



**HAL**  
open science

## **A reappraisal of the Border Cave 1 cranium (KwaZulu-Natal, South Africa)**

Amélie Beaudet, Lucinda Backwell, Lyn Wadley, Bernhard Zipfel, Paloma de la Peña, Hugo Reyes-Centeno, Francesco D'errico

### ► **To cite this version:**

Amélie Beaudet, Lucinda Backwell, Lyn Wadley, Bernhard Zipfel, Paloma de la Peña, et al.. A reappraisal of the Border Cave 1 cranium (KwaZulu-Natal, South Africa). *Quaternary Science Reviews*, 2022, 282, pp.107452. <10.1016/j.quascirev.2022.107452>. <hal-03860970>

**HAL Id: hal-03860970**

**<https://hal.science/hal-03860970v1>**

Submitted on 5 Jun 2025

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization


---

This is the **accepted version** of the journal article:

Beaudet, Amélie; D'Errico, Francesco; Backwell, Lucinda; [et al.]. «A reappraisal of the Border Cave 1 cranium (KwaZulu-Natal, South Africa)». *Quaternary Science Reviews*, Vol. 282 (April 2022) art. 107452. DOI 10.1016/j.quascirev.2022.107452

---

This version is available at <https://ddd.uab.cat/record/257654>

under the terms of the  <sup>IN</sup> COPYRIGHT license

1 **Title**

2 A reappraisal of the Border Cave 1 cranium (KwaZulu-Natal, South Africa)

3

4 **Authors**

5 Amélie Beaudet<sup>1,2,3\*</sup>, Francesco d’Errico<sup>4,5</sup>, Lucinda Backwell<sup>6,7,8</sup>, Lyn Wadley<sup>6</sup>, Bernhard  
6 Zipfel<sup>6</sup>, Paloma de la Peña<sup>6,8,9</sup>, Hugo Reyes-Centeno<sup>10,11\*</sup>

7

8 **Affiliations**

9 <sup>1</sup>Department of Archaeology, University of Cambridge, Cambridge, UK

10 <sup>2</sup>School of Geography, Archaeology and Environmental Studies, University of the  
11 Witwatersrand, Private Bag 3, WITS, 2050, South Africa

12 <sup>3</sup>Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona,  
13 Barcelona, Spain

14 <sup>4</sup>UMR 5199 CNRS De la Préhistoire à l’Actuel : Culture, Environnement, et Anthropologie  
15 (PACEA), Université Bordeaux, Talence, France

16 <sup>5</sup>SFF Centre for Early Sapiens Behaviour (SapienCE), University of Bergen, Bergen, Norway

17 <sup>6</sup>Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa

18 <sup>7</sup>Instituto Superior de Estudios Sociales (ISES-CONICET), Tucumán, Argentina

19 <sup>8</sup>Centre of Exploration for the Deep Human Journey, University of the Witwatersrand,  
20 Johannesburg, South Africa

21 <sup>9</sup>McDonald Archaeological Research Institute, University of Cambridge, Cambridge, UK

22 <sup>10</sup>Department of Anthropology, University of Kentucky, Lexington, Kentucky, USA

23 <sup>11</sup>William S. Webb Museum of Anthropology, University of Kentucky, Lexington, Kentucky,  
24 USA

25

26 **Keywords**

27 Middle Stone Age; South African fossil record; Hominin brain; Bony labyrinth; Cranial vault  
28 thickness

29

30 **Corresponding authors\***

31 A. Beaudet – aab88@cam.ac.uk

32 H. Reyes-Centeno – hugo.reyes-centeno@uky.edu

33

34 **Highlights**

- 35 • Border Cave 1 cranium, found in 1940-42, comes from alleged MSA deposits.
- 36 • In this paper we present a computer-assisted reappraisal of the Border Cave 1 cranium.
- 37 • The brain endocast has a globular shape similar to extant humans.
- 38 • Bone thickness distribution resembles that of Late Pleistocene fossil hominins.
- 39 • The semi-circular canals of the bony labyrinth show an ancestral configuration as
- 40 compared to the derived condition seen in Neanderthals.

41

## 42 **Abstract**

43 Besides providing a unique archaeological assemblage that documents the early emergence of  
44 complex behaviour in the human lineage, Border Cave (South Africa) is noteworthy for having  
45 yielded hominin remains of at least nine individuals, including the partial cranium Border Cave  
46 1. While the exact provenance of Border Cave 1 is unknown, sequence stratigraphy and ESR  
47 dating converge towards an age from about 82 to 170 ka. Here we present novel information  
48 about the brain, braincase and bony labyrinth of Border Cave 1 and discuss related evolutionary  
49 implications. We compare Border Cave 1 to specimens of Early and Middle Pleistocene *Homo*  
50 as well as to fossil and extant *Homo sapiens*. Virtual segmentation techniques were used to  
51 reconstruct the brain and bony labyrinth endocasts, assess the distribution of cranial bone  
52 thickness, and identify the vascular and sulcal imprints preserved on the inner surface of the  
53 braincase. Our results show that the overall morphology of the brain endocast approximates the  
54 globular shape of the modern human brain and differs from the long and low brains seen in  
55 Middle Pleistocene fossil hominins. The vascular imprints preserved on the right hemisphere  
56 indicate that the middle branch derives from the anterior branch, which is a pattern shared with  
57 Neanderthals and modern humans. Bone thickness distribution in the Border Cave 1 cranium  
58 resembles the patterns seen in Cro-Magnon 1 and Abri Pataud 1, which both share a diffuse  
59 distribution of thickened areas over the frontal region. Finally, the relative size and curvature  
60 of the semi-circular canals of the bony labyrinth conform to the ancestral configuration shared  
61 between Early and Late Pleistocene fossil hominins from Africa and the Levant, as well as  
62 modern humans, and distinct from the more derived condition documented within  
63 Neanderthals. We discuss the implications of our findings for understanding the biogeography,  
64 evolution, and, to some extent, behaviour of fossil *Homo sapiens*.

65

66

67

## 1. Introduction

Border Cave is a rock shelter located in KwaZulu-Natal (South Africa), about 400 m from the eSwatini border (Backwell et al., 2018). This site, which preserves deposits documenting about 250,000 years of cultural evolution with Middle and Late Stone Age occupations, has been successively excavated by Dart (1934), Cooke, Malan and Wells (1941-1942), Beaumont (1970-1975, 1987), Todd and Miller (1987) and Backwell, Wadley and d'Errico (since 2015) (rev. in Backwell et al., 2018). In addition to scientific activities, extraction of bat guano in 1940 exposed human remains and archaeological artefacts that were left in what is commonly referred to as Horton's dump. The sequence at Border Cave comprises 11 members (as defined by Beaumont 1978, 1994; Beaumont et al. 1978, 1992, see also Table 2 from Backwell et al., 2018) dated from  $227 \pm 11$  ka to 41.1-24 ka using electron spin resonance (ESR) and radiocarbon ( $^{14}\text{C}$ ) methods (d'Errico et al., 2012; Villa et al., 2012; Bird et al., 2003; Grün and Beaumont, 2001; Grün et al., 2003). In total, nine human individuals have been uncovered, including a nearly complete infant skeleton (Cooke et al., 1945; de Villiers, 1973; Tommy et al., 2021). The archaeological record from Border Cave illustrates the emergence of critical cultural innovations. In particular, the successive excavations revealed the presence of the earliest human burials associated with personal ornaments (i.e., the grave of an infant with a perforated *Conus* shell dated to 74 ka, Cooke et al., 1945; Grün and Beaumont 2001; Grün et al. 2003; d'Errico and Backwell, 2016), the early occurrence of Early Later Stone Age artefacts (Beaumont, 1978; d'Errico et al., 2012; Villa et al., 2012), and the use of grass bedding placed above ash layers before 200 ka (Wadley et al., 2020; for an overview see Backwell et al., 2018, this issue).

Bone fragments attributed to the Border Cave 1 (BC 1) cranium were found in Horton's dump (Figure 1A) during the excavations led by Cooke and colleagues from 1940 to 1942 (Cooke et al., 1945; rev. in de Villiers, 1973). Judging by the stratigraphy and the deposits exposed by Horton's excavations (Figure 1B), Cooke et al. (1945, p. 9) stated that 'It is [therefore] highly probable that this skull belongs at the latest to the uppermost phase of the Middle Stone Age occupation'. Moreover, based on the presence of adhering sediments (Beaumont et al., 1978; Beaumont, 1980), BC 1 has been suggested to derive from members 4 BS or 5 BS, dated respectively to  $77 \pm 2$  and to  $161 \pm 10 - 144 \pm 11$  ka (Grün and Beaumont 2001; Grün et al. 2003). Nonetheless, the hypothesis of a younger age has also been considered on the basis of its exceptional preservation in comparison to poorly preserved non-human faunal material derived from stratified MSA contexts (rev. in Grine, 2016). BC 1 preserves the frontal

102 bones and fragments of the parietal, temporal (including mastoid, tympanic and petrous parts)  
103 and occipital bones, and the right zygomatic. The cranium has been reconstructed using plaster  
104 by A.R. Hughes (Rightmire, 1979). Interestingly, the cranial morphology of BC 1,  
105 characterized by a broad frontal, glabellar protrusion and prominent superciliary eminences  
106 (Rightmire, 1979; Corruccini, 1991), has been described and interpreted as being either similar  
107 (e.g., de Villiers, 1973; Rightmire, 1979; Houghton and Thackeray, 2011) or different (e.g.,  
108 Campbell, 1984; Ambergen and Schaafsma, 1984; Van Vark et al., 1989; Corruccini, 1991)  
109 from extant *Homo sapiens*.

110 The African Middle Stone Age featured as pivotal in the evolutionary scenarios of  
111 human behaviour, as illustrated by the emergence of cultural innovations such as abstract  
112 engravings and drawings (e.g., Henshilwood et al., 2002, 2018), personal ornaments (e.g.,  
113 d’Errico and Backwell, 2016), or the use of mineral pigments (e.g., use of ochre, rev. in  
114 Hodgskiss, 2020). Two main models have been considered when tracking the origins of  
115 behavioural modernity; one that supports the idea of a biocultural ‘revolution’ in relation to the  
116 emergence and spread of modern *Homo sapiens* and specific cognitive abilities (e.g., Klein,  
117 2000), and a second model that relies on a more gradual process in response to external factors  
118 (rev. in McBrearty and Brooks, 2000; Scerri et al. 2018). The study of brain and cognition in  
119 fossil humans, and *in fine* the question of the nature and origins of the neural substrate  
120 associated with such behavioural innovations, has the potential to contribute to this debate  
121 (Bruner, 2021). For instance, the reconstruction and analysis of the brain endocast of fossil  
122 *Homo sapiens* specimens has demonstrated that the globular shape that characterizes the extant  
123 human brain emerged gradually over the last 100 ka, thus contradicting the hypothesis of a  
124 sudden event associated with a biocultural revolution (Neubauer et al., 2018). The modern  
125 human globular brain has been suggested to result from parietal and cerebellar bulging, and the  
126 onset of a specific phase (‘globularization’) during postnatal development (Bruner et al., 2003;  
127 Neubauer et al., 2018; Gunz et al., 2019). Because parietal areas and the cerebellum are  
128 involved in critical functions such as the coordination of movements, working and long-term  
129 memory, planning, language, or visuospatial integration, Neubauer et al. (2018) raised the  
130 possibility that brain globularization may have played a role in the emergence of behavioural  
131 innovations. Falsifying or verifying this hypothesis requires further investigation of the shape  
132 and organisation of fossil *Homo sapiens* brain endocasts, which is the primary material source  
133 of evidence for reconstructing hominin brain evolution, along with archaeological material,  
134 which represent a key source of information about past cognition. In addition to brain endocasts,

135 the patterning of cranial vault thickness may also reflect variation in the brain external surface  
136 (Balzeau, 2013; Anzelmo et al., 2015).

137 From a biological perspective, the temporal and spatial origins of *Homo sapiens* and  
138 emergence of human features have been a matter of intense discussions for decades. Iconic  
139 specimens like those of Qafzeh and Skhūl from the Middle East, dated respectively to ca. 82  
140 and 100 ka, those from Klasies River Mouth (88-93 ka), Florisbad (259 ka) and Border Cave  
141 in South Africa, and from Omo Kibish (195 ka) and Herto (154-160 ka) in Ethiopia, featured  
142 prominently in these debates until the discovery of new remains from the site of Jebel Irhoud  
143 in Morocco dated to 315 ka (Stringer, 2016; Hublin et al., 2017). From that point in time, a  
144 combination of factors has shaped human diversity and spatial distribution. Processes involved  
145 consist of a succession of expansion, dispersal, extinction and structuration events, influenced  
146 by climate change (Mirazón Lahr, 2016; d’Errico et al., 2018). Genetic, archaeological and  
147 palaeoanthropological evidence support the dispersal of *Homo sapiens* from Africa in multiple  
148 waves (rev. in Reyes-Centeno, 2016 and Tucci & Akey, 2016; Beyer et al., 2021). However,  
149 less is known about the polarity, timing and pattern of dispersals of *Homo sapiens* within Africa  
150 and the relative contribution of the different continental regions to the emergence of our lineage.  
151 One of the crucial aspects would be to determine if data from various sources could support or  
152 discard a possible African multiregional model and the possibility of structured populations  
153 living across the continent before the main out-of-Africa migration of modern humans (Scerri  
154 et al., 2018; Rito et al., 2019; Bergström et al., 2021). Besides its potential for discussing  
155 taxonomic status and phylogenetic relationships of fossil hominins, the morphology of the bony  
156 labyrinth has also been demonstrated to be a reliable marker for tracking modern human  
157 dispersals (Ponce de León et al., 2018); as such, the characterization of fossil human bony  
158 labyrinths should shed light on the migration patterns of *Homo sapiens* across and outside  
159 Africa.

160 The form of the brain and bony labyrinth are hypothesized to have co-evolved in *Homo*,  
161 with the configuration of the labyrinth and surrounding petrous pyramid linked to brain  
162 evolution via the spatial demands of the cerebellum in the posterior fossa and attachment of the  
163 tentorium cerebelli to the superiopetrosal margin (Spoor, 1997; Spoor et al., 2003). Given its  
164 geographical and chronological context, BC 1 has the potential to play a key role in our  
165 understanding of the evolution and behaviour of *Homo sapiens*, particularly since it is one of  
166 few well-conserved fossils retaining both the neurocranial and bony labyrinth structures with  
167 an associated archaeological record. Here we present novel information about the braincase

168 (i.e., brain endocast and cranial vault thickness) and the bony labyrinth of Border Cave 1 and  
169 discuss related evolutionary and potential behavioural implications.

170

## 171 **2. Materials and Methods**

172

### 173 *2.1. Materials*

174

175 The Border Cave 1 cranium (Figure 2) is housed in the Evolutionary Studies Institute at the  
176 University of the Witwatersrand (South Africa). Permission to study the specimen has been  
177 granted by the Fossil Access Advisory Panel of the Evolutionary Studies Institute of the  
178 University of the Witwatersrand. The brain of BC 1 was compared to brain endocasts of recent  
179 adult human crania curated in the Pretoria Bone Collection (L'Abbé et al., 2005) at the  
180 University of Pretoria (South Africa) (Beaudet et al., 2019) and fossil specimens for which we  
181 could reconstruct or access the brain endocast (i.e., Olduvai Hominin 9 (OH 9), Dinaledi  
182 Hominin 1 (DH 1), Bodo and Cro-Magnon 1; see Table 1 for additional details). Additionally,  
183 we used published descriptions of fossil brain endocasts and cranial vault thickness, as well as  
184 published measurements of fossil bony labyrinths from Early and Middle Pleistocene *Homo*  
185 along with fossil and extant *Homo sapiens* (Table 1).

186

### 187 *2.2. Methods*

188

189 The Border Cave 1 cranium was scanned at the microfocus X-ray tomography facility of the  
190 Palaeosciences Centre at the University of the Witwatersrand (South Africa), at a spatial  
191 resolution of 117.4  $\mu\text{m}$  (isotropic voxel size). Digital data of OH 9 and Bodo were provided by  
192 the Institute of Anthropology, University of Vienna (Austria) through the Digital Archive of  
193 Fossil Hominoids project and were scanned at Innsbruck (Austria) at a resolution of  
194 0.47x0.47x1 mm and of 0.49 x 0.49x1 mm, respectively). The cranium of Cro-Magnon 1 was  
195 scanned in Paris (France) with a resolution of 0.45x0.45x1 mm. The endocast of DH 1 was  
196 downloaded from MorphoSource (<http://n2t.net/ark:/87602/m4/M48481>).

197 The virtual brain endocasts were extracted from the BC 1, OH 9, Bodo and Cro-Magnon  
198 crania by using Endex software (Subsol et al., 2010; <http://liris.cnrs.fr/gilles.gesquiere/wiki/doku.php?id!4endex>). Sulcal and vascular imprints  
199 were automatically detected using a method for the detection of topographic variation in 3D  
200 meshes (Yoshizawa et al., 2007, 2008; Beaudet et al., 2016, 2019; de Jager et al., 2019;  
201

202 Dumoncel et al., 2021). The 3D surface of Border Cave 1 was also registered with the 3D  
203 surface of Cro-Magnon 1 for further comparison using the ‘Align’ module of Avizo v9.0  
204 software (Visualization Sciences Group Inc.)

205 To investigate topographic cranial vault thickness distributions in BC 1, a 3D colour  
206 map was generated using the ‘Surface Distance’ module of Avizo v9.0. This module  
207 automatically calculates distances between the inner and the outer cranial surfaces. The colour  
208 map was rendered on the outer surface using a colour scale ranging from dark blue (‘thinner’)  
209 to red (‘thicker’) (Beaudet et al., 2018).

210 The bony labyrinth morphology was reconstructed using Avizo v9.0 software. In this study  
211 we focused primarily on the semicircular canals. Measurements were taken in Avizo v2002.3.1  
212 (Thermo Fischer Scientific), following the protocols of Gunz et al. (2012) and Uhl et al. (2016),  
213 which consists of identifying the midpoint of the lumen in order to pinpoint landmarks defining  
214 the height and width of the labyrinth semicircular canals (Spoor, 1993; Spoor & Zonneveld,  
215 1995). Raw measurements were transformed into shape indices, retaining variables that  
216 maximized the number of fossil samples that could be included for comparison. In total, seven  
217 indices were used, including those conveying the arc of each semicircular canal (ASCh/w,  
218 PSCh/w, and LSCh/w), the sagittal labyrinth index (SLI), and the radius of curvature of each  
219 semicircular canal relative to the total canal radii (ASC%R, PSC%R, and LSC%R). These  
220 variables were used to explore shape affinities in a Principal Component Analysis (PCA),  
221 performed using PAST software (v4.05, Hammer et al., 2001). BC 1 was treated as an unknown  
222 specimen and projected onto the PCA space comprising the comparative sample.

223

### 224 **3. Results**

225

#### 226 *3.1. Brain endocast of BC 1*

227

##### 228 3.1.1. General description

229

230 This is an incomplete endocast lacking both temporal lobes and the entire ventral surface. There  
231 is no major distortion (Figure 3). The dorsal surface of the prefrontal cortex is relatively well  
232 preserved, notwithstanding a large crack that runs obliquely from the right posterior gyrus to  
233 the left inferior gyrus. The lateral surface of the left parietal lobe is preserved whereas the entire  
234 right parietal lobe is absent. A remnant of the left occipital lobe is visible. The endocast is  
235 overall rounded (i.e., rostro-caudally short and ventro-dorsally tall).

236 The frontal lobes are relatively broad as in Middle and Late Pleistocene human  
237 specimens such as Bodo and Cro-Magnon (Figure 3) and not pointed as in early Pleistocene  
238 hominins (Falk et al., 2000; Holloway et al., 2004; Beaudet et al., 2019). The overall shape of  
239 the endocast approximates the globular shape illustrated in our sample by Cro-Magnon (Figure  
240 S1) and the extant human individual (Figure 4), and by the endocast of Hofmeyr based on  
241 Figure 10 published by Grine et al. (2010). However, it differs from the rostro-caudally long  
242 and ventro-dorsally low endocasts seen in the Middle Pleistocene fossil hominins (e.g., *Homo*  
243 *erectus s.l.* OH 9 and *Homo naledi* DH 1 Figure 3, but also in KNM-ER 3733, KNM-WT 15000,  
244 Ngandong 14, Sambungmacan 3, Sangiran 2, Broken Hill 1, Sima de los Huesos, see Holloway  
245 et al., 2004, Poza-Rey et al., 2019), from Neanderthals (e.g., Amud 1, La Chapelle-aux-Saints  
246 1, La Ferrassie 1, Gánovce; see Holloway et al., 2004; Ogihara et al., 2017; Eisoova et al., 2019)  
247 and from the Middle Pleistocene specimens Jebel Irhoud 1 and 2, recently assigned to *Homo*  
248 *sapiens* (see Holloway et al., 2004; Neubauer et al., 2018).

249

### 250 3.1.2. Sulcal imprints

251

252 The fronto-marginal sulcus makes an incision in the left orbital margin (Figure 4A). Two  
253 furrows are detected on the dorsal surface of the left frontal lobe that might be remnants of the  
254 superior frontal sulci. Ventrally to the superior frontal sulci are two ventrodorsally-oriented  
255 furrows. The most rostral one could possibly be identified as part of the inferior frontal sulcus.  
256 The furrow that nearly connects the two vertical imprints might be part of the inferior frontal  
257 sulcus (following the pattern seen in Connolly, 1950 p. 186 Figure 132). Rostral to this series  
258 of furrows is a vertical imprint identified as the precentral sulcus. The caudal portion of the left  
259 parietal surface preserved is particularly convoluted. The most ventral sulcus, which is  
260 markedly arched, is identified as the caudal end of the middle temporal sulcus (a3 in Connolly,  
261 1950). The furrows located ventral to the middle temporal sulcus could be part of the superior  
262 temporal sulcus (a2 in Connolly, 1950; see pattern 236 p. 226). If this identification is correct,  
263 the bulge that is visible immediately above might correspond to the angular gyrus. On the right  
264 hemisphere, remnants of sulci are detected but are difficult to identify.

265 The sulcal pattern in Border Cave 1 does not show any substantial differences with the  
266 extant human sulcal pattern (i.e., spatial relationships between sulci, Connolly, 1950; de Jager  
267 et al., 2019) nor with fossil human specimens for which sulcal imprints are described (e.g., the  
268 *Homo naledi* specimen DH 3, the fossil *Homo sapiens* specimen Manot 1, Holloway et al.,  
269 2018; Grimaud-Hervé et al., 2020).

270

271 3.1.3. Vascular imprints

272

273 Vascular imprints that correspond to the middle meningeal vessels were detected on both  
274 hemispheres (Figure 4B). On the left hemisphere, the anterior branch runs from the temporo-  
275 orbital notch to the parietal lobe and bifurcates. The middle branch is connected to the anterior  
276 branch and stretches from the temporo-orbital notch to the dorsal part of the parietal lobe, above  
277 the intra-parietal sulcus. The frontal branch is well-developed and covers most of the rostral  
278 part of the frontal lobe. The posterior branch extends to the posterior lobe and is almost  
279 orthogonal to the anterior branch. Arborization of the posterior branch is observed and covers  
280 the region of the angular and supramarginal gyri. Traces of the middle and posterior branches  
281 are visible on the right hemisphere, but the branching pattern cannot be assessed as most of the  
282 parietal is missing. The transverse sinus is visible on both hemispheres.

283 In the Border Cave 1 endocast, both the anterior and posterior branches of the middle  
284 meningeal vessels are reticulated. In the left hemisphere, the middle branch derives from the  
285 anterior branch. As such, BC 1 is close to Neanderthals and modern humans in showing a more  
286 developed anterior branch from which the middle branch arises and a posterior branch nearly  
287 orthogonal to the anterior branch (Grimaud-Hervé, 1997; Grimaud-Hervé et al., 2000; Bruner  
288 et al., 2005), and differs from *Homo erectus* and *Homo naledi*, in which the middle branch  
289 derives from the posterior branch (Grimaud-Hervé, 1997; Grimaud-Hervé et al., 2000;  
290 Holloway et al., 2018), as well as from Florisbad, in which the posterior branch is more  
291 developed (Bruner and Lombard, 2020). In particular, this pattern (i.e., the fact that the middle  
292 branch derives from the anterior branch) is shared with Jebel Irhoud 1 and 2, Broken Hill 1,  
293 Salé, Omo 2, as and La Ferrassie 1 (Grimaud-Hervé, 2004).

294

295 3.2. *Cranial vault thickness distribution in BC 1*

296

297 The colour map in Figure 5 reveals that the frontal bone is particularly thick compared to the  
298 preserved portions of the parietal bones. In terms of thickness distribution, the maximum values  
299 are confined to the midline of the most anterior part of the frontal bone while the posterior  
300 regions show a more heterogeneous pattern with thickened areas being widely distributed.  
301 When compared to the cranial vault thickness cartographies of fossil hominins published in  
302 Balzeau (2013) and Beaudet et al. (2018), bone thickness distribution in the Border Cave 1  
303 cranium resembles the patterns seen in Cro-Magnon 1 and Abri Pataud 1, which both share a

304 diffuse distribution of thickened areas over the frontal region. However, it differs from the  
305 extant human condition that is characterized by a thickened area located in the bregmatic area  
306 (Balzeau, 2013; Beaudet et al., 2018).

307

### 308 3.3. *Bony labyrinth of BC 1*

309

#### 310 3.3.1. General description

311

312 The bony labyrinth endocast of Border Cave 1 is complete and retains all components of the  
313 semicircular canals, the vestibule, and the cochlea (Figure 6). While some details like the  
314 ampullae are well defined, others such as the oval window and shape of vestibule are less clearly  
315 demarcated. All canals exhibit a relatively high degree of torsion and the posterior canal, in  
316 particular, is relatively large and laterally extended, reminiscent of the condition in the Late  
317 Pleistocene hominin from Ishango, Democratic Republic of Congo (Crevecoeur et al., 2016).

318

#### 319 3.3.2. Multivariate analysis

320

321 Shape index values are reported in Figure 7 alongside the corresponding PCA plot. Therein,  
322 Neanderthals and modern Middle Pleistocene hominins from Eurasia are largely separated from  
323 recent Holocene *Homo sapiens* and *Homo erectus* along the main axis of variation (PC 1; Figure  
324 7). This separation is driven in large part by measures of the lateral canal (loadings: LSC%R =  
325 0.63, LSCh/w = 0.44), as well as the sagittal labyrinthine index (loading: SLI = 0.24)—a  
326 derived trait in Neanderthals (Spoor et al., 2003). While the Qafzeh-Skhūl series of early Late  
327 Pleistocene *Homo sapiens* is also largely separated from Neanderthals along PC 1, the Late  
328 Pleistocene *Homo sapiens* fossils are widely distributed. Along PC 2, the recent Holocene  
329 sample is largely separated from the *Homo erectus* specimens. When delimiting the  
330 comparative samples with convex hulls along the major axes of variation, Border Cave 1 is  
331 outside the range of all groups. It occupies a space characterizing labyrinths with relatively  
332 large, curved posterior canals (loading: PSC%R = -0.44) and is close to the OH 9 fossil from  
333 eastern Africa.

334

## 335 4. Discussion

336

337 Given the scarcity of fossil hominins attributed to *Homo sapiens* in Africa, Border Cave 1  
338 provides a unique opportunity to learn more about the evolution of this taxon. Here we discuss  
339 the implications of our results for (i) better understanding the evolution of the human brain and  
340 inner ear, and (ii) reconstructing the behavioural evolution of *Homo sapiens*.

341

#### 342 4.1. Human brain evolution

343

344 Our study of the brain endocast of BC 1 reveals a globular shape. If BC 1 is older than 120 ka,  
345 which is possible given the chronological range considered for this specimen (i.e., up to 170  
346 ka, Grün and Beaumont, 2001; Grün et al., 2003), this would imply that this specificity of our  
347 brain (also pointed out by Bruner et al., 2003 in their analysis of the evolutionary changes in  
348 the parietal and temporal regions) may have emerged earlier than previously suggested by  
349 published shape analysis of the endocasts of Middle and Late Pleistocene *Homo* specimens  
350 (Neubauer et al., 2018). Indeed, within this scenario, BC 1 would be grouped in the  
351 aforementioned paper within the geological age group 1, which is characterized by an elongated  
352 brain intermediate between *Homo erectus* and Neanderthals. If our results are confirmed by  
353 further quantitative analyses, the evolutionary history of the human brain might be more  
354 complex and would include an early emergence of the derived shape in some human groups  
355 during the Middle Pleistocene, supporting the idea that modern human traits may have evolved  
356 independently in different African regions due to semi-isolation of populations (Scerri et al.,  
357 2018). If BC 1 instead dates to a more recent time period (Klein, 1983), then it cannot be used  
358 to falsify the hypothesis of an early emergence of a globular brain. However, it will support  
359 model of a gradual change towards the derived shape observed in present-day humans and Late  
360 Pleistocene humans, providing a better idea of how the southern African human material fits  
361 within evolutionary scenarios of the human brain. Nonetheless, a reconstruction of the endocast  
362 of BC 1 coupled with morphometric geometric analyses would be necessary for our results to  
363 be directly comparable to Neubauer et al. (2018). Moreover, it is noteworthy that our study also  
364 revealed a modern pattern in terms of brain organization (sulcal imprints) and vascularization  
365 (middle meningeal vessel imprints). Additionally, the distribution of the cranial bone  
366 thickness similar to the topography of Cro-Magnon 1 (Balzeau, 2013).

367

#### 368 4.2. Human inner ear evolution

369

370 The analysis of the bony labyrinth shows that BC 1 retains a semicircular canal morphology  
371 found in *Homo erectus s.l.* and which is also retained in modern humans. This morphology is  
372 characterized by relatively larger vertical (anterior and posterior) canals in comparison to the  
373 derived condition in Neanderthals. However, BC 1 exhibits a relatively large and laterally  
374 extended posterior canal—a condition that is seldom observed in the fossil record and here for  
375 the first time in South Africa, but which is documented across the Pleistocene and mid-  
376 Holocene in eastern and Central Africa (Crevecoeur et al., 2016). Indeed, this feature drives the  
377 positioning of BC 1, OH 9, Ishango 37, and Lothagam 4b along the major axes of variation in  
378 multivariate space (Figure 7). As such, the bony labyrinth morphology of BC 1 is within the  
379 variation observed for either an early or later chronological scenario and cannot be used to  
380 adjudicate between the debates on whether it is an intrusive burial or one truly associated with  
381 the MSA. Notably, the possibly penecontemporaneous *Homo sapiens* from the Levant (Skhūl  
382 and Qafzeh) are separated from BC 1 along PC 2, instead overlapping with the sample of recent  
383 South African individuals in a shape space associated with relatively larger anterior canals  
384 (Figure 7). This is in contrast to the metrical analyses of BC 1's ectocranium exhibiting  
385 affinities with extant South Africans (Rightmire, 1979). Taken together, BC 1 appears to retain  
386 the ancestral bony labyrinth semicircular canal anatomy, including the relatively larger  
387 posterior canal dimensions found in OH 9 and Sangiran 4 that generally decrease in size over  
388 time, particularly outside of Africa. Nevertheless, we note that the SK 847 early *Homo* and the  
389 Daka *Homo erectus s.l.* specimens show a more varied semicircular canal morphology,  
390 overlapping with *Homo sapiens* in the former case and with Neanderthals in the latter case. As  
391 such, further samples from the Pleistocene of Africa are necessary for understanding the  
392 diversity and evolution of the bony labyrinth in *Homo* within and outside the continent.

393

#### 394 4.3. Behavioural and evolutionary implications

395

396 Inter-specific and diachronic changes in the brain and inner ear of fossil hominins, which are  
397 involved respectively in contributing to cognitive abilities and hearing and balance systems,  
398 may have critical behavioural implications. If we consider the hypothesis of an early emergence  
399 of the globular brain shape within the hominin lineage, and a possible relationship between  
400 brain globularization and changes in human behaviours, a derived brain shape in BC 1 raises  
401 interesting questions about potential correlations between the shape of the brain of the hominins  
402 inhabited Border Cave and cultural innovations documents in this site, such as the systematic  
403 maintenance of bedding grass as early as 200 ka (Neubauer et al., 2018; Wadley et al., 2020).

404 However, the polarity of the relationship between biological change and cultural innovations  
405 needs to be further explored in the future to decide if evidence from the fossil record (including  
406 from Border Cave) reflects gradual or punctuated evolutionary processes. While models of  
407 cognitive and cultural evolution tend to be dichotomized as processes of either genetic mutation  
408 and natural selection (i.e. where a sudden genetic change is responsible for key modifications  
409 in the brain and adaptive cognitive skills that contribute to cultural innovations; Klein, 2000)  
410 or gene flow and genetic drift (i.e. where ecological and demographic factors of population  
411 size, structure, and admixture are responsible for a gradual emergence of derived biocultural  
412 traits; Scerri et al., 2018), more nuanced evolutionary scenarios must also be considered (e.g.  
413 exaptations: d’Errico and Colagè, 2018; Colagè and d’Errico, 2020) alongside diverse  
414 theoretical frameworks (rev. in Sahle et al., 2018; Will et al., 2019).

415 In modern humans the bony labyrinth has primarily evolved as a result of genetic drift  
416 (Ponce de León et al., 2018), yet it clearly serves important functional roles in sound perception  
417 via the cochlea and in motor control via the semicircular canals during locomotion. It has  
418 therefore been hypothesized that variation in the bony labyrinth also reflects differences in  
419 sound perception and locomotor behaviour in hominins (Spoor et al., 2003; Braga et al., 2021).  
420 For example, the relatively larger vertical canals in *Homo erectus* and *Homo sapiens* are  
421 speculated to be a functional adaptation to a locomotor behavioural repertoire comprising  
422 habitual running and jumping (Spoor et al., 1994; Spoor et al., 2003), capacities that may have  
423 been essential for long-range dispersals and specialized subsistence practices (Bramble and  
424 Lieberman, 2004). Whether the relative differences we observe in posterior and anterior canal  
425 dimensions within *Homo sapiens* have a functional and behavioural association remains to be  
426 tested. New dating for BC 1, as well as quantitative shape analysis of the brain endocast and  
427 access to key southern African fossil human specimens (e.g., Hofmeyr; Grine et al., 2010;  
428 Saldanha, Drennan, 1953; Florisbad, Bruner and Lombard, 2020), will be required to  
429 appropriately test these interpretations from the brain endocast and bony labyrinth.

430 It is interesting to note that the brain and bony labyrinth structures in BC 1 convey  
431 distinct evolutionary signals, with the latter retaining an ancestral pattern and the former  
432 exhibiting a more derived shape and organization, which may question the co-evolutionary  
433 relationship between these two organs (Spoor, 1997; Spoor et al., 2003). In addition, the  
434 combination of derived and primitive features within fossil African *Homo sapiens* has been  
435 suggested to indicate a mosaic-like evolutionary process consistent with the view that modern  
436 humans emerged from structured populations in Africa (i.e., the ‘African multiregionalism’  
437 model, Scerri et al., 2018). Further studies explicitly studying brain and bony labyrinth

438 endocasts alongside the surrounding bone features will thus be necessary for testing these  
439 hypotheses.

440

## 441 **5. Conclusions**

442

443 In this study we described and compared a number of cranial features in Border Cave 1 that  
444 have the potential to shed light on the evolution of *Homo sapiens*. The brain endocast, including  
445 its shape, organization and vascularization, show similarities with modern humans, whereas the  
446 bony labyrinth exhibits ancestral features found in both *Homo erectus s.l.* and modern humans.  
447 While the relationship between features observed in brain and bony labyrinth endocasts needs  
448 to be explored further in relation to the archaeological record, our findings show that the  
449 assemblage at Border Cave documents the presence of humans with a derived brain and the  
450 emergence of key cultural innovations, emphasizing the role of this site in understanding *Homo*  
451 *sapiens* biological and cultural evolution. Additional evidence from key southern African  
452 specimens such as Hofmeyr, Saldanha, or Florisbad, along with new absolute dating of the  
453 fossil-bearing layers at Border Cave, would be crucial to test the hypotheses raised in this paper,  
454 in particular the ones dealing with the timing of the emergence of derived neuroanatomical  
455 traits. Lastly, the computer-assisted reconstruction of the BC 1 cranium, including the  
456 estimation of the missing parts, would help in quantifying cranial variation over the Middle  
457 Pleistocene and better understand hominin diversity (Mounier and Mirazón Lahr, 2019).

458

## 459 **Acknowledgements**

460 We thank the Fossil Access Advisory Panel and the Evolutionary Studies Institute (University  
461 of the Witwatersrand) for access to Border Cave 1, and Gideon Chinamatira for X-ray  
462 microtomographic acquisitions. We sincerely thank the Digital Archive of Fossil Hominoids  
463 team (<https://www.virtual-anthropology.com/>) and the Rising Star team (MorphoSource project  
464 ‘Rising Star’ ID 00000C124) for sharing data. We are grateful to the following institutions for  
465 their financial support: Bordeaux University, Centre for Early Sapiens Behaviour, DSI-NRF  
466 Centre of Excellence in Palaeosciences (Genus) (CEOOP2020-1), National Geographic Society  
467 (NGS-54810R-19), Grand Programme de Recherche ‘Human Past’ of the University of  
468 Bordeaux Initiative d’Excellence, National Research Foundation of South Africa (#129336),  
469 University of Bordeaux Programme Talents (Grant No. 191022-001), Research Council of  
470 Norway through its Centre’s of Excellence funding scheme, SapienCE (Project No. 262618),  
471 and National Science Foundation (#2131940-EduceLab: Infrastructure for Next-Generation

472 Heritage Science). We thank the Editors, Antoine Balzeau and one anonymous reviewer for  
473 their comments that contributed to improve the quality of this paper. Ethical clearance for the  
474 use of the extant human cranium was obtained from the Main Research Ethics committee of the  
475 Faculty of Health Sciences, University of Pretoria in February 2016.

476

## 477 **References**

- 478 Ambergen, A. W., Schaafsma, W., 1984. Interval estimates for posterior probabilities:  
479 Applications to Border Cave, in: van Vark, G.N., Howells, W.W. (Eds.), *Multivariate*  
480 *Statistical Methods in Physical Anthropology*. Reidel, Dordrecht, pp. 115–134.
- 481 Anzelmo, M., Ventrice, F., Barbeito-Andres, J., Pucciarelli, H.M., Sardi, M.L., 2015.  
482 Ontogenetic changes in cranial vault thickness in a modern sample of *Homo sapiens*.  
483 *Am. J. Hum. Biol.* 27, 475–485.
- 484 Backwell, L.R., d'Errico, F., Banks, W.E., de la Peña, P., Sievers, C., Stratford, D., Lennox,  
485 S.J., Wojcieszak, M., Bordy, E.M., Bradfield, J., Wadley, L., 2018. New Excavations at  
486 Border Cave, KwaZulu-Natal, South Africa. *J. Field Archaeol.* 43, 417–436,
- 487 Balzeau, A., 2013. Thickened cranial vault and parasagittal keeling: correlated traits and  
488 autapomorphies of *Homo erectus*? *J. Hum. Evol.* 64, 631–644.
- 489 Beaudet, A., Dumoncel, J., de Beer, F., Duployer, B., Durrleman, S., Gilissen, E., Hoffman, J.,  
490 Tenailleau, C., Thackeray, J.F., Braga, J., 2016. Morphoarchitectural variation in South  
491 African fossil cercopithecoid endocasts. *J. Hum. Evol.* 101, 65–78.
- 492 Beaudet, A., Carlson, K.J., Clarke, R.J., de Beer, F., Dhaene, J., Heaton, J., Pickering, T.R.,  
493 Stratford, D., 2018. Cranial vault thickness variation and inner structural organization  
494 in the StW 578 hominid cranium from Jacovec Cavern, South Africa. *J. Hum. Evol.*  
495 121, 204–220.
- 496 Beaudet, A., Clarke, R.J., de Jager, E., Bruxelles, L., Carlson, K.J., Crompton, R., de Beer, F.,  
497 Dhaene, J., Heaton, J.L., Jakata, K., Jashashvili, T., Kuman, K., McClymont, J.,  
498 Pickering, T.R., Stratford, D., 2019. The endocast of StW 573 (“Little Foot”) and  
499 hominin brain evolution. *J. Hum. Evol.* 126, 112–123.
- 500 Beaumont, P.B., 1980. On the age of Border Cave hominids 1–5. *Palaeontol. Afr.* 23, 21–33.
- 501 Beaumont, P.B., de Villiers, H., Vogel, J.C., 1978. Modern man in sub-saharan Africa prior to  
502 49,000 years B.P.: a review and evaluation with particular reference to Border Cave. *S.*  
503 *Afr. J. Sci.* 74, 409–419.
- 504 Beaumont, P.B., Miller, G., Vogel, J.C., 1992. Contemplating old clues to the impact of future  
505 greenhouse climates in South Africa. *S. Afr. J. Sci.* 88, 490–498.

506 Bergström, A., Stringer, C., Hajdinjak, M., Scerri, E.M.L., Skoglund, P., 2021. Origins of  
507 modern human ancestry. *Nature* 590, 229-237.

508 Beyer, R.M., Krapp, M., Eriksson, A., Manica, A., 2021. Climatic windows for human  
509 migration out of Africa in the past 300,000 years. *Nat. Commun.* 12, 4889.

510 Bird, M.I., Fifield, L.K., Santos, G.M., Beaumont, P.B., Zhou, Y., Di Tada, M.L., Hausladen,  
511 P.A., 2003. Radiocarbon dating from 40–60 ka BP at Border Cave, South Africa. *Quat.*  
512 *Sci. Rev.* 22, 943–947.

513 Bouchneb, L., Crevecoeur, I., 2009. The inner ear of Nazlet Khater 2 (Upper Paleolithic,  
514 Egypt). *J. Hum. Evol.* 56, 257–262.

515 Braga, J., Samir, C., Fradi, A., Feunteun, Y., Jakata, K., Zimmer, V.A., Zipfel, B., Thackeray,  
516 J. F., Macé, M., Wood, B.A., Grine, F.E., 2021. Cochlear shape distinguishes southern  
517 African early hominin taxa with unique auditory ecologies. *Sci. Rep.* 11, 17018.

518 Bramble, D.M., Lieberman, D.E., 2004. Endurance running and the evolution of *Homo*. *Nature*  
519 432, 345–352.

520 Broadfield, D.C., Holloway, R.L., Mowbray, K., Silvers, A., Yuan, M.S., Márquez, S., 2001.  
521 Endocast of Sambungmacan 3 (Sm 3): A new *Homo erectus* from Indonesia. *Anat. Rec.*  
522 262, 369–379.

523 Bruner, E., 2021. Evolving human brains: paleoneurology and the fate of Middle Pleistocene.  
524 *J. Archaeol. Method Theory* 28, 76–94.

525 Bruner, E., Lombard, M., 2020. The skull from Florisbad: a paleoneurological report. *J.*  
526 *Anthropol. Sci.* 98, 89–97.

527 Bruner, E., Manzi, G., Arsuaga, J.L., 2003. Encephalization and allometric trajectories in the  
528 genus *Homo*: evidence from the Neandertal and modern lineages. *Proc. Natl. Acad. Sci.*  
529 *U.S.A.* 100, 15335–15340.

530 Bruner, E., Mantini, S., Perna, A., Maffei, C., Manzi, G., 2005. Fractal dimension of the middle  
531 meningeal vessels: variation and evolution in *Homo erectus*, Neanderthals, and modern  
532 humans. *Eur. J. Morphol.* 42, 217–224.

533 Campbell, N.A., 1984. Some aspects of discrimination and allocation, in: van Vark, G.N.,  
534 Howells, W.W. (Eds.), *Multivariate Statistical Methods in Physical Anthropology*.  
535 Dordrecht, Reidel, pp. 177–192.

536 Colagè, I., d’Errico, F., 2020. Culture: the driving force of human cognition. *Top. Cogn. Sci.*  
537 12, 654-672.

538 Conde-Valverde, M., Quam, R., Martínez, I., Arsuaga, J.-L., Daura, J., Sanz, M., Zilhão, J.,  
539 2018. The bony labyrinth in the Aroeira 3 Middle Pleistocene cranium. *J. Hum. Evol.*  
540 124, 105–116.

541 Connolly, C.J., 1950. *External Morphology of the Primate Brain*. C.C. Thomas, Springfield.

542 Cooke, H.B.S., Malan, B.D., Wells, L.H., 1945. Fossil man in the Lebombo Mountains, South  
543 Africa: The Border Cave, Ingwavuma District, Zululand. *Man* 45, 6–13.

544 Corruccini, R.S., 1991. Metrical reconsideration of the Skhül IV and IX and Border Cave 1  
545 crania in the context of modern human origins. *Am. J. Phys. Anthropol.* 87, 433–445.

546 Coutinho-Nogueira, D., Coqueugniot, H., Santos, F., Tillier, A.-M., 2021. The bony labyrinth  
547 of Qafzeh 25 *Homo sapiens* from Israel. *Archaeol. Anthropol. Sci.* 13, 151.

548 Crevecoeur, I., Brooks, A., Ribot, I., Cornelissen, E., Semal, P., 2016. Late Stone Age human  
549 remains from Ishango (Democratic Republic of Congo): New insights on Late  
550 Pleistocene modern human diversity in Africa. *J. Hum. Evol.* 96, 35–57.

551 Drennan, M.R., 2020. The Saldanha skull and its associations. *Nature* 4383, 791–793.

552 d’Errico, F., Colagè, I., 2018. Cultural exaptation and cultural neural reuse: a mechanism for  
553 the emergence of modern culture and behavior. *Biol. Theory* 13, 213–227.

554 d’Errico, F., Backwell, L., 2016. Earliest evidence of personal ornaments associated with burial:  
555 the *Conus* shells from Border Cave. *J. Hum. Evol.* 93, 91–108.

556 d’Errico, F., Backwell, L.R., Villa, P., Degano, I., Lucejko, J., Bamford, M., Higham, T.,  
557 Colombini, M.P., Beaumont, P.B., 2012. Early Evidence of San Material Culture  
558 Represented by Organic Artifacts from Border Cave, South Africa. *Proc. Natl. Acad.*  
559 *Sci. U.S.A.* 109, 13214–13219.

560 d’Errico, F., Banks, W., Dan L. Warren, D.L., Sgubin, G., van Niekerk, K., Henshilwood, Ch.,  
561 Daniau, A-L, Sanchez Goni, M. F., 2017. Identifying Early Modern Human ecological  
562 niche expansions and associated cultural dynamics in the South African Middle Stone  
563 Age. *Proc Natl Acad Sci USA*, 114, 30: 7869-7876, doi: 10.1073/pnas.1620752114.

564 de Jager, E., Van Schoor, A.N., Hoffman, J.W., Oetlè, A.C., Fonta, C., Mescam, M., Risser,  
565 L., Beaudet, A., 2019. Sulcal pattern variation in extant human endocasts. *J. Anat.* 235,  
566 803–810.

567 de Villiers, H., 1973. Human skeletal remains from Border Cave, Ingwavuma District,  
568 KwaZulu, South Africa. *Ann. Transvaal Mus.* 28, 229–256.

569 Doboş, A, Soficaru, A, Trinkaus, E., 2010. The prehistory and paleontology of the Peştera  
570 Muierii (Romania): Université de Liège, Service de Préhistoire.

571 Dumoncel, J., Subsol, G., Durrleman, S., Bertrand, A., de Jager, E., Oettlé, A., Lockhat, Z.,  
572 Suleman, F.E., Beaudet, A., 2021. Are endocasts reliable proxies for brains? A 3D  
573 quantitative comparison of the extant human brain and endocast. *J. Anat.* 238, 480–488.

574 Eisová, S., Velemínský, P., Bruner, E., 2019. The Neanderthal endocast from Gánovce (Poprad,  
575 Slovak Republic). *J. Anthropol. Sci.* 96, 139–149.

576 Falk, D., Redmond Jr., J.C., Guyer, J., Conroy, G.C., Recheis, W., Weber, G.W., Seidler, H.,  
577 2000. Early hominid brain evolution: a new look at old endocasts. *J. Hum. Evol.* 38,  
578 695–717.

579 Gilbert, W.H., Asfaw, B., 2008. *Homo erectus*: Pleistocene evidence from the Middle Awash,  
580 Ethiopia. University of California Press, London.

581 Glantz, M., Viola, B., Wrinn, P., Chikisheva, T., Derevianko, A., Krivoschapkin, A., Islamov,  
582 U., Suleimanov, R., Ritzman, T., 2008. New hominin remains from Uzbekistan. *J. Hum.*  
583 *Evol.* 55, 223–237.

584 Gómez-Olivencia, A., Crevecoeur, I., Balzeau, A., 2015. La Ferrassie 8 Neandertal child  
585 reloaded: New remains and re-assessment of the original collection. *J. Hum. Evol.* 82,  
586 107–126.

587 Grine, F.E., 2016. The Late Quaternary hominins of Africa: The Skeletal Evidence from MIS  
588 6–2, in: Jones, S., Stewart, B.A. (Eds.), *Africa from MIS6–2: population dynamics and*  
589 *paleoenvironments*. Springer, Dordrecht, pp. 323–381.

590 Grine, F.E., Gunz, P., Betti-Nash, L., Neubauer, S., Morris, A.G., 2010. Reconstruction of the  
591 Late Pleistocene human skull from Hofmeyr, South Africa. *J. Hum. Evol.* 59, 1–15

592 Grimaud-Hervé, D., 1997. *L'évolution de l'encéphale chez Homo erectus et Homo sapiens.*  
593 *Exemples de l'Asie et de l'Europe*. CNRS, Paris.

594 Grimaud-Hervé, D., 2004. Endocranial vasculature, in: Holloway, R.L., Broadfield, D.C.,  
595 Yuan, M.S. (Eds.), *The Human Fossil Record: Brain Endocasts, the Paleoneurological*  
596 *Evidence*. Wiley-Liss, Hoboken, pp. 273–282.

597 Grimaud-Hervé, D., Albessard-Ball, L., Pokhojaev, A., Balzeau, A., Sarig, R., Latimer, B.,  
598 McDermott, Y., May, H., Hershkovitz, I., 2021. The endocast of the late Middle  
599 Paleolithic Manot 1 specimen, Western Galilee, Israel. *J. Hum. Evol.* 160, 102734.

600 Grün, R., Beaumont, P.B., 2001. Border Cave Revisited: A revised ESR chronology. *J. Hum.*  
601 *Evol.* 40, 467–482.

602 Grün, R., Beaumont, P.B., Tobias, P.V., Eggins, S., 2003. On the age of Border Cave 5 human  
603 mandible. *J. Hum. Evol.* 45, 155–167.

604 Guipert, G., de Lumley, M.-A., Tuffreau, A., Mafarta, B., 2011. A late Middle Pleistocene  
605 hominid: Biache-Saint-Vaast 2, North France. *C. R. Palevol* 10, 21–33.

606 Gunz, P., Ramsier, M., Kuhrig, M., Hublin, J.-J., Spoor, F., 2012. The mammalian bony  
607 labyrinth reconsidered, introducing a comprehensive geometric morphometric  
608 approach. *J. Anat.* 220, 529–543.

609 Gunz, P., Tilot, A.K., Wittfeld, K., Teumer, A., Shapland, C.Y., Erp van, T.G.M., Dannemann,  
610 M., Vernot, B., Neubauer, S., Guadalupe, T., Fernánde z, G., Brunner, H.G., Enard, W.,  
611 Fallon, J., Hosten, N., Völker, U., Profico, A., Vincenzo, F.D., Manzi, G., Kelso, J.,  
612 Pourcain, B.S., Hublin, J.-J., Franke, B., Pääbo, S., Macciardi, F., Grabe, H.J., Fisher,  
613 S.E., 2019. Neandertal introgression sheds light on modern human endocranial  
614 globularity. *Curr. Biol.* 29, 120–127.

615 Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2011. PAST: Paleontological statistics software  
616 package for education and data analysis. *Palaeontol. Electron.* 4.

617 Henshilwood, C.S., d’Errico, F., Yates, R., Jacobs, Z, Tribolo, C., Duller, G.A.T., Mercier, N.,  
618 Sealy, J.C., Valladas, H., Watts, I., Wintle, A.G., 2005. Emergence of modern human  
619 behavior: Middle Stone Age engravings from South Africa. *Science* 295, 1278.

620 Henshilwood, C.S., d’Errico, F., van Niekerk, K.L., Dayet, L., Queffelec, A., Pollarolo, L.,  
621 2018. An abstract drawing from the 73,000-year-old levels at Blombos Cave, South  
622 Africa. *Nature* 562, 115–118.

623 Hill, C.A., Radovčić, J., Frayer, D.W., 2014. Investigation of the semicircular canal variation  
624 in the Krapina Neandertals. *Am. J. Phys. Anthropol.* 154, 302–306.

625 Hodgskiss, T., 2020. Ochre use in the Middle Stone Age. *Oxford Research Encyclopedia of*  
626 *Anthropology*, <https://doi.org/10.1093/acrefore/9780190854584.013.51>

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

629 Holloway, R.L., Hurst, S.D., Garvin, H.M., Schoenemann, P.T., Vanti, W.B., Berger, L.R.,  
630 Hawks, J., 2018. Endocast morphology of *Homo naledi* from the Dinaledi Chamber,  
631 South Africa. *Proc. Natl. Acad. Sci. U.S.A.* 115, 5738–5743.

632 Houghton, K., Thackeray, J.F., 2011. Morphometric comparisons between crania of Late  
633 Pleistocene *Homo sapiens* from Border Cave (BC 1), Tuinplaas (TP 1) and modern  
634 southern African populations. *Trans. R. Soc. South Africa* 66, 159–162.

635 Hublin, J.-J., Ben-Ncer, A., Bailey, S.E., Freidline, S.E., Neubauer, S., Skinner, M.M.,  
636 Bergmann, I., Le Cabec, A., Benazzi, S., Harvati, K., Gunz, P., 2017. New fossils from

637           Jebel Irhoud, Morocco and the pan-African origin of *Homo sapiens*. *Nature* 546, 289–  
638           292.

639 Klein, R.G., 1983. The Stone Age prehistory of Southern Africa. *Annu. Rev. Anthropol.* 12,  
640           25-48.

641 Klein, R.G., 2000. Archeology and the evolution of human behavior. *Evol. Anthropol.* 9, 17–  
642           36.

643 L'Abbé, E.N., Loots, M., Meiring, J.H., 2005. The Pretoria Bone Collection: a modern South  
644           African skeletal sample. *Homo* 56, 197–205.

645 McBrearty, S., Brooks, A.S., 2000. The revolution that wasn't: a new interpretation of the origin  
646           of modern human behavior. *J. Hum. Evol.* 39, 453–563.

647 Neubauer, S., Hublin, J.-J., Gunz, P., 2018. The evolution of the modern human brain shape.  
648           *Sci. Adv.* 4, eaao5961.

649 Mirazón Lahr, M., 2016. The shaping of human diversity: filters, boundaries and transitions.  
650           *Phil. Trans. R. Soc. B* 371, 20150241.

651 Mounier, A., Mirazón Lahr, M., 2019. Deciphering African late middle Pleistocene hominin  
652           diversity and the origin of our species. *Nat. Comm.* 10, 3406.

653 Ogihara, N., Amano, H., Kikuchi, T., Morita, Y., Suzuki, H., Kondo, O., 2017. Digital  
654           reconstruction of Neanderthal and Early *Homo sapiens* endocasts, in: Bruner, E.,  
655           Ogihara, N., Tanabe, H. (Eds.), *Digital Endocasts: From Skulls to Brains*. Springer,  
656           Nagoya, pp. 9–32.

657 Ponce de León, M., Zollikofer, C., 2013. The internal cranial morphology of Oase 2, in: E.  
658           Trinkaus, S. Constantin, J. Zilhão (Eds.), *Life and Death at the Peștera cu Oase. A*  
659           *Setting for Modern Human Emergence in Europe*, Oxford University Press, New York,  
660           pp. 332–347.

661 Ponce de León, M.S., Koesbardiati, T., Weissmann, J.D., Milella, M., Reyna-Blanco, C.S.,  
662           Suwa, G., Kondo, O., Malaspinas, A.S., White, T.D., Zollikofer, C.P.E., 2018. Human  
663           bony labyrinth is an indicator of population history and dispersal from Africa. *Proc.*  
664           *Natl. Acad. Sci. U.S.A.* 115, 4128–4133.

665 Poza-Rey, E.M., Gómez-Robles, A., Arsuaga, J.L., 2019. Brain size and organization in the  
666           Middle Pleistocene hominins from Sima de los Huesos. Inferences from endocranial  
667           variation. *J. Hum. Evol.* 129, 67–90.

668 Quam, R., Lorenzo, C., Martínez, I., Gracia-Tellez, A., Arsuaga, J.L., 2016. The bony labyrinth  
669           of the middle Pleistocene Sima de los Huesos hominins (Sierra de Atapuerca, Spain). *J.*  
670           *Hum. Evol.* 90, 1–15.

671 Reyes-Centeno, H., 2016. Out of Africa and into Asia: Fossil and genetic evidence on modern  
672 human origins and dispersals. *Quat. Int.* 416, 249–262.

673 Rightmire, G.P., 1979. Implications of the Border Cave skeletal remains for Later Pleistocene  
674 human evolution. *Curr. Anthropol.* 20, 23–35.

675 Rito, T., Vieira, D., Silva, M., Conde-Sousa, E., Pereira, L., Mellars, P., Richards, M.B., Soares,  
676 P., 2019. A dispersal of *Homo sapiens* from southern to eastern Africa immediately  
677 preceded the out-of-Africa migration. *Sci. Rep.* 9, 4728.

678 Sahle, Y., Reyes-Centeno, H., Bentz, C., 2018. Modern human origins and dispersal: current  
679 state of knowledge and future directions. *Evol. Anthropol.* 27, 64–67.

680 Scerri, E.M.L., Thomas, M.G., Manica, A., Gunz, P., Stock, J.T., Stringer, C., Grove, M.,  
681 Groucutt, H.S., Timmermann, A., Rightmire, G.P., d’Errico, F., Tryon, C.A., Drake,  
682 N.A., Brooks, A.S., Dennell, R.W., Durbin, R., Henn, B.M., Lee-Thorp, J., deMenocal,  
683 P., Petraglia, M.D., Thompson, J.C., Scally, A., Chikhi, L., 2018. Did our species evolve  
684 in subdivided populations across Africa, and why does it matter? *Trends Ecol. Evol.* 33,  
685 582–594.

686 Spoor, F., 1997. Basicranial architecture and relative brain size of Sts 5 (*Australopithecus*  
687 *africanus*) and other Plio-Pleistocene hominids. *S. Afr. J. Sci.* 93, 182–186.

688 Spoor, F., Zonneveld, F., 1995. Morphometry of the primate bony labyrinth: a new method  
689 based on high-resolution computed tomography. *J. Anat.* 186, 271–286.

690 Spoor, F., Wood, B., Zonneveld, F., 1994. Implications of early hominid labyrinthine  
691 morphology for evolution of human bipedal locomotion. *Nature* 369, 645–648.

692 Spoor, F., Hublin, J., Braun, M., Zonneveld, F., 2003. The bony labyrinth of Neanderthals. *J.*  
693 *Hum. Evol.* 44, 141–165.

694 Stringer, C., 2016 The origin and evolution of *Homo sapiens*. *Phil. Trans. R. Soc. B* 371,  
695 20150237.

696 Subsol, G., Gesquière, G., Braga, J., Thackeray, F., 2010. 3D automatic methods to segment  
697 “virtual” endocasts: state of the art and future directions. *Am. J. Phys. Anthropol.*  
698 141(S50), 226–227 (abstract).

699 Tommy, K.A., Zipfel, B., Kibii, J., Carlson, K.J., 2021. Trabecular bone properties in the ilium  
700 of the Middle Paleolithic/Middle Stone Age Border Cave 3 *Homo sapiens* infant and  
701 the onset of independent gait. *J. Hum. Evol.* 155, 102984.

702 Tucci, S., Akey, J.M., 2016. A map of human wanderlust. *Nature* 538, 179–180.

703 Uhl, A., Reyes-Centeno, H., Grigorescu, D., Kranioti, E.F., Harvati, K., 2021. Inner ear  
704 morphology of the cioclovina early modern European calvaria from Romania. *Am. J.*  
705 *Biol. Anthropol.* 160, 62–70.

706 van Vark, G. N., Bilsborough, A., Dijkema, J., 1989. A further study of the morphological  
707 affinities of the Border Cave 1 cranium, with special reference to the origin of modern  
708 man. *Anthrop. Préhist.* 100, 43–56.

709 Villa, P., Soriano, T., Tsanova, T., Higham, F., d’Errico, L., R. Backwell, J., Lucejko,  
710 Beaumont, P.B., 2012. Border Cave and the Beginning of the Later Stone Age in South  
711 Africa. *Proc. Natl. Acad. Sci. U.S.A.* 109, 13208–13213.

712 Wadley, L., Esteban, I., de la Peña, P., Wojcieszak, M., Stratford, D., Lennox, S., d’Errico, F.,  
713 Rosso, D.E., Orange, F., Backwell, L., Sievers, C., 2020. Fire and grass-bedding  
714 construction 200 thousand years ago at Border Cave, South Africa. *Science*, 369, 863–  
715 866.

716 Will, M., Conard, N.J., Tryon, C.A., 2019. Timing and trajectory of cultural evolution on the  
717 African continent 200,000-30,000 years ago, in: Sahle, Y., Reyes-Centeno, H., Bentz,  
718 C. (Eds.), *Modern Human Origins and Dispersal*. Kerns Verlag, Tübingen, pp. 25-72.

719 Wu, X.-J., Crevecoeur, I., Liu, W., Xing, S., Trinkaus, E., 2014. Temporal labyrinths of eastern  
720 Eurasian Pleistocene humans. *Proc. Natl. Acad. Sci. U.S.A.* 111, 10509–10513.

721 Yoshizawa, S., Belyaev, A., Yokota, H., Seidel, H.-P., 2007. Fast and faithful geometric  
722 algorithm for detecting crest lines on meshes, in: *Proceedings of the 15th Pacific*  
723 *Conference on Computer Graphics and Applications*, pp. 231–237.

724 Yoshizawa, S., Belyaev, A., Yokota, H., Seidel, H.P., 2008. Fast, robust, and faithful methods  
725 for detecting crest lines on meshes. *Comput. Aided Geom. Des.* 25, 545–560.

726  
727  
728  
729  
730  
731  
732  
733  
734  
735  
736

737 **Tables**

738

739 **Table 1.** Comparative sample for the study of <sup>a</sup>brain imprints, <sup>b</sup>cranial vault thickness and  
740 <sup>c</sup>bony labyrinth.

Specimens	Sites	Dating (~ka)	Source
<i>early Homo</i>			
SK 847 <sup>c</sup>	Swartkrans (South Africa)	2190-1800	Spoor et al., 1994
<i>Homo erectus s.l.</i>			
KNM-ER 3733 <sup>a</sup>	Koobi Fora (Kenya)	1780	Holloway et al., 2004
Lantian <sup>c</sup>	Gongwangling (China)	1630	Wu et al., 2014
KNM-WT 15000 <sup>a</sup>	Nariokotome (Kenya)	1535	Holloway et al., 2004
Sangiran 2 <sup>a,c</sup> , 4 <sup>c</sup>	Sangiran (Indonesia)	1500	Holloway et al., 2004
OH 9 <sup>a,c</sup>	Olduvai Gorge (Tanzania)	1470	This study Holloway et al., 2004 Spoor et al., 1994
Daka <sup>c</sup>	Dakanihylo (Ethiopia)	1000	Gilbert and Asfaw, 2008
Sambungmacan 3 <sup>a</sup>	Sambungmacan (Indonesia)	200	Holloway et al., 2004 Broadfield et al., 2001
Ngandong 14 <sup>a</sup>	Solo River, (Indonesia)	200	Holloway et al., 2004
<i>Middle Pleistocene</i>			
Bodo <sup>a</sup>	Middle Awash (Ethiopia)	600	This study Holloway et al., 2004
SH 2 <sup>a</sup> , 2-9 <sup>a,c</sup> , 10 <sup>a</sup> , 11- 15 <sup>a,c</sup> , 16 <sup>a</sup> , 17 <sup>a,c</sup> , AT- 1907 <sup>c</sup>	Sima de los Huesos, Atapuerca (Spain)	430	Poza-Rey et al., 2019; Quam et al., 2016
Aroeira 3 <sup>c</sup>	Aroeira (Portugal)	436-389	Conde-Valverde et al., 2018
Hexian <sup>c</sup>	Longtan Cave (China)	412	Wu et al., 2014
Broken Hill 1 <sup>a</sup>	Kabwe (Zambia)	299	Holloway et al., 2004
Xujiayao 15 <sup>c</sup>	Xujiayao (China)	370-260	Wu et al., 2014
Steinheim <sup>c</sup>	Steinheim (Germany)	350	Spoor et al., 2003
Reilingen <sup>c</sup>	Reilingen (Germany)	300	Spoor et al., 2003

Florisbad <sup>a</sup>	Bloemfontein (South Africa)	259	Bruner and Lombard (2020)
BSV 2 <sup>c</sup>	Biache-Saint-Vaast (France)	200	Guipert et al., 2010
Abri Suard <sup>c</sup>	Abi Suard (France)	185-101	Spoor et al., 2003
<hr/>			
Neanderthal			
<hr/>			
Krapina 38.1 <sup>c</sup> , 38.12 <sup>c</sup> , 38.13 <sup>c</sup> , 39.13 <sup>c</sup> , 39.18 <sup>c</sup> , 39.20 <sup>c</sup> , 39.4 <sup>c</sup> , 39.8 <sup>c</sup>	Krapina (Croatia)	130	Hill et al., 2014
Tabūn C1 <sup>c</sup>	Mount Carmel (Israel)	122	Spoor et al., 2003
Gánovce <sup>a</sup>	Gánovce (Slovakia)	105	Eisová et al., 2019
Gibraltar 1 <sup>c</sup> , 2 <sup>c</sup>	Forbes' Quarry, Devil's Tower (Gibraltar)	130-24	Spoor et al., 2003
OR-1 <sup>c</sup>	Obi-Rakhmat (Uzbekistan)	90-60	Glantz et al., 2008
La Ferrassie 1 <sup>a,b</sup> , 2 <sup>c</sup> , 3 <sup>c</sup> , 8 <sup>c</sup>	La Ferrassie (France)	70	Spoor et al., 2003 Holloway et al., 2004 Balzeau, 2013 Gómez-Olivencia et al., 2015
Dederiyeh-93002 <sup>c</sup>	Dederiyeh (Syria)	70-50	Spoor et al., 2002
Amud 1 <sup>c</sup> , 7 <sup>c</sup>	Wadi Amud (Israel)	70-50	Coutinho-Nogueira et al., 2021
La Quina 5 <sup>c</sup> , 27 <sup>c</sup>	La Quina (France)	65	Spoor et al., 2003
Kebara 1 <sup>c</sup>	Mount Carmel (Israel)	60-48	Coutinho-Nogueira et al., 2021
Petit-Puymoyen 5 <sup>c</sup>	Petit-Puymoyen (France)	57-29	Spoor et al., 2003
Le Moustier 1 <sup>c</sup>	Le Moustier (France)	56-40	Spoor et al., 2003
Amud 1 <sup>c</sup>	Wadi Amud (Israel)	53	Holloway et al., 2004 Ogihara et al., 2017
La Chapelle-aux-Saints <sup>a,c</sup>	La Chapelle-aux-Saints (France)	52	Holloway et al., 2004 Ogihara et al., 2017 Spoor et al., 2003
Pech de l'Azé <sup>c</sup>	Pech de l'Azé (France)	51-41	Spoor et al., 2003
Feldhofer 1 <sup>a</sup>	Feldhofer (Germany)	40	Holloway et al., 2004
Spy I <sup>a,c</sup> , II <sup>a,c</sup>	Spy Cave (Belgium)	40	Holloway et al., 2004, Holloway, 1981

<hr/>			
<i>Homo naledi</i>			
<hr/>			
DH 1 <sup>a</sup> , DH 3 <sup>a</sup> , DH 4 <sup>a</sup> , DH 5 <sup>a</sup>	Rising Star Cave (South Africa)	236-335	Spoor et al., 2003  Holloway et al., 2018 This study
<hr/>			
<i>Homo sapiens</i>			
<hr/>			
Jebel Irhoud 1 <sup>a</sup> , 2 <sup>a</sup>	Jebel Irhoud (Morocco)	315	Neubauer et al., 2018 Holloway et al., 2004 Holloway, 1981
Skhūl I <sup>a,b</sup> , V <sup>a,c</sup>	Mount Carmel (Israel)	115	Balzeau, 2013 Ogihara et al., 2017 Coutinho-Nogueira et al., 2021
Qafzeh 3 <sup>c</sup> , 6 <sup>c</sup> , 7 <sup>c</sup> , 9 <sup>a,c</sup> , 11-13 <sup>c</sup> , 15 <sup>c</sup> , 21 <sup>c</sup> , 25 <sup>c</sup>	Mount of Precipitation (Israel)	115-92	Ogihara et al., 2017 Coutinho-Nogueira et al., 2021
Liujiang 1 <sup>c</sup>	Liujiang (China)	120-60	Wu et al., 2014
Manot 1 <sup>a</sup>	Manot Cave (Israel)	55	Grimaud-Hervé et al., 2020
NK 2 <sup>c</sup>	Nazlet Khater 2 (Egypt)	38	Bouchneb and Crevecoeur 2009
Hofmeyr <sup>a</sup>	Hofmeyr (South Africa)	36	Grine et al., 2010
Mladeč 1 <sup>a</sup>	Mladeč Caves (Czech Republic)	35	Ogihara et al., 2017
Abri Pataud 1 <sup>a,b,c</sup> , 3 <sup>c</sup>	Abri Pataud (France)	33-32	Spoor et al., 2003 Balzeau, 2013
Cro-Magnon 1 <sup>a,b,c</sup> , 3 <sup>a</sup>	Cro-Magnon (France)	30-31	This study Balzeau, 2013 Ogihara et al., 2017 Holloway et al., 2004
Muierii 2 <sup>c</sup>	Peștera Muierii (Romania)	30	Doboș et al., 2010
Cioclovina <sup>c</sup>	Peștera Cioclovina (Romania)	29	Uhl et al., 2016
Ish37 <sup>c</sup>	Ishango (Democratic Republic of Congo)	25-20	Crevecoeur et al., 2016
Laugerie Basse 1 <sup>c</sup>	Laugerie Basse (France)	15	Spoor et al., 2003

Combe Capelle <sup>a</sup>	France	8	Holloway et al., 2004
Lothagam 4b <sup>c</sup>	Kenya	7-5	Crevecoeur et al., 2016

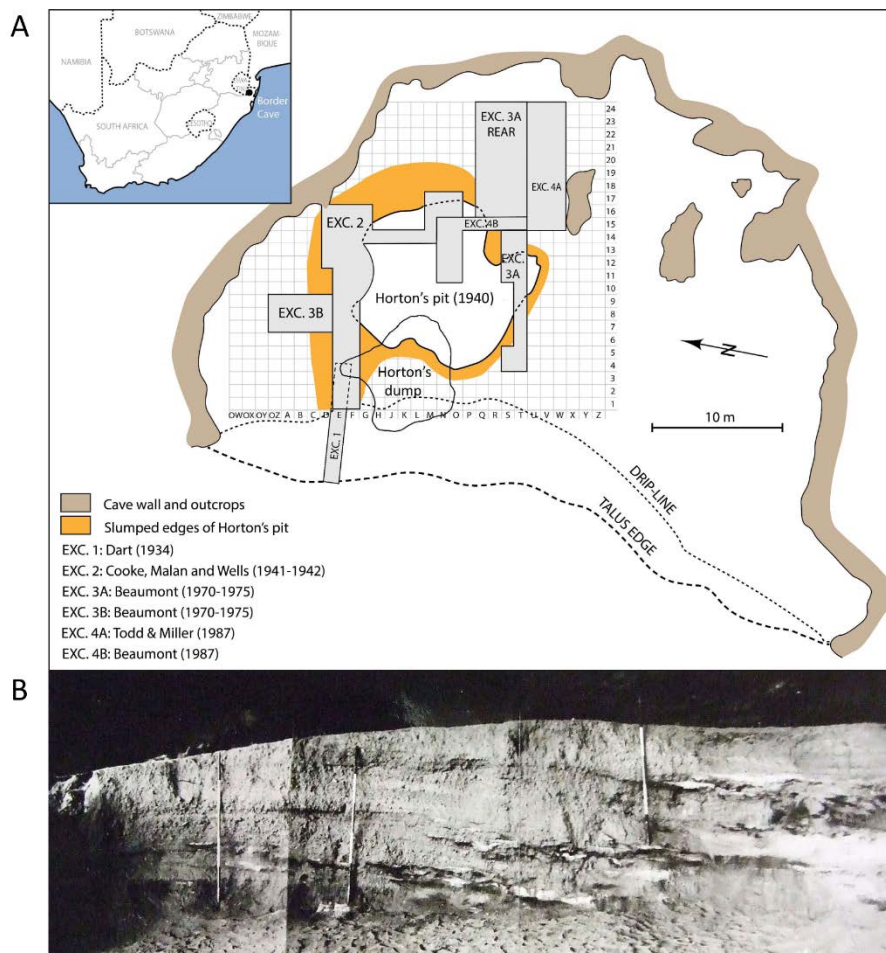
---

741

742 **Figure captions**

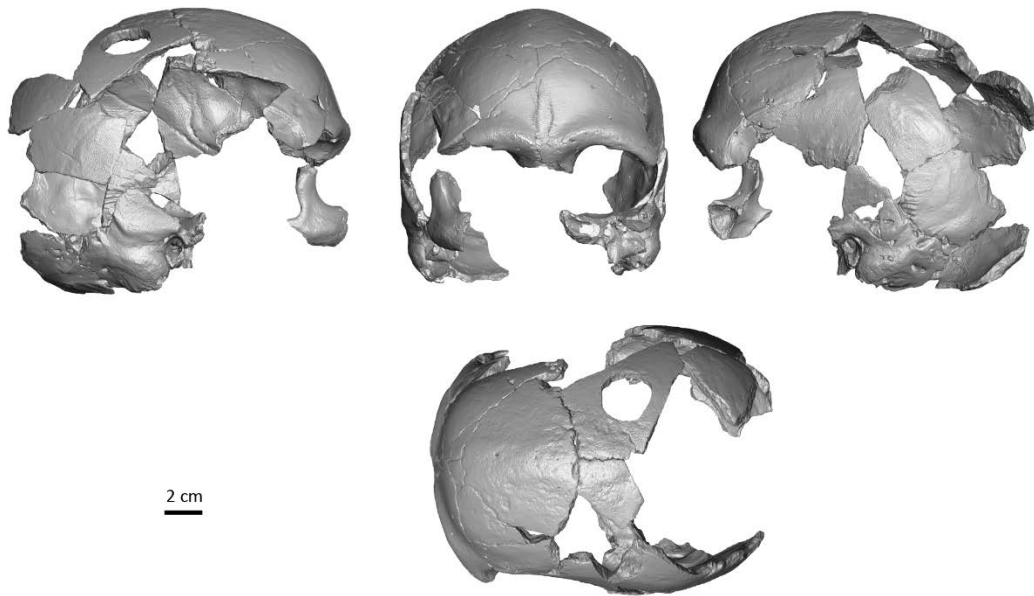
743

744 **Figure 1.** A plan (A) of Border Cave showing the location of the Horton's dump and a  
745 composite photograph (B) of the East face of Horton's pit taken in 1941 (from H.B.S. Cooke's  
746 interim report on excavation of Border Cave housed at the National Archives and Records  
747 Service of South Africa).



748

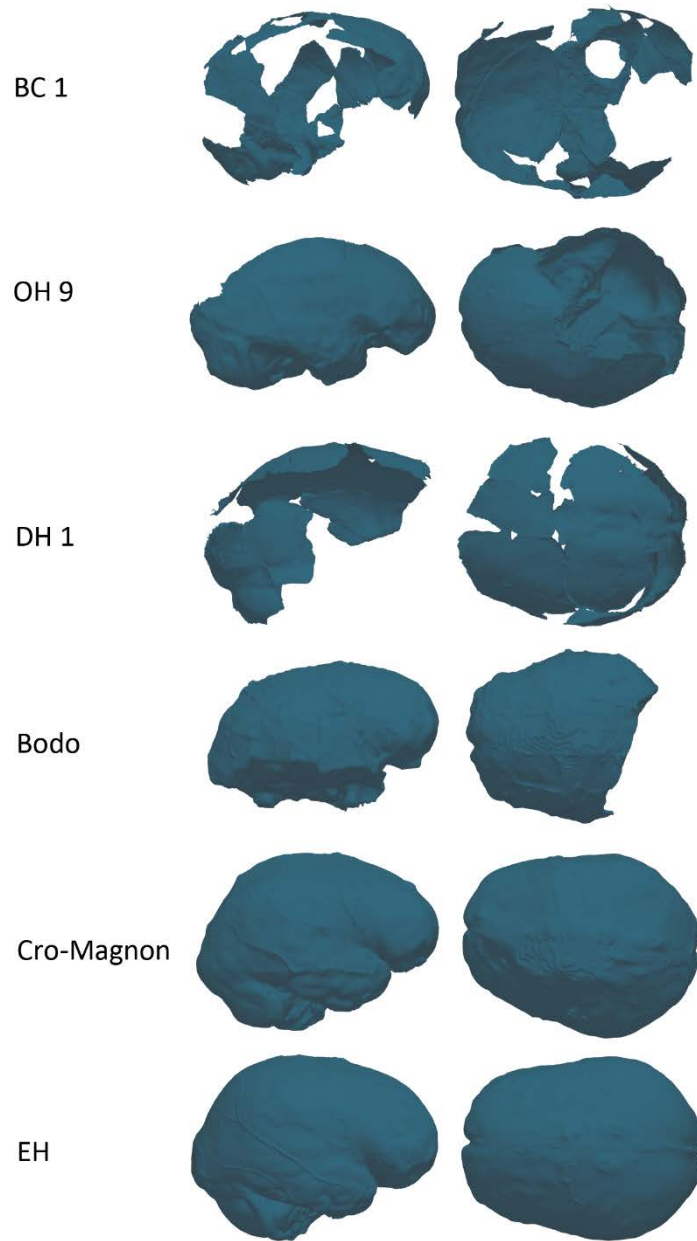
749 **Figure 2.** Virtual rendering of the Border Cave 1 cranium in lateral right (top left), anterior  
750 (top middle), lateral left (top right) and superior (bottom) views.



751

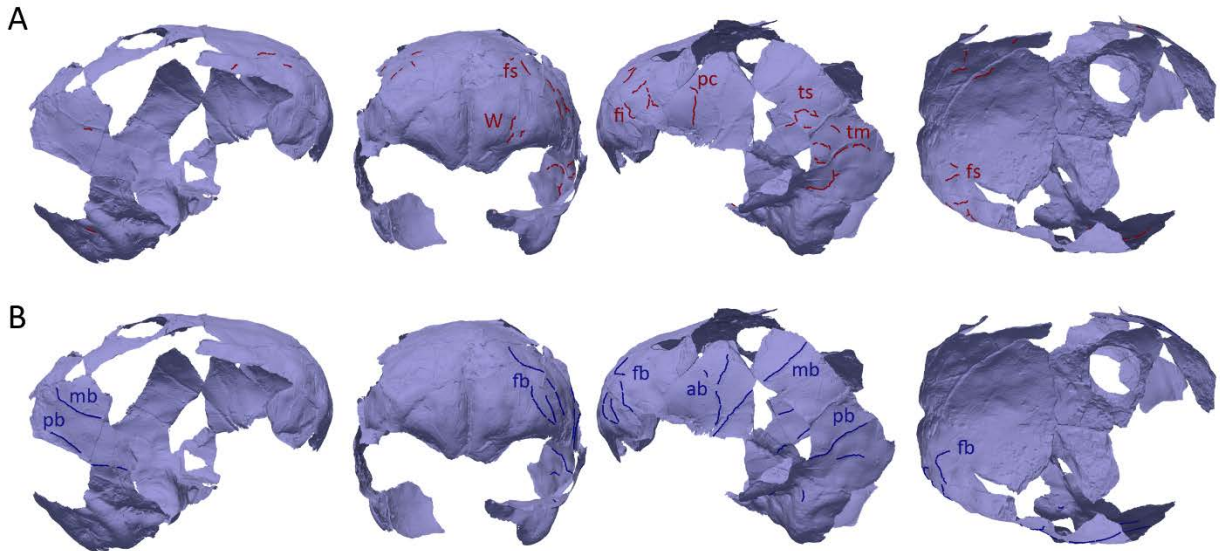
752

753 **Figure 3.** The endocasts of Border Cave 1 (BC 1), *Homo erectus* (OH 9, left side mirrored),  
754 *Homo naledi* (DH 1), African Middle Pleistocene *Homo* (Bodo), fossil (Cro-Magnon) and  
755 extant (EH) *Homo sapiens* in lateral right and superior views. Images not to scale.



756

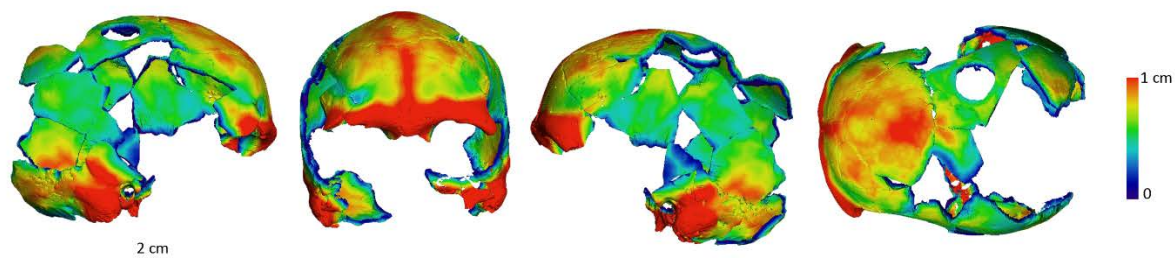
757 **Figure 4.** The sulcal (A) and vascular (B) imprints detected and identified in the Border Cave  
758 1 endocast in (from left to right) lateral right, anterior, lateral left and superior views. ab:  
759 anterior branch; fb: frontal branch; fi: inferior frontal sulcus; fs: superior frontal sulcus; ip:  
760 intraparietal sulcus; mb: middle branch; pb: postcentral sulcus; pc: precentral sulcus; ts: superior  
761 temporal sulcus; tm: middle temporal sulcus; W: fronto-marginal sulcus. Images not to scale.



762

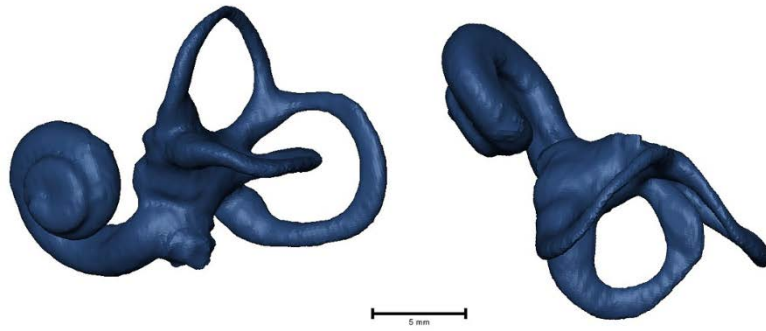
763

764 **Figure 5.** Cranial vault thickness cartographies of Border Cave 1 in (from left to right) lateral  
765 right, anterior, lateral left and superior views. Topographic thickness variation is rendered by  
766 a pseudocolor scale (in cm) ranging from thinner dark blue to thicker red.



767

768 **Figure 6.** Bony labyrinth endocast of Border Cave 1 in lateral (left) and superior (right)  
769 views.



770

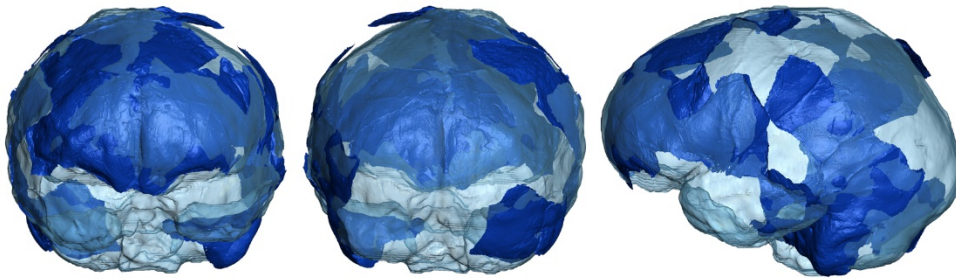


785 **Supplementary material**

786

787 **Figure S1.** Registration of the virtual renderings of the brain endocasts of Border Cave 1 (dark  
788 blue) and of Cro-Magnon 1 (light blue) in anterior (left), posterior (middle) and lateral left  
789 (right) views.

790



791