Temporal lobe sulcal pattern and the bony impressions in the middle cranial fossa. The case of the El Sidrón (Spain) neandertal sample.

Antonio Rosas[1], Angel Peña-Melián[2], Antonio García-Tabernero[1], Markus Bastir[1] and Marco de la Rasilla[3].

1 - Paleoanthropology Group MNCN-CSIC, Department of Paleobiology; Museo Nacional de Ciencias Naturales-CSIC. Calle José Gutiérrez Abascal 2, 28006 Madrid, Spain.

2 - Departamento de Anatomía y Embriología Humana I, Facultad de Medicina, Universidad Complutense de Madrid. 28040 Madrid, Spain.

3 - Área de Prehistoria, Departamento de Historia; Universidad de Oviedo. Calle Teniente Alfonso Martínez s/n, 33011 Oviedo, Spain.

* CORRESPONDING AUTHOR: Dr. Antonio Rosas. Department of Paleobiology. Museo Nacional de Ciencias Naturales (CSIC). C/ José Gutiérrez Abascal 2, 28006 Madrid (Spain). Phone +34 915668973. Fax +34 91564 50 78. e-mail: arosas@mncn.csic.es

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ABSTRACT

Correspondence between temporal lobe sulcal pattern and bony impressions on the middle cranial fossae (MCF) was analyzed. MCF bone remains (SD-359, SD-315 and SD-1219) from the El Sidrón (Spain) neandertal site are analyzed in this context. Direct comparison of the soft and hard tissues from the same individual was studied by means of: 1) dissection of two human heads; 2) optic (white light) surface scans; and 3) CT and Magnetic Resonance of the same head.

The inferior temporal sulcus and gyrus are the features most strongly influencing MCF bone surface. The Superior temporal sulcus and middle temporal and fusiform gyri also leave imprints. Temporal lobe form differs between *Homo sapiens* and neandertals. A wider and larger post-arcuate fossa (posterior limit of Brodmann area 20 and the anterior portion of area 37) is present in modern humans as compared to neandertals. However other traits of the MCF surface are similar in these two large-brained human groups.

A conspicuous variation is appreciated in the more vertical location of the inferior temporal gyrus in *H. sapiens*. In parallel, structures of the lower surface of the temporal lobe are more sagittally orientated. Grooves accommodating the fusiform and the lower temporal sulci become grossly parallel to the temporal squama. These differences can be understood within the context of a supero-lateral deployment of the lobe in *H. sapiens*, a pattern previously identified (Bastir et al. 2011). Regarding dural sinus pattern, a higher incidence of petrosquamous sinus is detected in neandertal samples.

INTRODUCTION

Presently, it is recognized that brain increase has experienced parallel evolution in different lineages of the genus Homo, e.g. H. sapiens and H. neanderthalensis. However, brains of modern humans and neandertals present substantial organizational differences of the parietal, occipital, and temporal lobes. For example, Bruner (2010) identified such constructional differences in the parietal area while Balzeau et al., (2012) found that that neandertal occipital lobes are relatively larger than those of modern humans. Recently, other differences have been detected. Thus, the visual system of neandertals is significantly larger than modern humans, with larger occipital visual areas (Pearce et al., 2013). In addition, Bastir et al., (2011) has shown that temporal poles are relatively larger in modern humans than in neandertals and other fossil hominins, but also that such enlargement is related to the temporal poles' forward projection relative to the midline. Functionally, the inferior temporal and fusiform gyri present ways of direct connection with the occipital visual areas. It is well known that, distally located visual areas can evolve in a coordinated mode, and independently of other functional areas (Barton, 2007). It could be expected that temporal visual areas were proportionally larger in neandertals as compared to modern humans.

The apomorphic condition of the modern human temporal lobes is also expressed in a comparatively wider lobe (even though neandertals and modern humans, both large-brained species, show an increment in the Middle Cranial Fossa (MCF) width). In modern humans the increase in the temporal lobe width has occurred medially in the area of the anterior-most poles, as well as superolaterally. Therefore, the modern humans temporal poles appear relatively wider, higher, longer and also projected forward relative to the midline (Bastir et al., 2011). Differing from modern humans, the evolution of the temporal lobes shape in neandertals does not include that relative elongation and the forwards deformation. Although there is an increase in relative width, the MCF poles (similar to the primitive condition), continue vertically low. This retention of the low position of the temporal poles, together with the relative length, could be interpreted as structural

elements according to the Bruner et al., (2003) hypothesis of an archaic pattern of neandertal encephalization.

In this context, the size and shape (structural) differences detected in the temporal lobe of *H. sapiens* could also imply differences in the cortical folding and sulcal pattern, as compared with other *Homo* species, and perhaps also on the drainage pattern of the dura mater sinuses. We want to test this hypothesis and pose the question: do temporal lobe structural differences have any reflection on its pattern of gyri and convolutions?

Temporal lobes are housed within the MCF, upon whose surface a large number of bony impressions can be appreciated. These impressions are originated from the adaptation of the internal surface of the cranial base to the sulci and gyri of the lower and lateral brain. The largely reabsorptive nature of growth dynamics at the cranial base (Duterloo and Enlow, 1970; Enlow, 1990) leads to the partial imprinting the cerebral surface on the cranial fossae and gives a process basis to this adaptation.

Presently, there is not a good and precise description of the correspondence between the cerebral sulcal pattern and the bony impressions of the MCF. So in this context, a more accurate knowledge of these correspondences is welcome.

In this work, size and external configuration of the temporal lobe are explored by means of a series of methodologies that allow the direct comparison of brain and cranial base in the same individual. On this basis, a detailed analysis of the physical correspondence between brain external anatomy of the temporal lobe (sulcal pattern) and the bony impressions on the middle cranial fossae was performed in order to describe and compare new temporal bone remains found at the El Sidrón (Asturias, Spain) neandertal site (Rosas et al., 2012).

MATERIAL AND METHODS

Internal aspect of three MCF fragments (mostly temporal bone) belonging to different individuals from the El Sidrón (Asturias, Spain) site, labeled SD-

359, SD-315 and SD-1219, are described. The age of the bone assemblage has been estimated at 49 kya (de Torres et al., 2010; Wood et al., 2013). The minimum number of individuals (MNI) identified at the site is 13 (Rosas et al., 2012, 2013).

Original fossil are compared to a large series of neandertal fossils. Dry skulls of the Oloriz Collection (Department of Human Anatomy and Embryology I, UCM, Spain, http://www.ucm.es/info/museoana/Colecciones/Craneos/index_english.htm) (see also Peña-Melian et al., 2011; Rosas et al., 2008) have been used as a reference sample for modern human variation.

Physical correspondence between brain external anatomy of the temporal lobe (sulcal pattern) and the bony impressions on the middle cranial fossae was assessed by means of three different and successive methods, based on the direct comparison of the soft (neuronal) and hard (bone) tissues from the same individuals. 1) We dissected two human heads at the Department of Human Anatomy and Embryology I (UCM). Visual inspections were recorded, and once the dura mater was removed, both left brain surface and middle cranial fossa were molded with high resolution silicone moldmaking rubber. Positive molds of polyurethane were used to explore morphological correspondence.

Positive cast of the molds was used to fit bone and brain surface, helping to define correspondence with staining of different colors for each anatomical detail (both sulcus and bony crests or fossae). Several direct and consistent correspondences were found. Sulcal pattern terminology follows Ono et al., (1991). Regarding osseous detailed anatomy we follow Grimaud-Hervè (1997), together with new nomina introduced for previously unconsidered characters. In parallel, a large collection of crania with opened calvaria, virtual specimens as well as reference books (Grimaud-Hervé, 1997; Holloway et al., 2004) was used for direct assessment of hard tissue variability.

Superposition of both brain and bone tissues was also explored using digital methods: 2) optic surface scans, and 3) computed tomography combined

with magnetic resonance scans. Two additional heads were submitted to computed tomography (CT) and magnetic resonance (MRI). Amira 4.0 (Visualization Sciences Group) has been used for processing both CT and MRI image datasets, registering them by semiautomatic methods by means of matching up the corresponding slices on the basis of the bony structures. Some error sources could be the overall decrease in brain size due to natural aging and also to the preservation processes (fixation with formaldehyde).

Geometric morphometrics analyses were performed in order to clarify spatial variation of the MCF. 14 landmarks were defined and digitized (Fig. 1) on 20 neandertals and 20 modern human CT scans. These landmarks were selected according to the capability to quantify relevant and homologisable features of endocranial bone morphology. These landmarks try to capture the morphology of the sulci and gyri of the temporal lobe, so they reflect not only osteological variation, but also variation related to soft-tissue structures (brain surface impressions). Standard Procrustes methods were used for shape analysis (Rohlf and Slice, 1990; Bookstein, 1991; O'Higgins, 2000). During generalized Procrustes analysis, the landmark configurations are translated to common origin, scaled to unit centroid size, and then rotated iteratively according to a best-fit criterion that minimizes overall Procrustes distance. Centroid size is used as a size measurement (i.e., the square root of the sum of squared distances of all landmarks to the centroid of the object). The metrics of shape are Procrustes distances (d), defined as the square root of the summed squared distances between Procrustes registered landmark configurations (Bookstein, 1991). Shape and size data were obtained and analysed by Principal Components Analysis using Morphologika 2.5 software (O'Higgins, 2000), (ET-software) (Evan Society, 2010) and MorphoJ integrated software package (Klingember, 2011).

The fossil specimens used in this study were: Le Moustier 1, La Ferrassie 1, La Chapelle-aux-Saints, Guattari 1, Spy I, Spy II, Gibraltar 1, Amud, Krapina 1, Krapina 3, together with 12 modern human skulls (Oloriz Collection).

RESULTS

Anatomical findings in human dissected material

A close correspondence among the individual sulcal pattern (*sensu* Ono et al., 1990) and the bony impressions of the MCF were detected (Fig. 2 and 3). The sylvian fissure does not leave any mark on the temporal bone and the superior temporal gyrus hardly leaves imprints. Superiorly, impressions located higher on the squama corresponds to the superior temporal sulcus. On the floor of the MCF, only the inferior temporal gyrus and part of the fusiform gyrus come into contact with the bone. The parahippocampal gyrus does not leave any imprint. The inferior temporal sulcus and the inferior temporal gyrus are the cerebral structures that most strongly influence the underlying MCF surface morphology. The superior temporal sulcus, the middle temporal gyrus, the occipitotemporal sulcus, and the fusiform gyrus also leave close imprints on the endocranial surface.

Temporal lobe surface impressions show a direct and consistent pattern of marks. Thus, longitudinal sulci produce longitudinal crests. In cases were longitudinal sulci are interrupted by transversal segments (e.g. vertical), a triangular-shaped bony imprint emerges usually. This is often found in the middle part of the inferior temporal gyrus, giving rise to the angular crests. Also, a confluence of sulci occurs at the lateral side of the temporal lobe, giving rise to a bony prominence, of variable form, but often with a shape of star that we call the star-shaped prominence

For the sake of clarity in the description of features, the MCF was divided into four regions: 1) temporal squama, 2) region of the temporal pole, 3) anterior (or cerebral) surface of the petrosal pyramid, and 4) basal region around the oval foramen.

Temporal squama

The squama is a region of the MCF that records a large number of crests and fossae, which are highly variable. There are marked impressions matching the superior and inferior temporal sulci, as well as impressions

matching middle and inferior temporal gyri. The limit of the bone remodeling fields: deposition (superior) and resorption (inferior) are located *grosso modo* in the line of the superior temporal sulcus.

The superior temporal sulci is evidenced by means of a highly variable series of crests discontinuously located from the pole region to the distal end of the temporal squama, where its position coincides with the vertical projection of the lateral sulcus (Sylvian fissure) bifurcation.

The inferior temporal sulcus leaves some imprints in a variable series of crests located in the middle-lower part of the squama. In the anterior end, impressions of the inferior temporal sulcus may reach the pole region, whereas the most posterior ones are located in the postero-lateral border of the pyramid crest. Depending on the number of interruptions of the inferior temporal sulcus (*sensu* Ono et el., 1990), a series of crests of longitudinal and/or oblique orientation can be identified, which in turn delineate some fossae, variably defined, which correspond to segments of the inferior temporal gyrus. An anterior segment corresponds to the Brodmann area 20 (Brodmann, 1909) (Fig. 2), and a posterior segment corresponds to the Brodmann area 37. The posterior portion of the area 20 is housed in a well defined and constant bony depression, located at the lateral lope of the arcuate eminence, and we name this structure post-arcuate fossa. Posterior to it, there can be a crest which delimits the most anterior portion of the Brodmann area 37 (Fig. 2).

Region of the temporal pole

It corresponds to the cerebral surface of the greater wing of the sphenoid, usually covered by the lesser wings. Brodmann area 38 is located on it (Fig. 2).

The bony impressions in this region of the MCF are variable. On its supero-lateral portion, crests left by the superior temporal sulcus can be found. On its middle portion, crests appear that may correspond to the inferior temporal sulcus , whereas in its most basal are, close to the oval foramen region, impressions can be identified that correspond to the parallel segment of the inferior temporal sulcus. Between the crests left by temporal

sulci fossae of variable depth are located, corresponding to the middle and inferior temporal gyri.

Anterior (cerebral) aspect of the petrous pyramid

The area of the temporal lobe which contacts to a bone support includes: basal part of the inferior temporal gyrus, anterior half of the occipito-temporal sulcus and the anterior half of the fusiform gyrus.

The inferior temporal gyrus rests upon the posterior margin of the arcuate eminence. This latter structure is, in turn, run by a crest of an anterior-lateral orientation which matches with the occipito-temporal sulcus, here named as occipito-temporal crest (Fig. 2).

On the other side, the fusiform gyrus rests upon the anterior margin of the arcuate eminence. Occasionally, it forms a depression or groove here named as fusiform fossa (Fig. 2). In the anterior end of the petrous pyramid a second eminence is found, of a lesser relief, located between the fusiform fossa and the trigeminal cave. We call the relief, upon which the anterior portion of the fusiform gyrus rests post-trigeminal eminence (Fig. 2).

Region of the oval foramen

An area located around the oval and spinosum foramina can be distinguished within the MCF, upon which the most anterior portion of the inferior temporal gyrus rests.

Lateral to the oval foramen, and located on the spheno-squamosal suture, is located a bony elevation, from which radiate small crests of variable extends and number from its top star-shaped prominence), and was present in all analyzed skulls, either in modern humans or in neandertals. The star-shaped prominence corresponds to a secondary segment of the inferior temporal sulcus, running parallel to it (Fig. 2). This secondary segment is variable in deepness and configuration but it always leaves a relief in the region of the foramina.

Description of the internal aspect features of the El Sidrón temporal bones.

SD-359

State of preservation. The specimen SD-359 is a left temporal bone taphonomically distorted, with a cracked surface (Fig. 4). It preserves an almost complete squama, but with a highly fragmented part articulating with the greater wing of the sphenoid. The petrosal pyramid is present though its anterior third and part of its posterior side are missing. A perforation of taphonomical origin is present in the middle of the squama. Size of the bone is relatively small, perhaps belonging to an adult female. A detailed location of anatomical features is recorded in Fig. 1.

Squama. The incisura parietal can be observed in the posterior area (Fig. 4, 1). Also the parietomastoid suture is visible in this area (Fig. 4, 2). On the squama, the beveled of the petrosquamousal suture can be observed but not its typical crests and indentations (Fig. 4, 3). At the anterior and superior region, the middle meningeal artery and associated veins groove (anterior branch) can be appreciated (Fig. 4, 4). Posterior to this groove, the imprint of a collateral branch of the inferior temporal sulcus is visible (Fig. 4, 5). Two fossae separate this crest, one is posteriorly located and corresponds to the temporal inferior gyrus, in a position where Brodmann area 37 is located (Fig. 4, 6). The other fossa, anteriorly located, coincides with Brodmann area 20 (Fig. 4, 7). Inferior to these details, a groove is appreciated (Fig. 4, 8), which corresponds to the inferior border of the inferior temporal gyrus, located between the squama and petrosal portion. This groove is forwardly extended and makes the vertex of an ample dihedral angle between the anterior face of the petrosal portion and the squama. In the anterior and inferior region of the squama, the star-shaped eminence can be observed (Fig. 4, 9). This is the imprint of a radial branch of the inferior temporal sulcus, at the surroundings of the temporal pole.

Anterior (or cerebral) aspect of the petrous portion. The arcuate eminence appears as a weak protuberance located in the middle area of this aspect (Fig. 4, 10). Anteriorly, and slightly lateral, the *tegmen tympani* can be appreciated (Fig. 4, 11). The anterior border of the petrous portion (pyramidal crest) (Fig. 4, 12) extends all along the petrous pyramid, lodging

the groove for the superior petrosal sinus (Fig. 4, 13). Posteriorly, the petrosquamous sinus groove (Fig. 4, 14) connects with the start of the sigmoid sinus groove (Fig. 4, 15).

A foramen for a branch of the middle meningeal vein (Fig. 4, 16) can be observed between the arcuate eminence and the petrosquamous sinus groove. In the anterior portion of the petrous pyramid fragment, and slightly lateral, close to the star-shaped eminence, a concavity is observed (Fig. 4, 17), which may correspond to the inner opening of the carotid canal.

Posterior (or cerebellar) aspect. Due to its bad preservation, only the internal acoustic meatus and ductus can be appreciated anteriorly, which are filled with sediment (Fig. 4, 18). Inferior and posterior to it, a notch corresponding to the vestibular aqueduct is present (Fig. 4, 19). Posteriorly, and located in the mastoid region, a wide groove for the left sigmoid sinus is visible (Fig. 4, 15), upon which a mastoid foramen is located (Fig. 4, 20). This foramen is usually located on the occipitomastoid suture; the lateral portion to the mastoid foramen belongs to the cerebellar fossa of the occipital bone (Fig. 4, 21). At the start of the inner side of the sigmoid sinus groove, some crests for the attachment of the tentorium cerebelli are present (Fig. 4, 22).

SD-315

State of preservation. SD-315 is a fragment of a left middle cranial fossa, mostly temporal bone, including the lower half of the squama and most of the petrous pyramid, the anterior (apex) end of which is missing (Fig. 5, A & B). Anterior to the squama, remnants of greater wing of the sphenoid bone are preserved. The sphenosquamous suture may be appreciated (Fig. 5A, 1). Also, a notch resulting from the absence of the wall separating foramina ovale and spinosum is present (Fig. 5A, 2). SD-315 also preserves a small portion of the mastoid process, adjacent to the base of the petrous pyramid (Fig. 5B, 1).

Squama. The parietal incisura is appreciated at the posterior portion of SD-315 (Fig. 5A, 3), whereas the articular suture for the greater wing of the sphenoid is clearly visible in the anterior portion of the specimen (Fig. 5A, 1). On the endocraneal surface, two blunt crests are observed, one is located anterior y vertical (Fig. 5A, 4), while the other one is backwardly placed, larger and horizontal, parallel to the greater axis of the petrosal pyramid (Fig. 5A, 5). These two crests are separated by a wide but short groove (Fig. 5A, 6), corresponding to middle meningeal groove. These crests delimit two ample fossae, imprints of the inferior temporal gyrus (Fig. 5A, 7 and 8). The start of the middle meningeal groove is located in the anteroinferior part of the squama (Fig. 5A, 9), taking its origin at the posterior border of the foramen spinosum.

Anterior (or cerebral) aspect of the petrous portion. The cerebral aspect of SD-315 is relatively wide. The arcuate eminence (Fig. 5A, 10) appears as a low protuberance, close to the squama and relatively remote from the anterior border (pyramidal crest). Anteriorly to this eminence, a slightly depressed area can be observed, which corresponds to the *tegmen tympani* (Fig. 5A, 11). Posterior to the arcuate eminence appears a fossa related to the inferior temporal gyrus (Brodmann area 37) (Fig. 5A, 12). In the anterior third of the petrosal portion, a large part of the root of the carotidean groove is taphonomically lost, being visible its internal surface (Fig. 5A, 13). Posterior to this groove, a narrow channel left by the major superficial petrous nerve can be seen, which elongates backwards (Fig. 5A, 14), but without reaching the Fallopian hiatus. On the medial area of the rest of the root of the carotidean groove, an ample fossa is appreciated (Fig. 5A, 15), (trigeminal cave). The groove for the superior petrosal sinus runs by the anterior border (Fig. 5A, 16). At the posterior end of the pyramid the petrosquamous sinus groove is clearly visible (Fig. 5A, 17).

Posterior (or cerebellar) aspect. This aspect is vertical in its anterior half but slightly concave in its posterior half (Fig. 5B, 2 and 3). Anteriorly, the internal acoustic meatus is located (Fig. 5B, 4), which is filled of sediment, and from which a wide groove emerge, directed in a forward direction, by which VII y VIII cranial pairs run. Both internal acoustic meatus perimeter

as well as the groove emerging from it present very smooth borders. Posterior to the internal acoustic meatus, a slightly depressed area is present, with several lines of fracture, where the inner foramen of the vestibular aqueduct is located (Fig. 5B, 5). The subarcuate fossa is missing due to the breakage of the area (Fig. 5B, 6). The superior petrosal groove is better seen on the anterior border of the pyramidal crest in its posterior third (Fig. 5B, 7). In the anterior most end of the petrous pyramid, it is clearly visible the petrosquamous sinus groove (Fig. 5B, 8), which is joined to the start of the sigmoid sinus groove (Fig. 5B, 9). Also, a connection of the sigmoid and superior petrosal sinuses grooves is detected (Fig. 5B, 10).

SD-1219

State of preservation. This specimen is composed by a left temporal bone, articulated to a fragment of parietal bone and most of the occipital bone (Fig. 6 A & B) (Rosas et al., 2008). The temporal bone preserves two third of its petrosal portion while only a small part of the squama is preserved (Fig. 6A, 1). Likewise, the endocraneal aspect of the mastoid process apophysis is preserved.

Squama**.** A part of the conserved area has lost the internal table. The squama is posterosuperiorly articulated with a fragment of parietal bone, being present the parieto-squamous suture (Fig. 6A, 2), and more inferiorly, the parietal incisura (Fig. 6A, 3). Inferiorly, the occipitomastoid suture for the articulation with the occipital bone is also preserved and well delimited (Fig. 6A, 4). The groove for the posterior branch of the middle meningeal groove runs on the boundary between the pretrosal portion and the squama (Fig. 6A, 5). This groove crosses a large fossa corresponding to the inferior temporal gyrus (Brodmann area 37) (Fig. 6A, 6), and extends in the parietal bone. Groove for the petroescamous sinus covers from the inferior portion of the squama and meets with the grove of the middle meningeal artery and veins (Fig. 6A, 7).

Anterior (or cerebral) aspect of the petrous portion. A strong and well marked arcuate eminence is visible on this aspect (Fig. 6A, 8), which seems to be laterally extended until the origin of the squama by means of a bony

bun. Anteriorly, an area slightly depressed corresponding to the *tegmen tympani* is detected (Fig. 6A, 9).

Posterior (or cerebellar) aspect**.** A well defined pyramidal crest defines a neat limit between the cerebral and the cerebellar aspects (Fig. 6A, 10). On its three posterior thirds, the groove of the superior petrosous sinus is well marked (Fig. 6A, 11, Fig. 6B, 1), flanked by two sharp crests, clearly connected to the groove of the sigmoid sinus (Fig. 6B, 2). Posteriorly, the petroesquamous sinus is conspicuous and connects to the start of the sigmoid sinus (Fig. 6B, 3). Anteriorly, the internal acoustic meatus can be appreciated (Fig. 6A, 12), with smooth borders, which give rise to a short internal auditive groove, filled with sediments. Posteriorly, between the anterior border and the internal auditive meatus, a depressed area is located, upon which a notch, possibly corresponding to the subarquate hiatus, is detected (Fig. 6A, 13). Inferiorly, the free border of the petrous pyramid forms the jugular notch (Fig. 6A, 14), which makes part of the jugular foramen at the time of joining the lateral masses of the occipital bone (Fig. 6A, 15). Posteriorly, on the endocraneal aspect of the mastoid apophysis, a wide groove for the sigmoid sinus is appreciated (Fig. 6A, 16 and 6B, 2), which extends to reaching the jugular foramen. This groove is flanked by two sharp crests, and close to the jugular notch, a mastoid foramen filled of sediment is observed (Fig. 6B, 4). Just anterior to the sigmoid sinus groove, the internal foramen of the aqueduct of vestibule is present (Fig. 6A, 17), where the endolymphatic sac is located.

Geometric morphometrics and comparative analyses

Average shape of the neandertal and modern human samples was different, despite a large overlap (Fig. 7). The El Sidrón temporal bone occupies a central position in the morphospace, clearly located within the neandertal variation. With this set of data, neandertals seem to present a larger range of variation and a noticeable asymmetry in their temporal lobe imprint configuration.

Considering cerebral imprints, two major anatomical structures are involved in the variation: 1) the vertical location of the inferior temporal sulcus, and 2) the orientation of the occipitotemporal sulcus (and fusiform gyrus). Taken as a whole, the form of the temporal lobe shows a marked difference between *Homo sapiens* and neandertals. The most obvious variation is appreciated in the more vertical location of the inferior temporal gyrus in *H. sapiens*. In parallel, structures of the lower surface of the temporal lobe are arranged in a more sagittal orientation. Grooves accommodating the fusiform and the lower temporal sulci become grossly parallel to the temporal squama. These differences can be understood within the context of a supero-lateral expansion (deployment) of the lobe in *H. sapiens* in which a lateral displacement of the basal temporal lobe occurs together with a superior displacement of the lateral sulci and gyri.

Regarding dural sinus pattern, a higher incidence of petrosquamous sinus is detected among Neandertal samples compared to modern humans (Table 1).

DISCUSSION

The fossil evidence of middle cranial fossa from the El Sidrón site (mainly temporal bone fragments) records a number of anatomical features, most of them located on the anterior (cerebral) face of the petrosal and on the lower most part of the temporal squama. Putting them into a comparative context, the El Sidrón specimens share a common pattern with other neandertals and occupy a central position in the distribution close to the neandertal average (e.g. SD-315).

On the whole, the bony impressions of MCF show a different configuration in Neandertal and modern humans. Thus, a wider and larger post-arcuate fossa (Fig. 2) seems to be present in modern humans as compared to neandertals. This area corresponds to the posterior limit of Brodmann area 20 and the anterior portion of Brodmann area 37. Other traits of the MCF surface do not show, however, evidence of dissimilarity between these two large-brained human groups. On the whole, our data suggest a relative

expansion of the inferolateral surface of the temporal lobe and a modification of the temporal pole, with a possible enlargement of the Brodmann areas 20, 37 and 38. The possible functional implications of these differences need to be explored.

Previous analyses have emphasized significant spatial evolutionary differences in the configuration of the temporal lobe in modern humans compared with other large-brained humans (Bastir et al., 2008; 2011), which fits with previously recognized overall endocraneal scaling differences (Bruner et al., 2003; Gunz et al., 2010). In modern humans, an apomorphic pattern locates the temporal lobe pole in a more anterior, lateral and upward position. Once a fine anatomical correspondence of the temporal lobe circumvolution pattern on its bony base has been clarified, we put forward the hypothesis that the temporal pole is differentially occupied among human species. Thus, temporal pole is defined in Neandertals by the middle and lower temporal gyri, while the pole is mostly defined by the superior and middle temporal gyrus in anatomically modern humans. In both species, however, cytoarchitecture of the temporal pole – corresponding to Brodmann area 38 - is different to that of the middle and superior temporal gyri. In turn, it is currently considered that this area is composed of different cytoarchitectonic, chemoarchitectonic and pathological markers, which reveals this region more complex than previously thought (Ding et al., 2009). Further analyses need to test this proposition as well as the functional implications of these cortical reorganizations. Also, size differences in the specific portions of the temporal lobe need to be explored.

Even though speculative, the possible functional implications of these changes could be as follows. Concerning the temporal lobe, functions related to social behavior as well as theory of mind may be involved. In modern humans, the occipital visual areas could be of a lesser extension than that of neandertals, perhaps at the expense of an increment of the complex associative cortex (cognitive) (Pearce et al., 2013). In this way, the visual ventral way receiving information from the occipital visual areas, which are distributed by Brodmann areas 21, 20 and 37, could be involved

in cognitive complex functions related to the visual world such as the recognition of familiar objects or faces and its emotional and social repercussion as well as a a large capability of visual attention. Also, an increased capacity of expression of happiness and laughing, perhaps as part of the social functions (Satow et al., 2003).

Finally, as previously mentioned, a higher incidence of petrosquamous sinuses is detected among Neandertal samples compared to modern humans (Table 1). In *Homo sapiens*, the petrosquamous sinus becomes differentiated during the embryonic life, being originally a duct of a large caliber, which runs from the transverse sinus to the roof of the temporomandibular joint (TMJ), to be linked, through a foramen, with the external jugular vein. From the fetal life on, this sinus begins to diminish (Butler, 1957), disappearing in the last three months of gestation (Marsot-Dupuch et al., 2001). Nonetheless, there are some discrepancies considering the disappearance of the petrosquamous sinus. There are references of the presence of this sinus during the adult life (Marsot-Dupuch et al., 2001; Gray's anatomy, 1995), and even preoperational findings which may cause a grave insult during intervention (An et al., 2011). Consequently, the elevated incidence of this sinus in neandertal adult population can be hypothesized as maintenance of a fetal feature during the adult life, serving to maintaining a communication between the intra and extracranial venous circulation by means of the external jugular vein system.

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