**University of
Zurich**^{UZH}

**Zurich Open Repository and
Archive**

University of Zurich
University Library
Strickhofstrasse 39
CH-8057 Zurich
www.zora.uzh.ch

Year: 2019

Virtual reconstruction and re-evaluation of the Neanderthal frontal bone from Carigüela Cave (Granada, Spain)

Jiménez-Arenas, Juan Manuel ; Bienvenu, Thibault ; Toro-Moyano, Isidro ; Ponce de León, Marcia S ;
Zollikofer, Christoph P E

Abstract: During several consecutive excavations from the 1950s to the 1990s the cave of Carigüela de Píñar (Granada, Baetic System, Southeast of the Iberian Peninsula) has yielded an important sample of Neanderthal fossils. Among these finds is a fragmentary frontal bone of an immature individual (CE-05877), which was described earlier. Here we present a new virtual reconstruction and a quantitative analysis of its three-dimensional morphology. Geometric morphometric analyses show that the Carigüela frontal falls within the range of shape variation of 6–7 year-old Neanderthals, and clearly outside the range of variation exhibited by same-age modern humans. Compared to other Neanderthals of similar age, Carigüela has a relatively wide nasal bridge and low frontal profile. Re-analysis of the fossil's endocranial imprints in the light of cerebral sulcal variability in modern humans indicates that only a reduced number of brain sulci can be identified reliably. Overall, the Carigüela fossil provides further support for the view that Neanderthals and modern humans exhibit distinct frontal bone morphologies, while their cerebral frontal lobes exhibit largely similar but highly variable sulcal patterns.

DOI: <https://doi.org/10.1016/j.quascirev.2019.03.014>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-183883>

Journal Article

Accepted Version

The following work is licensed under a Creative Commons: Attribution-NonCommercial-NoDerivatives 4.0 International (CC BY-NC-ND 4.0) License.

Originally published at:

Jiménez-Arenas, Juan Manuel; Bienvenu, Thibault; Toro-Moyano, Isidro; Ponce de León, Marcia S; Zollikofer, Christoph P E (2019). Virtual reconstruction and re-evaluation of the Neanderthal frontal bone from Carigüela Cave (Granada, Spain). *Quaternary Science Reviews*, 217:89-97.

DOI: <https://doi.org/10.1016/j.quascirev.2019.03.014>

Manuscript Details

Manuscript number	JQSR_2019_11
Title	Virtual reconstruction and re-evaluation of the Neanderthal frontal bone from Carigüela Cave (Granada, Spain)

Abstract

During several consecutive excavations from the 1950s to the 1990s the cave of Carigüela de Píñar (Granada, Baetic System, Southeast of the Iberian Peninsula) has yielded an important sample of Neanderthal fossils. Among these finds is a fragmentary frontal bone of an immature individual, which was described earlier. Here we present a new virtual reconstruction and a quantitative analysis of its three-dimensional morphology. Geometric morphometric analyses show that the Carigüela frontal falls within the shape variation of 6-7 year old Neanderthals, and clearly outside the shape variation exhibited by same-age modern humans. Compared other Neanderthals of similar age, Carigüela has a relatively wide nasal bridge and low frontal profile. Re-analysis of the fossil's endocranial imprints indicates that only a reduced number of brain sulci can be identified reliably. Overall, results indicate that endocranial (and brain) structural differences between Neanderthal and modern human frontal lobes are less striking than generally assumed.

Submission Files Included in this PDF

File Name [File Type]

Jimenez-Arenas_et-al_QSR-Highlights.docx [Highlights]

Jimenez-Arenas_et-al_QSR-manuscript.doc [Manuscript File]

Figure1.tif [Figure]

Figure2.tif [Figure]

Figure3.tif [Figure]

Figure4.tif [Figure]

Figure5.tif [Figure]

Figure6.tif [Figure]

Figure7.tif [Figure]

Table1.doc [Table]

To view all the submission files, including those not included in the PDF, click on the manuscript title on your EVISE Homepage, then click 'Download zip file'.

Research Data Related to this Submission

There are no linked research data sets for this submission. The following reason is given:
Data will be made available on request

Highlights

- We present a virtual reconstruction of the Neanderthal frontal bone for Carigüela Cave (Granada, Spain).
- The Carigüela frontal falls within the shape variation of 6-7 year old Neanderthals.
- Re-analysis of the fossil's endocranial imprints indicates that only a reduced number of brain sulci can be identified reliably.
- Endocranial structural differences between Neanderthal and modern human frontal lobes are less striking than generally assumed.

Virtual reconstruction and re-evaluation of the Neanderthal frontal bone from Carigüela Cave (Granada, Spain)

Juan Manuel Jiménez-Arenas¹

Departamento de Prehistoria y Arqueología (University of Granada, Spain)
Campus Universitario de Cartuja, Facultad de Filosofía y Letras. 18071 Granada
(Spain)

Instituto Universitario de la Paz y los Conflictos (University of Granada, Spain)
C/Rector Lopez Argüeta, s/n. Edificio de Documentación Científica. 18071 Granada
(Spain)

Department of Anthropology (University of Zurich, Switzerland). Winterthurerstrasse
190□CH- 8057 Zürich (Switzerland)

jumajia@ugr.es

Thibault Bienvenu

Department of Anthropology (University of Zurich, Switzerland). Winterthurerstrasse
190□CH- 8057 Zürich (Switzerland)

Thibaultbienvenu@hotmail.com

Isidro Toro-Moyano

Museo Arqueológico y Etnológico de Granada (Spain). Carrera del Darro 41-43.
18010 Granada (Spain)

isidro.toro@juntadeandalucia.es

Marcia S. Ponce de León

Department of Anthropology (University of Zurich, Switzerland). Winterthurerstrasse
190□CH- 8057 Zürich (Switzerland).

marcia@aim.uzh.ch

Christoph P.E. Zollikofer

Department of Anthropology (University of Zurich, Switzerland). Winterthurerstrasse
190□CH- 8057 Zürich (Switzerland).

zolli@aim.uzh.ch

Abstract

¹ Corresponding Author. Permanent Address: Depto. de Prehistoria y Arqueología. Facultad de Filosofía y Letras. Campus de Cartuja, s/n. 18071. Granada (Spain)

During several consecutive excavations from the 1950s to the 1990s the cave of Carigüela de Píñar (Granada, Baetic System, Southeast of the Iberian Peninsula) has yielded an important sample of Neanderthal fossils. Among these finds is a fragmentary frontal bone of an immature individual, which was described earlier. Here we present a new virtual reconstruction and a quantitative analysis of its three-dimensional morphology. Geometric morphometric analyses show that the Carigüela frontal falls within the shape variation of 6-7 year old Neanderthals, and clearly outside the shape variation exhibited by same-age modern humans. Compared other Neanderthals of similar age, Carigüela has a relatively wide nasal bridge and low frontal profile. Re-analysis of the fossil's endocranial imprints indicates that only a reduced number of brain sulci can be identified reliably. Overall, results indicate that endocranial (and brain) structural differences between Neanderthal and modern human frontal lobes are less striking than generally assumed.

Keywords

Neanderthal, frontal bone, platycephaly, nasal bridge, frontal lobe, Broca cap, encephalic beak.

Introduction

The cave of Carigüela de Píñar (Granada, Baetic System, Southeast of the Iberian Peninsula) comprises one of the most complete stratigraphic sequences documenting a Mousterian techno-complex and human activity from the Upper Pleistocene to the Holocene (Vega Toscano, 1988). These cave sediments have been key to the interpretation of local climate conditions (Carrión, 1990, 1992; Carrión et al. 1999; Fernández et al., 2007) and to document the late presence of Neanderthals in this region (Fernández et al., 2007). Excavations at Carigüela Cave were initiated by J. C. Spahni during the 1950s, and resumed by a team of Washington State University in the late 1960s and early 1970s. In addition to lithic tools (Vega Toscano, 1988), these excavations also yielded direct fossil evidence of *Homo neanderthalensis* (Fusté, 1956; García Sánchez, 1960; de Lumley & García Sánchez, 1971; de Lumley, 1973; García Sánchez et al., 1994; Jiménez-Arenas et al., 2016). Among the fossil finds, a frontal bone of an immature individual (CE-05877) stands out due to its exceptional state of preservation. It was found in two fragments, the first one on May 4 and the second one on May 22, 1955 in level 7 of the so-called Carigüela II (C-II) sequence. Fusté (1956) provided a preliminary description of its endocranial morphology. Later on, García Sánchez (1960) included the specimen in a description of all human fossils from Carigüela. Detailed comparative analyses of the specimen's external and internal morphology were provided by de Lumley and García Sánchez (1971) and de Lumley (1973).

CE-05877 was attributed to *H. neanderthalensis* based on the morphology of the supraorbital torus, a comparatively platycephalic midsagittal profile and in the purportedly lower development of the frontal lobes (Fusté, 1956), postorbital constriction and greater interorbital width than in *H. sapiens* (García Sánchez, 1960). The individual age of the specimen was estimated to 5-7 years (age group M1), based on craniometric dimensions and the unfused inferiormost part of the metopic suture (11 mm over nasion) (de Lumley & García Sánchez, 1971; de Lumley, 1973).

While these previous studies have provided detailed descriptions and metric analyses of the external morphology of the Carigüela frontal bone, several questions remain open and will be addressed here. First, as observed by García Sánchez (1960: 26), the taphonomic deformation of the specimen likely affects the validity of its current physical reconstruction and the outcome of previous metric analyses. Using techniques of virtual fossil reconstruction, we provide a new reconstruction of

the specimen, and derive a new set of metric data and quantitative comparative analyses. Furthermore, we perform a 3D geometric morphometric analysis of the frontal bone using a comparative sample including immature to adult specimens of *Homo erectus*, *H. heidelbergensis*, Neanderthals and modern humans. The second aim of our study is to re-analyze the endocranial imprints preserved on the Carigüela specimen. The morphology of the endocranial surface has been assessed based on drawings that resemble a cortical surface more than actual endocranial imprints (de Lumley and García Sánchez, 1971: p. 53, Fig. 13). Ascribing cortical gyri and sulci to endocranial imprints, however, needs to take into account potential ambiguities. Using an extended comparative sample of Neanderthal and modern human endocasts, we provide a re-interpretation of the endocranial imprints of the Carigüela frontal.

Materials and Methods

CE-05877 fossil is housed at the Museo Arqueológico y Etnográfico de Granada (Granada, Spain). Originally it was covered by a calcareous concretion that was removed in the Anatomy Laboratory of the University of Granada. Simultaneously, samples were taken to analyze the degree of fossilization and finally it was coated with paraffin. The fossil was handed over for study to Manuel García Sánchez in two fragments, who performed a physical reconstruction.

Virtual reconstruction: CE-05877 was scanned on a medical computed tomography (CT) device at the Centro de Diagnóstico Médico in Granada (Philips Brilliance 64-array helical CT). Scanning parameters were as follows: slice thickness 1 mm, voltage 110 kV, electric current 50 mA. Software packages Avizo 7.0 (Visualization Sciences Group Inc.) and GeoMagic were used for 3D isosurface extraction and post-processing. The virtual reconstruction was performed following standard procedures of fragment positioning and mirror-image completion (Zollikofer and Ponce de León, 2005). Specifically, the reconstruction proceeded as follows: 1) all plaster fillings were removed digitally; 2) the Devil's Tower and Teshik-Tash immature Neanderthals were used as a reference to superimpose both the Carigüela frontal left and right parts; 3) the smaller left part of the Carigüela frontal was mirror-imaged to the right side and fitted accordingly; 4) finally, the adjusted mirror-imaged left part was mirrored back to the left side.

Geometric morphometric analysis: The fossil comparative sample comprises 24 individuals (Table 1); 8 *H. erectus* (KNM-ER 1813, KNM-ER 3733, KNM-WT 15000 [Nariokotome], Dmanisi hominids D 2700, D 2280, D 2282, D 3444, D 4500), *H. heidelbergensis* (Broken Hill and Steinheim), 14 Neanderthals (Dederiyeh 1 and 2, Pech de l'Azé, Engis, Gibraltar 1 and 2, Roc de Marsal 2, Subalyuk 2, La Quina 18, Teshik Tash, Le Moustier, Amud 1, La Ferrassie and Tabun 1). The modern human sample consists of 63 individuals representing fetal to adult stages (Table 1). Modern human crania are from the collections of the Anthropological Institute and Museum of the University of Zurich, the Natural History Museum of London, and the Bosma collection (Peabody Museum, Harvard University). The sample was categorized into 7 age classes (fetus; neonate; dM1, dM2 fully erupted; M1, M2, M3 fully erupted).

The Carigüela frontal bone misses most of the upper part of the frontal squama, and the coronal suture is only preserved in its lowermost parts. Nevertheless, the following landmarks could be identified on the specimen and were used for the geometric morphometric analysis: nasion, glabella, maxillofrontale (R/L), foramen supraorbitale (R/L), frontomale orbitale (R/L), pterion (R/L), mid nasion-bregma, and foramen caecum. Geometric morphometric analysis was then performed according to standard procedures (Dryden and Mardia 1998): following generalized procrustes analysis, morphological variation in multivariate shape space was analyzed with principal components analysis (PCA), and frontal bone morphologies corresponding to extreme positions in shape space were visualized with thin-plate spline morphing procedures, using the well-preserved Gibraltar 2 frontal bone as a template.

Analysis of endocranial imprints and outlines: The Neanderthal endocranial sample comprises five specimens: Engis 2, Subalyuk 2, Roc de Marsal, Gibraltar 2 (complete deciduous dentition, age group dM2), and Teshik Tash (age group M1). The modern human sample comprises 27 immature specimens (17 and 10 specimens representing age classes dM2 and M1, respectively). All specimens were CT-scanned and their endocasts virtually extracted using methods described in Bienvenu et al. (2011). Comparative Neanderthal specimens have been virtually reconstructed as described earlier (Ponce de León et al., 2016; Zollikofer et al., 2017).

A comparison of endocranial outlines in lateral, frontal and inferior views was performed as follows: Endocasts of all specimens of the sample were oriented in

lateral view with the frontal and occipital poles on a horizontal plane (Falk et al., 1994). Incomplete Neanderthal endocasts were oriented visually, based on estimates of the occipital pole location. Once all specimens had the same orientation, location in space was also standardized by superimposing the midsagittal planes and translating all endocasts so that their most anterior point (frontal pole) abutted on the same coronal plane and their most inferior point on frontal lobe (olfactory bulb) abutted on the same transverse plane. Right lateral and inferior views of the specimens were captured orthogonally, i.e. without perspective distortion. Endocasts were further cut straight coronally at the level of the most anterior temporal pole, and the posterior portion was removed so as to keep only the frontal lobes. When temporal poles were not preserved (Carigüela, Engis 2, Gibraltar2), the cross-section was realized through the preserved parts of the coronal suture. Anterior views of the cut endocasts were captured orthogonally. Projected contours of the superimposed endocasts were drawn in right lateral, inferior and anterior views. Orthogonal projection results in right contours being equivalent to mirrored left contours, inferior contours being equivalent to mirrored superior contours, and anterior contours being equivalent to mirrored posterior contours, in such a way that three views suffice to describe the general shape of endocasts.

Results

General state of preservation

Comparison with frontal bones of other immature Neanderthal specimens shows that the Carigüela specimen preserves about 50% of the total endocranial surface of the frontal bone (Figure 1); the upper half of the frontal squama is missing, such that the endocast largely represents the anterior portions of the frontal lobes, including the cortical regions underlying Broca's Cap. Also, the new virtual reconstruction has revealed a gap between the two main fragments of the frontal bone, extending from superomedially to inferolaterally toward the left orbital roof. The left orbital roof is preserved on its lateral side, while its right counterpart is present, except for the most medial part. In the midplane region, the endocast is preserved anterior to foramen caecum. Comparison of the preserved parts of the frontal bone with their mirror-imaged counterparts confirms earlier observations (de Lumley and García Sánchez, 1971; de Lumley, 1973) on postmortem deformation: the fragment representing the

left side of the frontal bone appears flattened out compared to the right side, indicating plastic distortion due to taphonomic forces.

3D Geometric Morphometrics

Figure 2 shows the results of the 3D geometric morphometric analysis. PC1 comprises 32% of total variance and reflects changes in frontal bone morphology along taxon-specific ontogenetic trajectories, as well as inter-taxon variation from relatively paedomorphic (low PC1 scores) to peramorphic (high PC1 scores) shapes. Shape variation along this axis is most conspicuous in terms of width of the orbital relative to the squamal portions of the frontal bone, and relative length of nasal bridge. PC2 comprises 15% of total variance and captures variation in frontal squama height and nasal bridge width. Along this axis, specimens with relatively low frontal squamae and wide nasal bones are located toward low PC2 scores, and individuals with relatively high squamae and narrow nasal bones are located toward high PC2 scores. Neanderthals exhibit consistently lower PC2 scores than modern human and *H. erectus* specimens, and the Carigüela specimen exhibits one of the lowest PC2 scores, indicating a low frontal squama and wide nasal bridge, resulting in a wide interorbital distance. Figure 2 shows that Neanderthals (as well as *H. heidelbergensis* and *H. erectus*) have consistently higher PC1 scores than *H. sapiens* at any given ontogenetic stage, indicating that the human frontal squama is distinctly more rounded (paedomorphic) than that of fossil hominids of comparable individual age. Within the Neanderthal sample, the Carigüela frontal bone has a PC1 score that best corresponds to age group M1.

Endocranial imprints and inferred soft tissue structures

There is a well developed frontal crest which corresponds to a deep interhemispheric fissure (Figure 3, red tube). This fissure bifurcates superiorly into two branches delineating the borders of the superior sagittal sinus (big dural vein). The frontal poles do not exhibit petalial asymmetry. There are several small dimples on the anterior portion of the endocast (Figure 3, green tubes), one possibly being part of the left superior frontal sulcus as identified by de Lumley (1973) and Fusté (1956). There are also several well defined orbital gyral and sulcal imprints (Figure 3, orange tubes), especially visible on the better preserved right orbital surface. Those orbital sulci are small branches difficult to ascribe to standard sulci. Moreover, various nomenclatures

exist to describe those sulci. As a consequence, we do not attempt here to identify them individually.

Well defined sulcal imprints also appear in the lateral inferior portions of the Carigüela frontal endocast (Figure 3, purple tubes). On both sides, we identify a triradiate sulcus as the inferior frontal sulcus *fi*. Anterior to it is a depression running obliquely anteriorly and superiorly, which we define as the middle frontal sulcus *fm* or alternately as the fronto-marginal sulcus of Wernicke *W*. On the right side, *fm* (or *W*) is separate from *fi* by what de Lumley (1973) calls a "pli de passage" ("bridging convolution"), while on the left side, it is continuous to *fi*. Identification of this sulcus we name *fm* or *W* has been very problematic. Indeed, taking into account both sides, it received four different names from two different authors (Fusté 1956; de Lumley 1973) (Figure 3). On the left side, we do not consider this sulcus as the anterior branch of *fi* as suggested by de Lumley (1973) because this would involve too much asymmetry in the relative location of this branch between both hemispheres and there wouldn't be any left-side equivalent for right *fm*.

Endocranial outline analysis

Contrary to Fusté (1956) and de Lumley (1973), the frontal region of Carigüela does not appear to be "reduced" compared to modern humans. While we agree that the Carigüela frontal has a low endocranium (Figure 4), we do not observe reduction in length nor anterior narrowing. The Carigüela frontal region even appears to us wider and longer compared to most modern human endocasts. Quantification of endocranial outline shape confirms those observations concerning Carigüela (Figure 5). Compared to modern humans, Neanderthals have wide and low frontals (platycephaly). In Neanderthals, frontal width and frontal height increase together at a low pace relative to frontal length (Figure 5, solid and dotted red lines), while in modern humans, they also increase together but at a much higher pace (Figure 5, solid and dotted blue lines), so that no modern human endocast shows the combination of a wide and low frontal as in Neanderthals. The relationship between frontal width and frontal height is conserved in Neanderthals and modern humans (Figure 5, dashed lines).

While endocasts were standardized for orientation and location (Figure 4a), proper shape comparison further needs to adjust for differences in size. Accordingly, we tried two different scalings, one relative to maximum frontal length (from the level of

temporal poles/coronal suture to the level of frontal poles, Figure 4b) and one relative to maximum frontal width (at the level of temporal poles/coronal suture, Figure 4c). After scaling for frontal length, the Carigüela frontal appears even lower (Figure 4b) compared to the modern sample, as other Neanderthals do overall. The strong dorsal flattening of the Carigüela specimen (Figure 4b) is probably overemphasized due to its long frontal lobes (Figure 4a, lateral view). When scaling for frontal width, the Carigüela specimen does not depart as much from other Neanderthals (Figure 4c). However, all the Neanderthal endocasts then appear homogeneous in their general shape, more flattened dorsally than modern humans. Small height relative to width (Figure 5, dashed lines) is indeed the definition of platycephaly, which is considered a typical feature of Neanderthal endocasts. Neanderthal platycephaly is probably visually exaggerated in Figure 4c, because Neanderthals have larger frontal width relative to maximum endocranial length than modern humans (Bruner and Holloway, 2010). This makes Neanderthal endocasts look overall shorter than modern human ones (Figure 4c), which contributes to the visual effect of Neanderthal low dorsal endocranial surface.

As Fusté (1956), de Lumley and García (1971) and de Lumley (1973) pointed out, we observe that the preserved right orbital surface is very concave inferiorly with a very steep medial border associated to a projecting olfactory bulb (known as encephalic beak or bec).

Discussion

Although the Carigüela frontal bone is incomplete, the preservation of several anatomical landmarks has permitted to us to carry out a 3D geometric morphometric analysis. The position of this specimen along the axis of ontogenetic shape change (PC1) indicates an individual age corresponding to age group M1. This is consistent with previous age estimates [García Sánchez (1960): 7-8 y; de Lumley (1973): 4-8 y]. The position of Carigüela along PC2 (which separates modern human from Neanderthal frontal bone shapes) confirms its taxonomic status as a Neanderthal (Fusté, 1956).

From a general point of view, this study confirms previously described differences between the frontal bone morphologies of modern humans and Neanderthals (e.g.

Gunz and Bulygina, 2012). Furthermore, a geometric morphometric analysis of endocranial shape differences between Neanderthals and modern humans (Ponce de León et al. 2016) indicates that these differences are already present at birth, thus reflecting fundamental differences between brain morphologies of the two species. During postnatal development, these differences are accentuated due to more intense facial growth in the Neanderthals, and not due to differences in postnatal brain development, as postulated earlier (Gunz et al., 2010; 2012)

Though bregma is absent in Carigüela, the position of mid-bregma permits to us to confirm that the Carigüela child frontal squama height must be considered the lowest among Neanderthal infants (Fig. 2) as de Lumley (1973) claims previously. In addition, endocranial measurements show that Carigüela presents a long frontal such as de Lumley (1973) previously shown as well. On the other hand, the prominent width of the Carigüela nasal bridge was also highlighted by García Sánchez and de Lumley (García Sánchez, 1960; de Lumley and García Sánchez, 1971; de Lumley, 1973). In fact, de Lumley (1973) established that the interorbital width of Carigüela infant exceeds those measured in other Neanderthal infants. Our analysis confirms the presence of such feature, which is considered as a plesiomorphy preserved in the Neanderthals (Trinkaus, 2006). Our analysis shows that in relative terms orbital width of the Carigüela child is that expected for its age group.

The identification of the sulci and gyri on the Carigüela frontal endocast is tentative, for five well known reasons

- i) the *inter-rater variability* in sulcal identification/interpretation, especially on endocasts. This is a topic which most known example is the longstanding debate about Taung's lunate sulcus (e.g. Holloway et al., 2004a; Falk, 2009). The Carigüela endocast contributes to fuel this question: a) the sulcus on the left side defined in the present paper as inferior frontal sulcus is considered as the incisure of Broca's cap by de Lumley and García Sánchez (1971) and de Lumley (1973), and as the fronto-marginal sulcus of Wernicke by Fusté (1956); b) the middle frontal sulcus or fronto-marginal sulcus of Wernicke on the left side (this work) is named inferior frontal sulcus by de Lumley and García Sánchez (1971) and de Lumley (1973), and middle frontal sulcus by Fusté (1956); c) the middle frontal sulcus or fronto-marginal sulcus of Wernicke on the left side (this work) is named

inferior frontal sulcus by de Lumley and García Sánchez (1971) and de Lumley (1973), and middle frontal sulcus by Fusté (1956); d) the middle frontal sulcus or fronto-marginal sulcus of Wernicke on the right side (this work) is named anterior horizontal ramus of Sylvian fissure by de Lumley and García Sánchez (1971) and de Lumley (1973), and subfrontal sulcus by Fusté (1956); e) lastly, the inferior frontal sulcus on the right side (defined in this work) is considered as the incisure of Broca's cap by de Lumley and García Sánchez (1971) and de Lumley (1973). Moreover, there are several imprints described previously, which we do not identify as sulci.

- ii) the local *absence of correspondence* between the brain and the endocast:
"there is frequent fusion of furrows on the cast which are separate on the brain, and continuous sulci of the brain are often represented as interrupted on the cast" (Connolly, 1950, p. 323), Once more, the new virtual reconstruction of the Carigüela endocast helps us to illustrate this aspect. The reduction of the number of identifiable sulci is particularly evident in comparison with the de Lumley and García Sánchez reconstruction [de Lumley and García Sánchez (1971), de Lumley (1973)]. Moreover, the drawings provided by these authors remind more of the cortical surface than the actual endocranial one.
- iii) the *intraspecific variability*, not only in the degree of imprints left by the brain on the inner table and associated brain-endocast correspondence, but also in brain sulcal patterning itself (Connolly, 1950), In fact and in spite of its fragmentary preservation, the Carigüela endocranial imprints show conspicuous left/right asymmetry. For instance, although *fi* is triradiate on both sides, *fm* is separate from *fi* on the right side while on the left one both fissures are continuous.
- iv) the uncertain inter-taxon *homology of sulci*, especially when dealing with fossils: we do not have any Neanderthal brain to make sure that Neanderthal sulci can be interpreted using the same sulcal system framework as modern humans, even though comparative anatomy of extant primate species contributed a lot to the knowledge of interspecific sulcal homology (Connolly, 1950),

- v) the *incompleteness* of the Carigüela endocast, which prevents a comprehensive view of the sulcal pattern for this specimen.

Concerning the sulcal pattern of the Carigüela frontal endocast, it is relevant to point out, like Fusté already did in 1956, that brain fissuration does not essentially depart from that in modern humans, and overall does not appear rougher as would have been expected apropos Neanderthals by some researchers, especially decades ago. Most notably, the Carigüela Broca's cap, likely corresponding to a brain region involved in speech production in modern humans, forms a protruding bulge as in most modern human endocasts.

In humans, Broca's cap has traditionally been ascribed to *pars triangularis*, the portion of inferior frontal gyrus comprised between ascending and horizontal rami of Sylvian fissure and corresponding to Brodmann Area BA 45 (Balzeau et al., 2014), even though broader definitions including the full inferior frontal gyrus have been proposed (Holloway et al. 2004b). However, recent digital mapping of the brain-endocast relationship in modern humans suggests that endocast Broca's cap rather corresponds to *pars orbitalis*, the part of the inferior frontal gyrus anterior to horizontal ramus of Sylvian fissure and corresponding to Brodmann Area BA 47 (see figure B3 in Zollikofer and Ponce de León, 2013). In a related way, the sulcus we identify as *fi* on the Carigüela frontal endocast has its main course contouring Broca's cap bulge anteriorly and superiorly, which is a valid identification only if Broca's cap indeed corresponds to *pars orbitalis*/BA 47 who is the most anterior end of inferior frontal gyrus. If our interpretation of Broca's cap and *fi* is correct, then the sulcus we label *fm* (or *W*) on the right side is too anterior to be the horizontal ramus of Sylvian fissure *R'* as suggested by de Lumley (1973). In the same way, the inferior branch of *fi* cannot be the incisure of Broca's cap *ic* either. Moreover, both Fusté (1956) and de Lumley (1973) observed the ascending ramus of Sylvian fissure in the very posterior end of the Carigüela frontal endocast. Not only we do not observe any sulcus in this location, but were it the case, we doubt this sulcus could correspond to the ascending ramus of Sylvian fissure, as the ascending ramus should be more posterior according to our view of the Carigüela sulcal pattern.

"Reduction" of the frontal lobes in Carigüela, as pointed by Fusté (1956) and de Lumley and García Sánchez (1971) and de Lumley (1973), should be nuanced. Indeed contour superimposition shows that the Carigüela frontal lobes are neither

narrower nor shorter than modern human frontal lobes. However, their dorsal surface appears lower and flatter, even more so than in other Neanderthals. Concluding that the Carigüela frontal lobes are reduced in height would be a shortcut though, as their orbital surface flares infero-laterally like in other Neanderthals. To sum up, compared to modern humans, what Neanderthals lose superiorly, they gain it inferiorly, as if there were a reallocation of the neural tissue. What it means in terms of brain functional differences between the two groups remains to be determined.

The Carigüela encephalic beak seems absolutely and relatively wider than in modern humans (Figure 4, anterior views). Its presumed projection in anterior view is visually exaggerated due to largely missing medial orbital surface. The preserved lateral orbital surfaces in Carigüela are indeed projecting more inferiorly than in modern humans, so that we predict that a complete orbital surface in Carigüela would make its encephalic beak appear even less protruding in anterior view than in modern humans. Infero-lateral projection of the orbital surface seems to be a consistent pattern within Neanderthals overall (Figure 4, anterior views). Moreover, in Carigüela as in other Neanderthals overall, the encephalic beak projects more anteriorly than in modern humans (Figure 4, lateral views). We believe that the sharpness of the encephalic beak in Neanderthals would be better characterized in lateral view (anterior projection of the beak) than it has been classically so far in anterior view: indeed the beak in anterior view is not more protruding in Neanderthals than it is in modern humans; instead it may even be more blunt.

Conclusions

The new virtual reconstruction of the Carigüela frontal bone has shown that a hiatus exists between the two main bone fragments, and that the left fragment representing the orbital region is located more medially and posteriorly than in the current physical reconstruction. A 3D geometric morphometric analysis of frontal bone shape in an comparative ontogenetic sample yields an individual age estimate for Carigüela in the range of 4-6 years (M1 fully erupted). Carigüela exhibits characteristic features of Neanderthal frontal bone morphology, such as a low squama and a wide nasal bridge. Overall, even though the Carigüela frontal endocast definitely falls within frontal endocranial *shape* variation known from the Neanderthal group, *structural* differences between Neanderthal and modern human frontal lobes are not as striking

as the conventional wisdom assumes. To illustrate this statement, we chose to manually refit a modern human endocranial model (picked up on purpose for its resemblance to Carigüela) onto the Carigüela frontal endocranial model (Figure 6). Registration was rigid with isometric scaling; modern human endocranial model had to be virtually grown from 1200 cc to 1500 cc. The Carigüela postmortem distortion is obvious in the flattened left frontal surface. Biological differences between Carigüela and the modern human endocranial model prevent any close registration. The anterior projection of the encephalic beak, flattening of the dorsal surface, and expansion of the orbital surface appear very clearly in Carigüela compared to the modern human endocranial model. We further compared the sulcal pattern around Broca's cap in both specimens (Figure 7). In Carigüela as in the modern human, Broca's cap is limited anteriorly by one sulcus (*fi*) with branches (united or separate) radiating in multiple directions. Anterior to *fi* is a sulcus (*fm* or *W*) which is subparallel to the most anterior branch of *fi*, and which may be continuous to or separate from it. To summarize, as for the frontal lobes, Neanderthals and modern humans have different endocranial shapes but a similar endocranial structure (endocranial imprints reflecting brain sulcal pattern). The relative independence between endocranial shape and structure in Neanderthals was already suggested by Connolly (1950, p. 349): "There appears to be no occasion, therefore, for seeking any special cranial condition peculiar to Neanderthal Man, such as platycephaly, influencing the formation of fissural markings".

Acknowledgements

We would like to thank Junta de Andalucía for giving access to Carigüela frontal bone. Also to the editors of this special issue, José Carrión, Clive Finlayson and Carles Lalueza-Fox for inviting us to contribute to this volume. This research has been funded by the Junta de Andalucía, Spain (Research Group HUM-607).

References

Balzeau, A., Gilissen, E., Holloway, R.L., Prima, S., Grimaud-Hervé, D., 2014. Variations in size, shape and asymmetries of the third frontal convolution in hominids: paleoneurological implications for hominin evolution and the origin of language. *Journal of Human Evolution* 76, 116-128.

Bruner, E., Holloway, R.L., 2010. A bivariate approach to the widening of the frontal lobes in the genus *Homo*. *Journal of Human Evolution* 58, 138-146.

Carrión, J.S., 1990. Tesis doctoral sobre análisis polínico en la Cueva de la Carihuela. Departamento de Biología Vegetal, Universidad de Murcia, Murcia (unpublished).

Carrión, J.S., 1992. Late Quaternary pollen sequence from Carihuela Cave, Southeastern Spain. *Review of Palaeobotany and Palynology* 71, 37-77.

Carrión, J.S., Munuera, M., Navarro, C., Burjachs, F., Dupré, M., Walker, M., 1999. Palaeoecological potential of pollen records in caves: the case of Mediterranean Spain. *Quaternary Science Reviews* 18, 67-78.

Connolly, C.J., 1950. External morphology of the primate brain. Charles C. Thomas, Springfield.

de Lumley, M.A., 1973. Anténéandertaliens et néandertaliens du bassin méditerranéen occidental européen (Études Quaternaires: Géologie, Paléontologie, Préhistoire, Mémoire n° 2). Editions du Laboratoire de Paléontologie Humaine et de Préhistoire, Marseille.

de Lumley, M.A., García-Sánchez, M., 1971. L'enfant néandertalien de Carigüela à Piñar (Andalousie). *L'Anthropologie* 75, 29-56.

Falk, D., 2009. The natural endocast of Taung (*Australopithecus africanus*): Insights from the unpublished papers of Raymond Arthur Dart, *Yearbook of Physical Anthropology* 52, 49-65.

Falk, D., Hildebolt, C., Vannier, M., 1994. Relationship of squamosal suture to asterion on external skull surfaces versus endocasts of pongids: Implications for Hadar Early Hominid AL 162-28. *American Journal of Physical Anthropology* 93, 435-439.

Fernández, S., Carrión, J.S., Fuentes, N., González-Sampériz, P., Montoya, E., Gil Romera, G., Vega Toscano, L.G., Riquelme, J.A., 2007. Palynology of Carihuela Cave, southern Spain: completing the record. *Geobios* 40: 75-90.

Fuste, M., 1956. Morfología cerebral de un ejemplar neandertalense procedente de la cueva de La Carigüela, Piñar (Granada). *Trabajos del Instituto 'Bernardino de Sahagún', de Antropología y Etnografía* XV-1, 27-39.

García-Sánchez, M., 1960. Restos humanos del paleolítico medio y superior y del eneolítico de Píñar (Granada). Trabajos del Insituto "Bernardino de Sahagún" de Antropología y Etnografía 15, 19-78.

García-Sánchez, M., Tillier, A.M., Garralda, M.D., Vega, G., 1994. Les dents d'enfant des niveaux moustériens de la grotte de Carihuela (Grenade, Espagne). *Paléo* 6, 79-88.

Gunz, P., Neubauer, S., Maureille, B., Hublin, J.-J., 2010. Brain development after birth differs between Neanderthals and modern humans. *Current Biology* 20(21), R921-R922.

Gunz, P., Bulygina, E., 2012. The Mousterian child from Teshik-Tash is a Neanderthal: a geometric morphometric study of the frontal bone. *American Journal of Physical Anthropology* 149, 365-379.

Gunz, P., Neubauer, S., Golovanova, L., Doronichev, V., Maureille, B., Hublin, J.-J., 2012. A uniquely modern human pattern of endocranial development. Insights from a new cranial reconstruction of the Neandertal newborn from Mezmaiskaya. *Journal of Human Evolution* 62, 300-313.

Holloway, R.L., Clarke, R.J., Tobias, P.V., 2004a. Posterior lunate sulcus in *Australopithecus africanus*: Was Dart right? | Sulcus lunatus postérieur chez *Australopithecus africanus*: Dart avait-il raison? *Comptes Rendus - Palevol* 3, 285-291.

Holloway, R.L., Broadfield, D.C., Yuan, M.S., 2004b. *The Human Fossil Record. Volume Three: Brain Endocasts - The Paleoneurological Evidence*. Wiley-Liss, Hoboken.

Jiménez-Arenas, J.M., Toro-Moyano, I., Margvelashvili, A., Ponce de León, M., Alba-Tercedor, J., Carrión, J., Cortés, M., Lalueza-Fox, C., Riquelme, J.A., Zollikofer, C.P.E., 2016. Digging in the museum: Preliminary report on three unpublished Neanderthal teeth from Carigüela Cave (Píñar, Granada, Spain). *American Journal of Physical Anthropology* 159(S62), 185-186.

Ponce de León, M.S, Bienvenu, T., Akazawa, T., Zollikofer, C.P., 2016, Brain development is similar in Neanderthals and modern humans. *Current Biology* 226, R665-666.

Trinkaus, E., 2006. Modern Human versus Neandertal evolutionary distinctiveness. *Current Anthropology* 47, 597-620.

Vega Toscano, L.G., 1988. *El Paleolítico medio del sureste español y Andalucía oriental*. PhD Dissertation. Departamento de Prehistoria, Universidad Complutense, Madrid (unpublished).

Zollikofer, C.P.E., Ponce de León, M.S., 2013. Pandora's growing box: Inferring the evolution and development of hominin brains from endocasts. *Evolutionary Anthropology* 22, 20-33.

Zollikofer, C.P.E., Bienvenu, T., Ponce de León, M.S., 2017. Effects of cranial integration on hominid endocranial shape. *Journal of Anatomy* 230, 85-105.

Figure legends

Figure 1: Carigüela frontal bone (yellow). The Gibraltar 2 Devil's Tower frontal bone (gray semi-transparent) is superimposed onto Carigüela via rigid registration and isometric scaling to complete missing parts. From left to right: right lateral view, left lateral view, superior view, inferior view, anterior view, posterior (endocranial) view. Scalebar 10 cm.

Figure 2: Geometric-morphometric analysis of shape variation of the inferior portion of the frontal bone. The graph shows variation in shape space along PC1 and PC2. Colors indicate taxonomic affiliation; Neanderthals (filled black circles), Carigüela (black square), modern humans (open circles), *H. heidelbergensis* (black-gray), *H. erectus* (gray). Marker sizes are proportional to endocranial volume. The human sample comprises fetal to adult specimens; the Neanderthal sample comprises specimens with dM1 erupted to adult specimens. Landmarks used for shape analysis are nasion, glabella, maxillofrontale R/L, foramen supraorbitale R/L, frontomale orbitale R/L, pterion R/L, mid nasion-bregma, and foramen caecum. The 3D-visualizations are based on the frontal bone of the Gibraltar 2 (Devil's Tower) specimen. Only parts preserved in Carigüela are shown. PC1 characterizes intraspecific shape change along ontogenetic trajectories, as well as interspecific variation from paedomorphic (left) to peramorphic (right) shapes. Note that Neanderthals assume an intermediate position in shape space between paedomorphic modern humans and peramorphic *H. erectus/heidelbergensis*. PC2 characterizes variation between high and low frontal squamae independent of ontogenetic stage.

Figure 3: Carigüela frontal endocranial surface. Blue side, endocast (convex face); yellow side, endocranial cavity (concave face). From left to right: right lateral view, left lateral view, superior view, inferior view, anterior view, posterior view (as it is a frontal portion, posterior view shows the endocranial cavity and not the endocast). Upper row, specular appearance. Lower row, matte appearance with sulci displayed as thin flexible tubes and tentatively identified. Sulci colors: red, interhemispheric fissure; purple, major sulci (longer/deeper furrows on the endocast) on the lateral frontal surface; orange, orbital sulci; green, secondary sulci (short/shallow dimples on the endocast) on the lateral frontal surface. Sulci abbreviations (most following Connolly 1950): *fi*, inferior frontal sulcus; *fm*, middle frontal sulcus; *fs*, superior frontal sulcus; *ic*, incisure of Broca's cap; *ihf*, interhemispheric fissure; *R'*, anterior horizontal ramus of Sylvian fissure; *sf*, subfrontal sulcus; *W*, fronto-marginal sulcus of Wernicke. Labelling in parentheses corresponds to sulcal identifications from de Lumley and García Sánchez (1971) and de Lumley (1973; black font) when different from our own interpretations, and from Fusté (1956; gray font) when different from our own and de Lumley and García Sánchez's interpretations. Scalebar 10 cm.

Figure 4: Superimposed projected endocranial contours in right lateral (left column), inferior (middle column) and anterior (right column) views (see text for sample). For contours in anterior view, the posterior portions of endocasts from the level of temporal poles were removed so as to retrieve contours corresponding to the frontal lobes only. Blue contours correspond to modern humans, red contours to Neanderthals. The Carigüela endocranial surface is displayed with dull colors in the background of each contour superimposition, and its projected contours are highlighted in bold red. Endocasts were oriented in right lateral view with frontal and occipital poles defining the horizontal (approximate orientation for Carigüela, as the occipital poles are not preserved). Then the midsagittal planes of all endocasts were superimposed (dashed line) and endocasts were aligned with their frontal poles abutting the same coronal plane (dotted line) and the inferior point of the olfactory bulb adjacent to the same transverse plane (dashdotted line). a, unscaled contours. Scalebar 10 cm. b, contours scaled relative to maximum frontal length. c, contours scaled relative to maximum frontal width.

Figure 5: Graph representing endocranial outline dimensions. Neanderthals are in red, modern humans are in blue. Carigüela is represented by the star symbol. Regression lines: solid lines, frontal length vs frontal width; dotted lines (and empty symbols), frontal length vs frontal height; dashed lines, frontal width vs frontal height. Engis 2 and Roc de Marsal frontal width was measured for the right hemisphere to the midsagittal plane, then doubled. Carigüela frontal height was measured after reconstruction of the missing portions with the Gibraltar 2 Devil's Tower specimen (see Figure 1).

Figure 6: Upper row: Carigüela frontal endocranial surface (red, front face of the surface = endocast; black, back face of the surface = endocranial cavity). Second row from top: modern human endocast (cranial specimen of presumed similar age as Carigüela with first molar erupted). Scalebar for upper two rows: 10 cm. Third row: same modern human endocast (gray) manually rotated, translated and isometrically scaled to fit the Carigüela frontal endocranial surface (red). Bottom row: same as third row with modern human endocast semi-transparent; Carigüela endocranial cavity appears through transparency as black color. From left to right: right lateral view, left lateral view, superior view, inferior view, anterior view.

Figure 7: Upper row: modern human endocast (same specimen as in Figure 6). Lower row: Carigüela frontal endocranial surface (blue, front face of the surface = endocast; yellow, back face of the surface = endocranial cavity). Sulcal pattern around Broca's cap (BC) is highlighted with purple tubes. *fi*, inferior frontal sulcus; *fm*, middle frontal sulcus. Scalebar: 10 cm. From left to right: right lateral view, anterior view, left lateral view.

Table 1: Comparative sample structure for the geometric morphometric analysis of the frontal bone, summarized per species and age class.

	fetus	neonate	dM1	dM2	M1	M2	M3	Total
<i>H. erectus</i>	—	—	—	—	—	2	6	8
<i>H. heidelbergensis</i>	—	—	—	—	—	—	2	2
<i>H. neanderthalensis</i>	—	—	2	5	2	1	4	14
<i>H. sapiens</i>	10	6	4	17	10	8	8	63