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1 **Title**

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

3

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26 **Keywords**

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

29

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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*.

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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 ± 11 ka to 41.1-24 ka using electron spin resonance (ESR) and radiocarbon (^{14}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 ± 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 μm (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

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476

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737 **Tables**

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739 **Table 1.** Comparative sample for the study of ^abrain imprints, ^bcranial vault thickness and
740 ^cbony labyrinth.

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

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

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

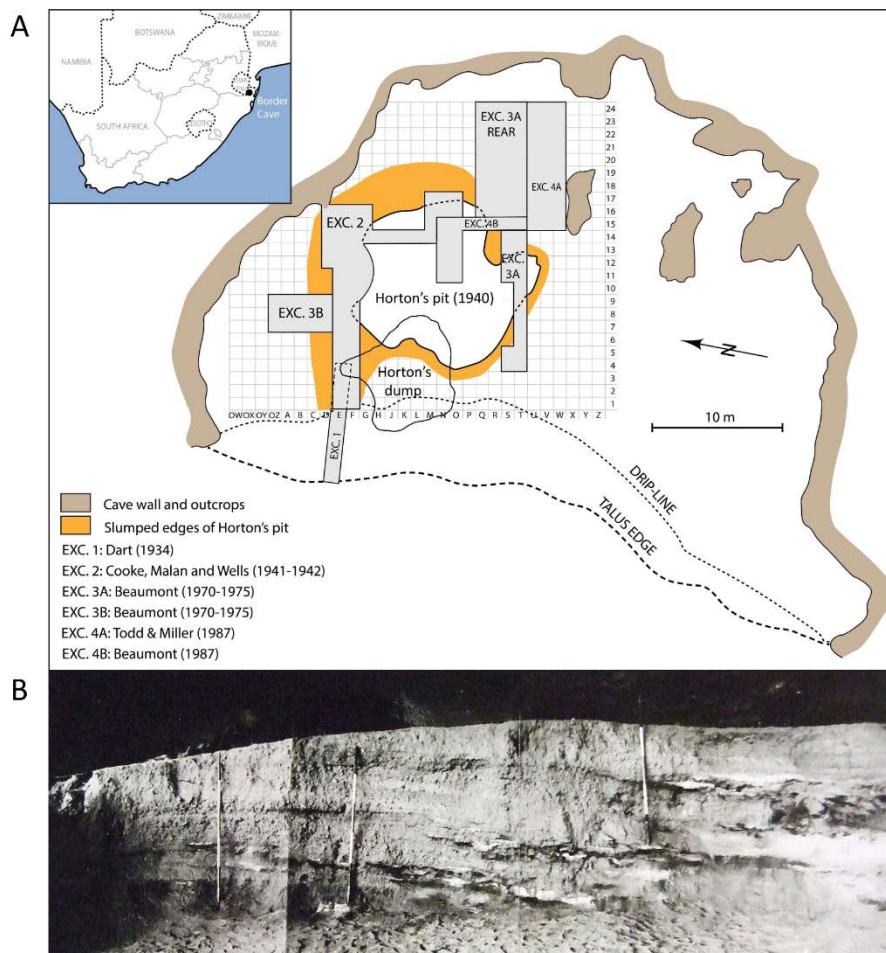
Combe Capelle ^a	France	8	Holloway et al., 2004
Lothagam 4b ^c	Kenya	7-5	Crevecoeur et al., 2016

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742 **Figure captions**

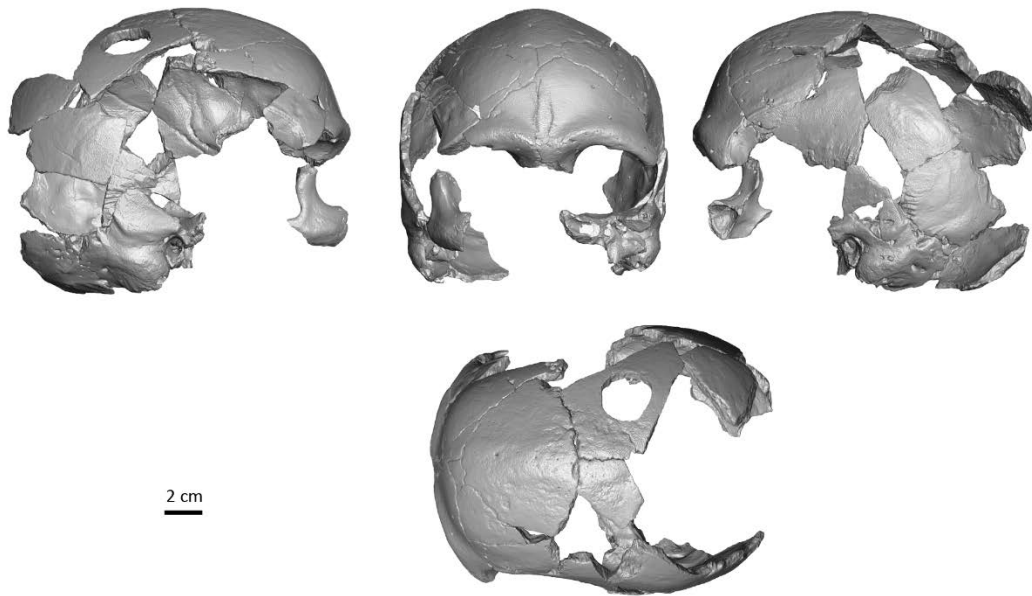
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744 **Figure 1.** A plan (A) of Border Cave showing the location of the Horton's dump and a
745 composite photograph (B) of the East face of Horton's pit taken in 1941 (from H.B.S. Cooke's
746 interim report on excavation of Border Cave housed at the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



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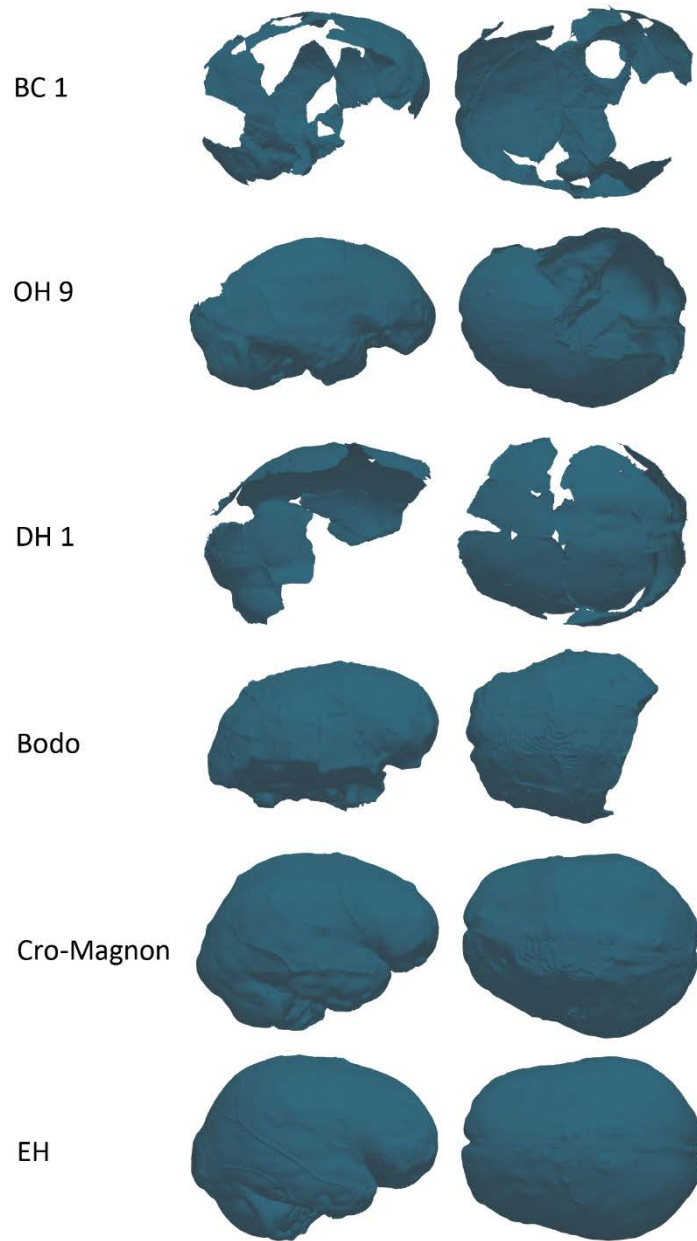
749 **Figure 2.** Virtual rendering of the Border Cave 1 cranium in lateral right (top left), anterior
750 (top middle), lateral left (top right) and superior (bottom) views.



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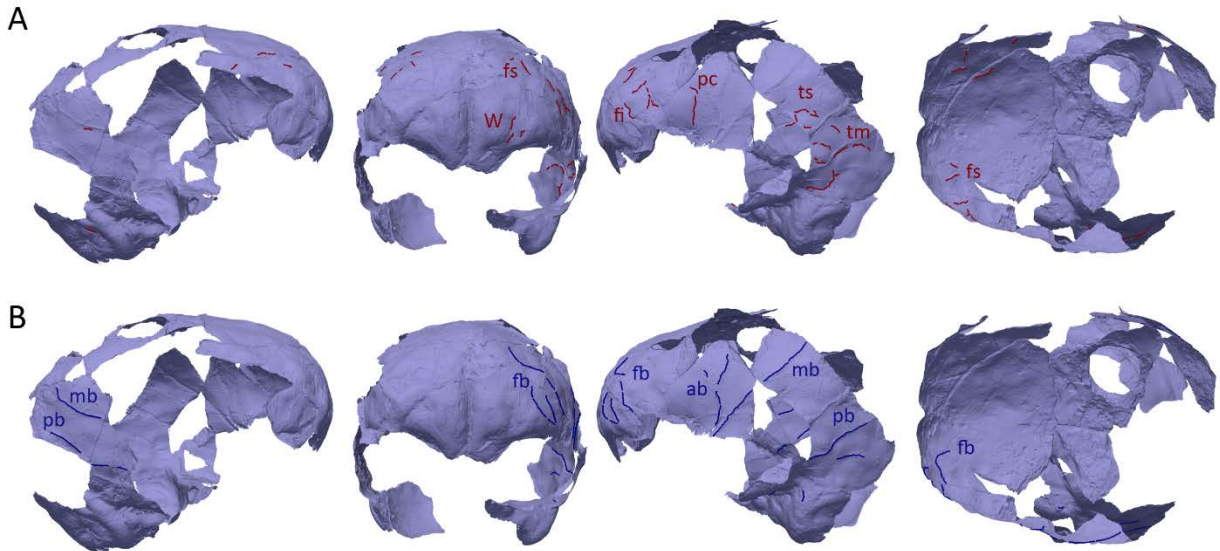
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753 **Figure 3.** The endocasts of Border Cave 1 (BC 1), *Homo erectus* (OH 9, left side mirrored),
754 *Homo naledi* (DH 1), African Middle Pleistocene *Homo* (Bodo), fossil (Cro-Magnon) and
755 extant (EH) *Homo sapiens* in lateral right and superior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



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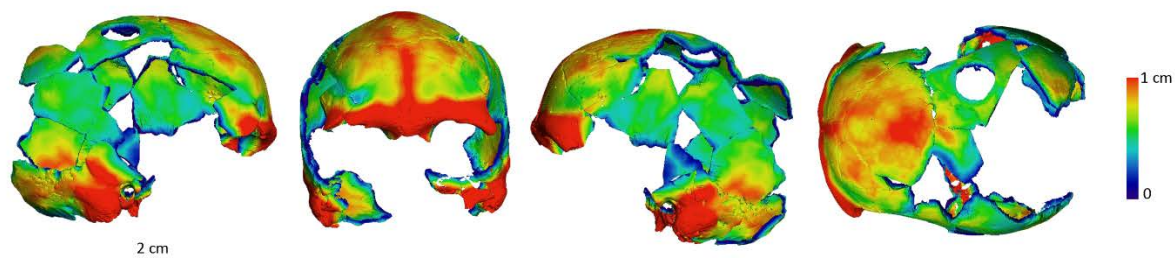
757 **Figure 4.** The sulcal (A) and vascular (B) imprints detected and identified in the Border Cave
758 1 endocast in (from left to right) lateral right, anterior, lateral left and superior views. ab:
759 anterior branch; fb: frontal branch; fi: inferior frontal sulcus; fs: superior frontal sulcus;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



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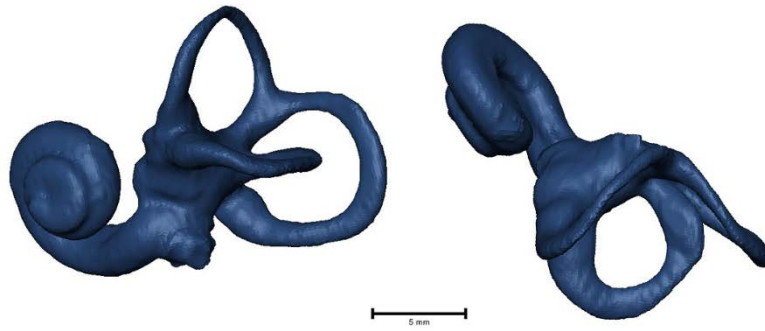
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764 **Figure 5.** Cranial vault thickness cartographies of Border Cave 1 in (from left to right) lateral
765 right, anterior, lateral left and superior views. Topographic thickness variation is rendered by
766 a pseudocolor scale (in cm) ranging from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



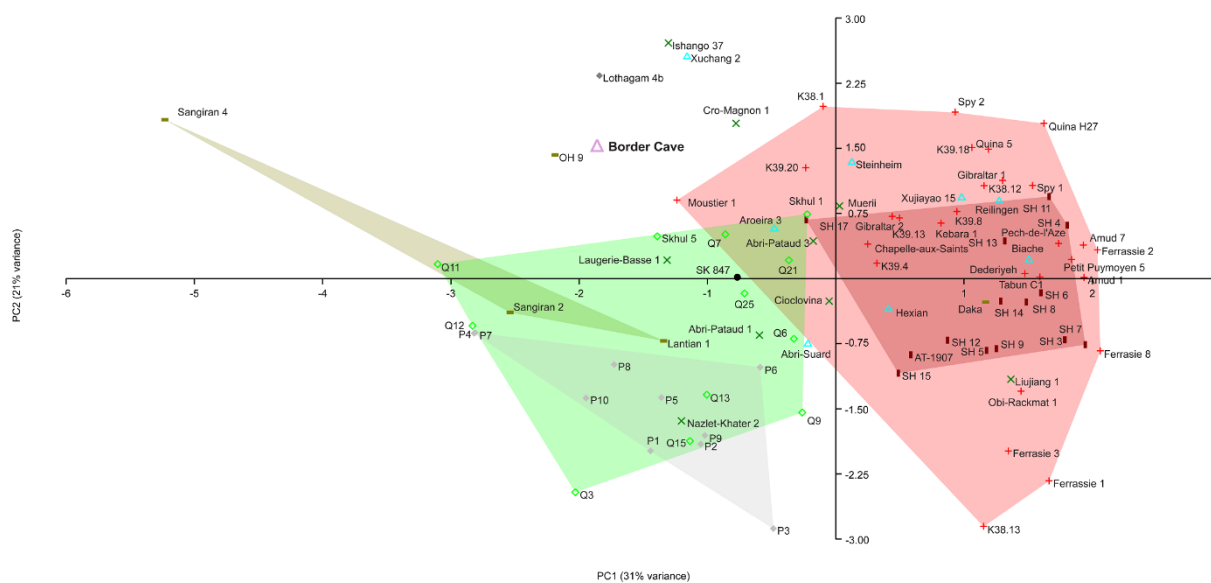
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768 **Figure 6.** Bony labyrinth endocast of Border Cave 1 in lateral (left) and superior (right)
769 views.



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771 **Figure 7.** Principal component analysis of seven bony labyrinth variables measuring the arc of
 772 each semicircular canal (in mm: ASCh/w=88.3, PSCh/w=101.1, and LSCh/w=89.3), the
 773 sagittal labyrinth index (SLI=43.6), and the radius of curvature of each semicircular canal
 774 relative to the total canal radii (ASC%R=35.4, PSC%R=37.9, and LSC%R=26.7). Convex hulls
 775 delimited for Neanderthals (red crosses), the Middle Pleistocene Sima de los Huesos Atapuerca
 776 hominins (crimson red bars), the early Late Pleistocene *Homo sapiens* from Skhul and Qafzeh
 777 (green diamonds), extant humans from Pretoria, South Africa (gray diamonds), and *Homo*
 778 *erectus s.l.* from Asia (tan bars). Acronyms: P: Pretoria; S: Skhul; K: Krapina. Symbols: Late
 779 Pleistocene fossils: green Xs; Middle Pleistocene fossils: turquoise triangles; Border Cave 1:
 780 violet triangle.



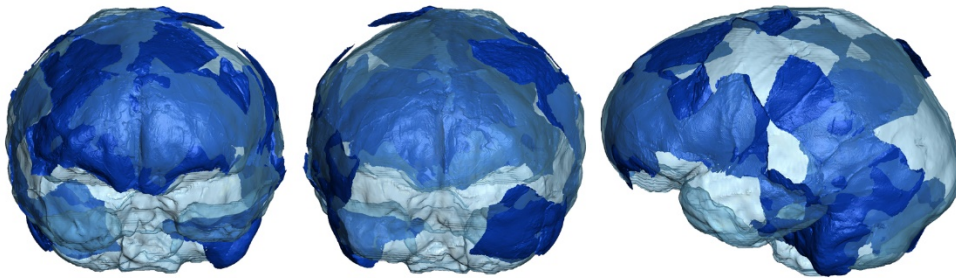
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785 **Supplementary material**

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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.

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