landmarks are situated on sutural intersections. However, individual developmental stages may influence their localisation when fontanelles are opened or when sutures are obliterated. Less confidence can be placed in type II or III landmarks (*sensu 34*, *35*) 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, center 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 according to various orientations: perpendicular to the external or internal cranial surface or by searching 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 structures and position and development of the endocranial impressions (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 taphonomical history must be considered since these factors can influence original 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 (Figure 1, 2). Indeed, this plane is clearly reproducible in both Neandertal 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. So, we have used computed tomography (CT) data to obtain a large number of measurements concerning CVT. 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 on the whole data set, which extends perpendicularly to the cranial thickness on its full extension. On each individual's corresponding slice, the boundary between the bone and the surrounding air was identified by manual segmentation (SMM: *Seuillage Manuel Multiple* or *Multiple Manual Thresholding*, [*36*]). 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 defin-

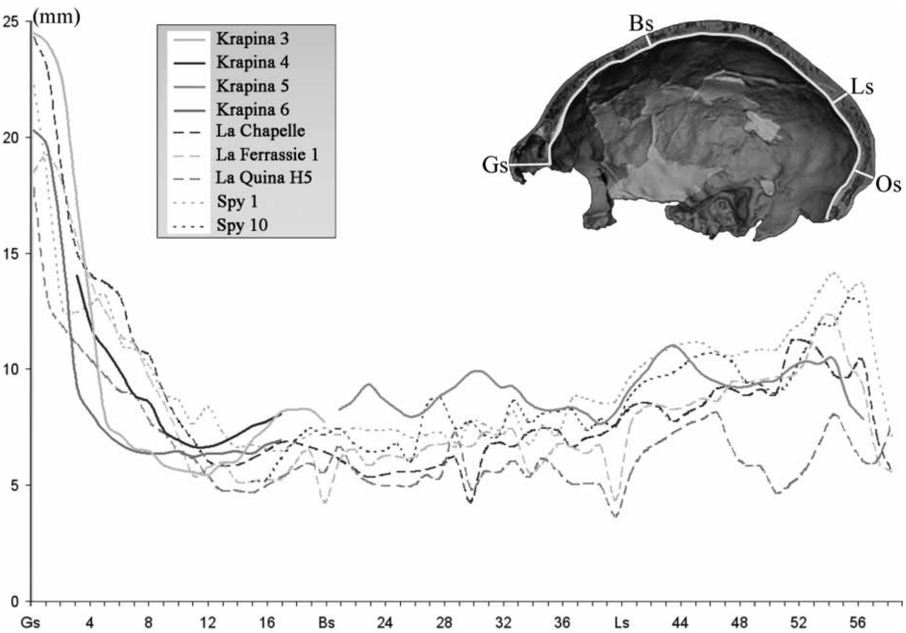

Figure 2. *Variations in the thickness of the cranial vault (in mm) along the mid-sagittal plane for the Neandertal specimens from Krapina and Western Europe (individual results). The cranial thickness is quantified from the sagittal glabella (Gs) to the foramen magnum, and the graphical representation of the data corresponds to the successive landmarks from left to right.*

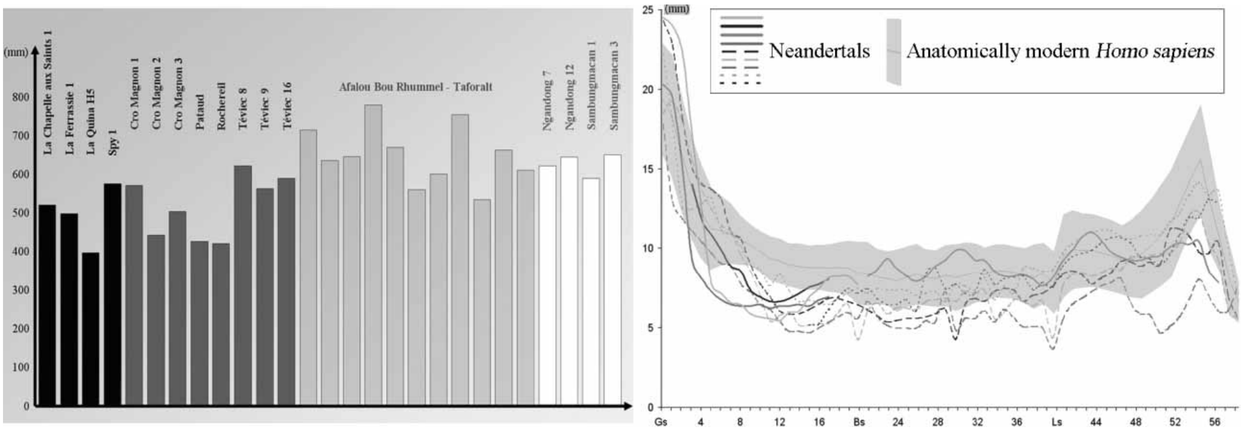

Figure 3. *Combined vault thickness for the 60 landmarks along the mid-sagittal plane for Neandertal (in black), European and African anatomically modern* Homo sapiens *(in gray) and Asian* Homo erectus *(in white) individuals; and variations in the thickness of the cranial vault (in mm) along the mid-sagittal plane for the Neandertal specimens from Krapina and Western Europe (individuals results) and the variation of the mean value plus or minus one standard deviation for the fossil anatomically modern* Homo sapiens *(gray area).*

ed (*37–38*). The manual segmentation has to be made each time the attenuation coefficient of one of the elements varies all along the interface. It allows for accurate identification of the interface between two structures, despite local fluctuation in CT numbers *(36)*. This segmentation protocol allowed the isolation of the exact area corresponding to the bone extension in order to quantify CVT. The spatial resolution limitations of the HMH methodology are known to overestimate thickness values when very thin distances are measured (see e.g., *37*). However, the elements quantified in this study do not reach this limit (e.g., thickness was always more than 1mm thick when it was possible to quantify it). There are no overflow artefacts in the analysed datasets and we have used a specific protocol to precisely isolate the different components of the images.

The only limitation to this study is related to the spatial resolution of the datasets and to the partial volume averaging artefact, which is inherent to CT. We estimate that errors in measurements do not exceed ± 0.23 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. Once the mid-sagittal plane is identified and the segmentation procedures are completed, 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 a completely opened sagittal suture, which could have resulted in a null thickness value. Moreover, the analysed plane includes the internal frontal crest and the internal occipital crest for all the analysed Neandertals. It is also the case for the most part of the comparative sample, even if these morphological areas are less pronounced and sometimes partially outside the mid-sagittal plane or incompletely preserved. 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 of the vault thickness on 60 landmarks on the whole mid-sagittal plane.

Our whole thickness dataset is affected by the development of the frontal and occipital superstructures as well as by those of the bregmatic eminence or keels. However, the inclusion of these morphological features in our study afforded a better discussion when comparing morphologies of Neandertals with those of anatomically modern *Homo sapiens*. Figure 1 and Figure 2 give cranial vault thickness metrical data, based on the analytical protocol described above and illustrate the variation of the cranial vault thickness (in mm, Y axis) all along the mid-sagittal plane (from Gs to the foramen magnum from left to right, X axis). The left side of the Figure 3 gives the combined vault thickness for the 60 landmarks along the mid-sagittal plane. 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.

RESULTS

Variation within the Neandertals

Krapina 3 preserves most of the face, the right half of the frontal bone, portions of the right parietal bone, fragmentary portions of the sphenoid, a piece of the nuchal plane on the right side and the complete right temporal bone. The mid-sagittal plane goes through a very developed internal frontal crest. In this orientation, the connection between the area just above the frontal torus and the frontal squama is not perfect, causing an important and probably slightly amplified decrease in thickness between these two parts in the analysed plane. Thickness was estimated for a few measurements in the middle part of the frontal squama because of a fracture. Thickness is maximal at the sagittal glabella (24.5 mm) and decreases rapidly and regularly posteriorly (see Figure 1). Values vary between 5.5 – 6.0 mm in the middle part of the frontal squama and are greater while getting closer to the sagittal bregma (around 8.2 mm).

Krapina 4 comprises the frontal bone including the right part of the frontal torus and the partial left parietal bone. The mid-sagittal plane is preserved for the frontal bone from posteriorly to the frontal torus to around 1.5 cm anterior to the sagittal bregma. Thickness (Figure 1) is around 14 mm at the most anterior preserved point of the frontal bone and decreases as far as the middle part of the frontal squama (where the minimal value is 6.6 mm). Thickness increases in direction to the sagittal bregma, with a maximal value of 8 mm for the most posterior preserved part of the frontal bone in this orientation.

Krapina 5 includes portion of the two parietals, the right temporal bone and the occipital bone. The actual reconstitution of this skull does not allow the identification of a CT slice going through the parietal bones and the occipital bone and corresponding to the mid-sagittal plane because of the lack of connexion between the different bone fragments and their conservation state. In this context, we quantified the variation of the thickness of the parietal bones on one hand, and of the occipital bone on the other hand, on two different reconstructed CT slices with slightly different orientations. The first image goes through the junction of the parietal bones. We had to estimate some measurements because of the presence of the sagittal suture, but thickness variation can be estimated between 8.0 mm and 9.8 mm along the junction of the parietal bones (Figure 1). For the occipital bone, thickness increases from 9.0 mm to 11.0 mm just posteriorly to the sagittal lambda. Values are lower in the middle part of the occipital squama (minimal value of 9.2 mm) and gets higher while getting closer to the sagittal external occipital protuberance, with a maximal value in this area of 10.4 mm.

Krapina 6 comprises the upper face, the entire frontal torus, and some elements on the right side of the frontal squama, as well as parts of the right parietal bone and of the occipital bone. In the mid-sagittal plane, we could quantify the thickness for nearly all the frontal bone. Thickness (Figure 1) is maximal at the sagittal glabella (20.3 mm). Values vary between 6.2 mm and 6.7 mm in the middle part of the frontal squama. Thickness is more important in direction to the sagittal bregma, with a maximal value of 6.9 mm for the most posterior preserved part of the frontal bone in this orientation. We could not quantify thickness on a large number of landmarks on the parietal and occipital bones because of their preservation state. Thickness of the preserved part of the occipital bone, which corresponds to the area of the external occipital protuberance, is around 11–12 mm.

La Chapelle aux Saints 1, La Ferrassie 1, La Quina H5 and Spy 1 are preserved on nearly all the extension of their respective mid-sagittal plane. Spy 10 does not include the frontal bone in this orientation but comprises well preserved parietal and occipital bones. Theses individuals show some variability in terms of thickness values but maintain a similar pattern of distribution of the cranial vault thickness all along the mid-sagittal plane (*36*).

The preservation state of the Krapina fossils does not allow statistical comparison with the western European Neandertal for the distribution of the cranial vault thickness on the whole sagittal plane. Nevertheless, the available data permits comparisons for the thickness of the different cranial bones between these two samples (Figure 2). For the frontal bone, Krapina 3 (Figure 2) and La Chapelle aux Saints 1 have the maximal values for the thickness at the sagittal glabella (24.5 mm). Krapina 3 has great values for the thickness of the anterior part of the frontal bone because of a very developed internal frontal crest. However, thickness in this area is only slightly greater than in La Chapelle aux Saints. Krapina 6 is well into the variability of the others Neandertals for this part of the frontal bone (Figure 2), and its thickness values are close to those of Spy 1. All the analysed Neandertal specimens share a similar variation of the thickness in the area posterior to the frontal torus. Indeed, values decrease rapidly and regularly from the area of the frontal torus to the middle part of the frontal squama. The thickness for the most anterior preserved part of the frontal bone of Krapina 4 is in the middle part of the variability of the others Neandertals (Figure 2). This individual also shares with the others fossils a similar decreasing in thickness values in direction to the middle part of the frontal squama. In the middle part of the frontal squama, the thickness for all the Neandertal individuals varies between 5.5 mm – 9.0 mm, and the Krapina fossils are in the middle part of this variation. Thickness is more important in direction to the sagittal bregma with a variation for the complete sample between 5.9 mm – 8.2 mm. Krapina 3, Krapina 4 and Krapina 6 have values for the thickness of the most posterior preserved part of their frontal bone in the upper part of the variability. For the parietal bones, the available data from

Krapina concern Krapina 5. Variations of thickness at the junction of the parietal bones are influenced by the presence of the sagittal suture, resulting in varying values from one point to the neighbouring one. However, these data allow estimating general thickness of this area (Figure 2). Krapina 5 has the greatest values among the Neandertal sample with a variation between 8.0 mm and 9.8 mm. In this area, thickness varies between 6.5 mm and 8.6 mm for Spy 10 and between 4.8 mm and 7.0 mm for La Quina H5 who are the two extremes individuals, at the exclusion of Krapina 5. For the occipital bone, the available data from Krapina concern Krapina 5. This individual shares with the Neandertal individuals from Western Europe a similar pattern of distribution of the occipital bone thickness in the mid-sagittal plane. Thickness values increase from the sagittal lambda to the middle part of the occipital squama, decrease posteriorly to this area and increase again in direction to the sagittal external occipital protuberance (Figure 2). Krapina 5 has thickness values in the middle part of the occipital squama within the variability of the other Neandertals and in its upper part. The maximal thickness in this area for Krapina 5 is 11.0 mm, whereas it is around 8.0 mm for La Quina H5, 8.5 mm for La Ferrassie 1, 9.0 mm for La Chapelle aux Saints 1, 10.0 mm for Spy 10 and 11.0 mm for Spy 1. The thickness at the sagittal external occipital protuberance for Krapina 5 (10.0 mm), as well as for Krapina 6 (11.0 mm–12.0 mm), is within the variability of the other Neandertals (around 8.0 mm for La Quina H5, 10.0 mm for La Chapelle aux Saints 1, 12.0 mm for La Ferrassie 1 and Spy 10 and 14.0 mm for Spy 1). So, the thickness of Krapina 5 is greater in the middle part of the occipital squama than at the sagittal external occipital protuberance. Finally, the thickness of the nuchal plane decreases from the occipital superstructures to the foramen magnum in a similar way and with similar values for all the analysed Neandertal specimens.

Comparison with anatomically modern *Homo sapiens*

With regard to the distribution and to the variation of the thickness all along the analysed plane, the Afalou Bou Rhummel and Taforalt skulls (n=12) present well developed superstructures. The Cro Magnon (n=3). Pataud (n=1), Rochereil (n=1) and Téviec (n=3) individuals yielded absolute thickness values around or lesser than the mean for the Afalou Bou Rhummel and Taforalt individuals. However, all these individuals share the same pattern of cranial vault thickness distribution along the mid-sagittal plane (*36*). In comparison with previous studies (*11, 15, 39–43*), the cranial thickness values of our *Homo sapiens* sample are outside the variation of these actual populations but are within the variability observed on fossil samples *(44)*.

Figure 3 illustrates the comparison of cranial vault thickness between Neandertals and anatomically modern *Homo sapiens*. The bar graph on the left side of this image gives values of combined vault thickness for the 60 landmarks along the mid-sagittal plane. We could not use the Krapina fossils for this analysis because of their incomplete preservation. The analysed Neandertal individuals have values for the combined vault thickness from 396 mm for La Quina H5, 497 mm for La Ferrassie 1, 517 mm for La Chapelle aux Saints 1, to 574 mm for Spy 1. The European anatomically modern *Homo sapiens* (n=8) have a range between 417 mm – 617 mm and the African anatomically modern *Homo sapiens* (n=11) have a range between 528 mm – 778 mm. The mean value for the Neandertal fossils is significantly less than the mean value for the anatomically modern *Homo sapiens* ($t = -17.705$, $p < 0.01$). Finally, Asian *Homo erectus* fossils from the Ngandong and Sambungmacan sites (n = 4) have values for this variable between 620 mm – 648 mm *(45)*. So, these Neandertal specimens have individual values for the combined vault thickness in the mid--sagittal plane within the inferior variability of anatomically modern *Homo sapiens* and below the values of the Ngandong and Sambungmacan *Homo erectus*.

The right part of the Figure 3 presents the comparison of the cranial vault thickness distribution between Neandertals and anatomically modern *Homo sapiens* all along the mid-sagittal plane. The individual results are shown for the Neandertals whereas the gray area illustrates the variation of the mean value plus or minus one standard deviation for the comparative sample (the gray line in the middle part of this distribution is the mean value, n = 19). The thickness for the Neandertal specimens exceed the variation shown for the comparative sample only for a few landmarks for Krapina 3 and La Chapelle aux Saints 1 in the anterior part of the frontal bone because of the great development of the internal frontal crest in these two individuals. One of the individual from Afalou has a value for the thickness at the sagittal glabella of 25.0 mm, which is above the values for the Neandertal fossils. On the opposite side, all the other Neandertal individuals yielded values all along the extension of the analysed plane within or below the represented variation of the comparison material.

In terms of variation of cranial vault thickness, the Neandertal specimens present some particularities compared to anatomically modern *Homo sapiens*. The analysed Neandertal and *Homo sapiens* specimens share similar thickness values in the area of the frontal superstructures. However, thickness in these Neandertals decreases rapidly and regularly from the area of the frontal torus to the middle part of the frontal squama whereas this variation is less abrupt in the comparative sample, resulting in greater value for the thickness of the middle part of the frontal squama. The variation along the junction of the parietal bones shares similar characteristics for the two analysed samples, but the Neandertals have lower values for the thickness in this area. On the occipital bone, both samples exhibit an increase of the thickness in the middle part of the occipital squama. On the opposite side, Neandertals only show a relatively reduced increase of thickness in direction to the sagittal external occipital protuberance whereas the comparative sample has an important thickening in this area.

DISCUSSION

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 few thickness data are used. CVT was quantified all along the mid-sagittal plane on a large number of landmarks. So, we compared the thickness of the frontal bone for Krapina 3, Krapina 4 and Krapina 6 with five West European Neandertals. Krapina 5 was compared with this sample for the thickness of the parietal bones and of the occipital bone. Moreover, the Neandertal sample was compared to anatomically modern *Homo sapiens*.

Krapina 3 and La Chapelle aux Saints 1 have the greater values for the thickness at the glabellar point whereas Krapina 6 is well into the variability of the whole sample of Neandertal specimens. Similarly, the thickness for the most anterior preserved part of the frontal bone of Krapina 4 is in the middle part of the variability of the other Neandertals. All the analysed Neandertals share a common pattern in the area posterior to the frontal torus with decreasing in thickness values in direction to the middle part of the frontal squama. Finally, Krapina 3, Krapina 4 and Krapina 6 have values for the thickness of the most posterior preserved part of their frontal bone in the upper part of the variability observed for the Neandertal sample. Overall, the Krapina fossils are not different from the Western European Neandertals for the values and the variation of the thickness of the frontal bone in the mid-sagittal plane. For the parietal bones, Krapina 5 has the maximal values among the Neandertal sample and a similar pattern of thickness variation. For the occipital bone, Krapina 5 shares with the Neandertal individuals from Western Europe a similar pattern of distribution of the occipital bone thickness in the mid-sagittal plane. Moreover, Krapina 5 has thickness values in the middle part of the occipital squama within the variability of the other Neandertals and in its upper part. The thickness at the sagittal external occipital protuberance for Krapina 5 (10.0 mm) is within the variability of the other Neandertals. So, the values for the cranial vault thickness in the mid-sagittal plane for Krapina 3, Krapina 4, Krapina 5 and Krapina 6 enter and complete the variation observed in the La Chapelle aux Saints 1, La Ferrassie 1, La Quina H5, Spy 1 and Spy 10 Neandertals. Moreover, all these individuals share a similar pattern of thickness variation all along the analysed plane (Figure 2).

These data also highlight the ambiguous relation between cranial vault thickness and sexual attribution of Neandertal specimens. In the analysed sample Krapina 4, Krapina 5, La Chapelle aux Saints 1, La Ferrassie 1 and Spy 10 are generally recognized as male individuals whereas Krapina 3, Krapina 6, La Quina H5 and Spy 1 are proposed to be female individuals, with some variations in sexual attribution depending on the author *(e.g., 6, 9, 46–50)*. Our results on cranial vault thickness do not permit to put in evidence a clear distinction between these two sub-samples. For example, Krapina 3 and 6 as well as Spy 1 have thickness values for the anterior part of the frontal bone equal or superior to those of La Chapelle aux Saints 1 and La Ferrassie 1. Similarly, for the posterior part of the frontal bone the individuals are classified in the order Krapina 3-Krapina 4-La Chapelle aux Saints 1-Krapina 6-Spy 1-Spy 10-La Ferrassie 1-La Quina H5 from high to low thickness values. Finally, Spy 10, presumably a male, has values for its cranial vault thickness below to those of Spy 1, presumably a female, on the most part of the landmarks analysed along the mid-sagittal plane. Consequently, the cranial vault thickness in the mid-sagittal plane, which however includes the frontal and occipital superstructures, appears not to be a discriminating indicator for sexual determination in Neandertals. CVT seems to be influenced by a size/robustness related component and it is this set of correlated features which is probably more meaningful to clarify sexual attribution when are considered the extreme individuals of the variation (e.g., the parietal bone of Krapina 5 *(6)*; or La Quina H5 which has the lower value for CVT, smaller cranial dimensions and less pronounced cranial superstructures of Neandertal sample).

The anatomically modern *Homo sapiens* individuals from European superior Palaeolithic sites (Cro Magnon 1, 2, 3, Pataud 1 and Rochereil), from Mesolithic European sites (Téviec 8, 9, 16) and North African Epi-Palaeolithic sites of Afalou Bou Rhummel and Taforalt are known to be robust (*27–29*) and are not considered representative for the whole variation in *Homo sapiens*. Nevertheless, these points do not influence the results of the hypothesis testing conduced here. Indeed, the purpose is to test if Neandertal individuals have thickened cranial bones. For the combined vault thickness in the mid-sagittal plane (Figure 3), the analysed Neandertal specimens have values within the inferior variability of European anatomically modern *Homo sapiens* and inferior to the values of the Ngandong and Sambungmacan *Homo erectus*. When is considered the cranial vault thickness distribution all along the mid-sagittal plane, the thickness for the Neandertal specimens exceed the values obtained on the comparative sample only for a few landmarks for Krapina 3 and La Chapelle aux Saints 1 in the anterior part of the frontal bone but all the other thickness data for Neandertal individuals are within or below the represented variation of the comparison material. So, these results illustrate that Neandertal individuals cannot be considered as exhibiting thicker cranial vault than anatomically modern *Homo sapiens*, when fossil individuals are considered in this comparative sample.

In terms of variation of cranial vault thickness, the Neandertal specimens present some particularities compared to anatomically modern *Homo sapiens*. The thickness in the Neandertal individuals decreases rapidly and regularly from the area of the frontal torus to the middle part of the frontal squama, whereas this variation is less abrupt in the comparative sample, resulting in greater value for the thickness of the middle part of the frontal squama. The variation along the junction of the parietal bones shares similar characteristics for the two analysed samples, but the Neandertals have lower value for the thickness in this area. On the occipital bone, both samples exhibit an increase of the thickness in the middle part of the occipital squama. On the opposite side, Neandertals only show a reduced increase of thickness in direction to the sagittal external occipital protuberance whereas the comparative sample has an important thickening in this area. Finally, the suprainiac fossa only induces a reduced variation of CVT and is not responsible for the important decreasing of thickness values between the middle part of the occipital squama and the occipital superstructures. So, the Neandertals are particular for the variation of the thickness in the area of the occipital superstructures whereas anatomically modern *Homo sapiens* and Ngandong and Sambungmacan *Homo erectus* share similar characteristics (*45*).

Additional work is needed to understand the variation of the cranial vault thickness in fossil hominids and its possible phylogenetic implications. Similar analyses and comparative studies remain to be done on all the different chronological groups of Asian *Homo erectus*, on the African, the older European and the Georgian fossils.

CONCLUSIONS

The purpose of this study was to present new evidence about the characteristics of the Krapina fossils compared to Western European Neandertals as well as specific characters of the Neandertals about cranial vault thickness. These results illustrate that the values for the cranial vault thickness in the mid-sagittal plane for Krapina 3, Krapina 4, Krapina 5 and Krapina 6 overlap and exceed the variation observed in the La Chapelle aux Saints 1, La Ferrassie 1, La Quina H5, Spy 1 and Spy 10 Neandertals. While variable, all these individuals share a similar pattern of thickness all along the analysed plane. Based on the variation observed in this sample, the cranial vault thickness in the mid-sagittal plane appears not to be an important indicator of sex in Neandertals. Finally, our results illustrate that the Neandertals are particular for the variation of the thickness in the mid-sagittal plane whereas anatomically modern *Homo sapiens* and Ngandong and Sambungmacan *Homo erectus* share similar characteristics (*45*). It reflects that the cranial vault in Neandertals had overall thinner vault bones than in the comparative sample. This evidence supports previous anatomical distinctions between Neandertals and *Homo sapiens* for the skull (*27, 51–53*) contrary to others who argue for morphological continuity between Neandertals and *Homo sapiens* in Europe (*54–56*).

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