Quaternary Science Reviews 282 (2022) 107452

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

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

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ARTICLE INFO

Article history:
Received 12 January 2022
Received in revised form
1 March 2022
Accepted 3 March 2022
Available online 23 March 2022

Handling Editor: Donatella Magri

Keywords:
Middle Stone Age
South African fossil record
Hominin brain
Bony labyrinth
Cranial vault thickness

ABSTRACT

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

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,

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https://doi.org/10.1016/j.quascirev.2022.107452
0277-3791/

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 burial associated with a personal ornament (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).

Bone fragments attributed to the Border Cave 1 (BC 1) cranium were found in Horton's dump (Fig. 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 (Fig. 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 ± 10–144 ± 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 bones and fragments of the parietal, temporal (including mastoid, tympanic and petrous parts) and occipital bones, and the right zygomatic. The cranium has been reconstructed using plaster by A.R. Hughes (Rightmire, 1979). Interestingly, the cranial morphology of BC 1, characterized by a broad frontal, glabellar protrusion and prominent superciliary eminences (Rightmire, 1979; Corruccini, 1991), has been described and interpreted as being either similar (e.g., de Villiers, 1973; Rightmire, 1979; Houghton and Thackeray, 2011) or different (e.g., Campbell, 1984; Ambergen and Schaafsma, 1984; van Vark et al., 1989; Corruccini, 1991) from extant *Homo sapiens*.

The African Middle Stone Age features as pivotal in the evolutionary scenarios of human behaviour, as illustrated by the emergence of cultural innovations such as abstract engravings and drawings (e.g., Henshilwood et al., 2005; 2018), personal ornaments (e.g., d'Errico and Backwell, 2016), or the use of mineral pigments (e.g., use of ochre, rev. in Hodgskiss, 2020). Two main models have been considered when tracking the origins of behavioural modernity; one that supports the idea of a biocultural 'revolution' in relation to the emergence and spread of modern *Homo sapiens* and specific cognitive abilities (e.g., Klein, 2000), and a second model that relies on a more gradual process in response to external factors (rev. in McBrearty and Brooks, 2000; Scerri et al., 2018). The study of brain and cognition in fossil humans, and *in fine* the question of the nature and origins of the neural substrate associated with such behavioural innovations, has the potential to contribute to this debate (Bruner, 2021). For instance, the reconstruction and analysis of the brain endocast of fossil *Homo sapiens* specimens has demonstrated that the globular shape that characterizes the extant human brain emerged gradually over the last 100 ka, thus contradicting the hypothesis of a sudden event associated with a biocultural revolution (Neubauer et al., 2018). The modern human globular brain has been suggested to result from parietal and cerebellar bulging, and the onset of a specific phase ('globularization') during postnatal development (Bruner et al., 2003; Neubauer et al., 2018; Gunz et al., 2019). Because parietal areas and the cerebellum are involved in critical functions such as the coordination of movements, working and long-term memory, planning, language, or visuospatial integration, Neubauer et al. (2018) raised the possibility that brain globularization may have played a role in the emergence of behavioural innovations. Falsifying or verifying this hypothesis requires further investigation of the shape and organisation of fossil *Homo sapiens* brain endocasts, which is the primary material source of evidence for reconstructing hominin brain evolution, along with archaeological material, which represents a key source of information about past cognition. In addition to brain endocasts, the patterning of cranial vault thickness may also reflect variation in the brain external surface (Balzeau, 2013; Anzelmo et al., 2015).

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

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

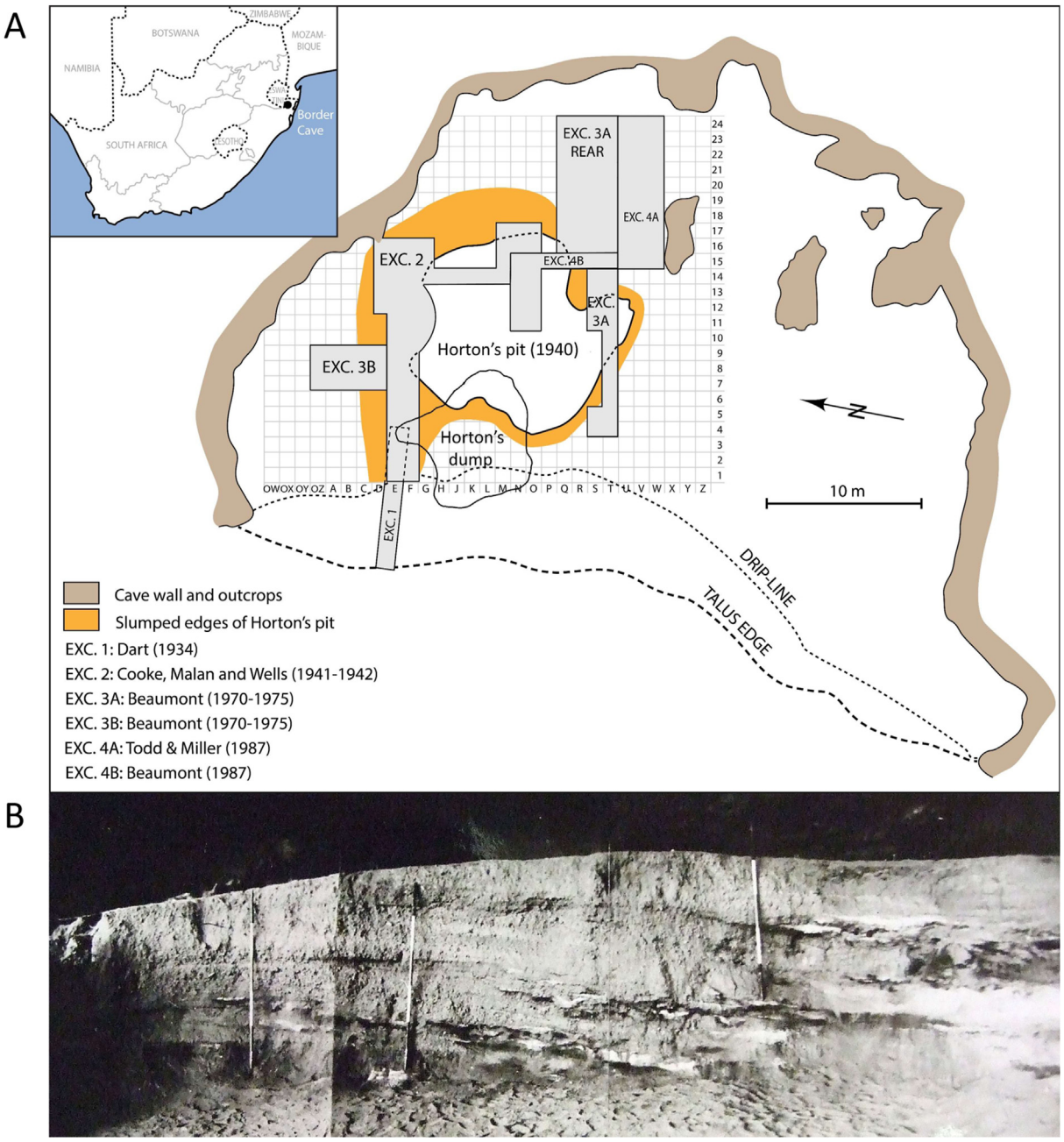

Fig. 1. A plan (A) of Border Cave showing the location of Horton's dump and a composite photograph (B) of the East face of Horton's pit taken in 1941 (from H.B.S. Cooke's interim report on excavation of Border Cave housed at the National Archives and Records Service of South Africa).

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

2. Materials and methods

2.1. Materials

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

2.2. Methods

The Border Cave 1 cranium was scanned at the microfocus X-ray tomography facility of the Palaeosciences Centre at the University

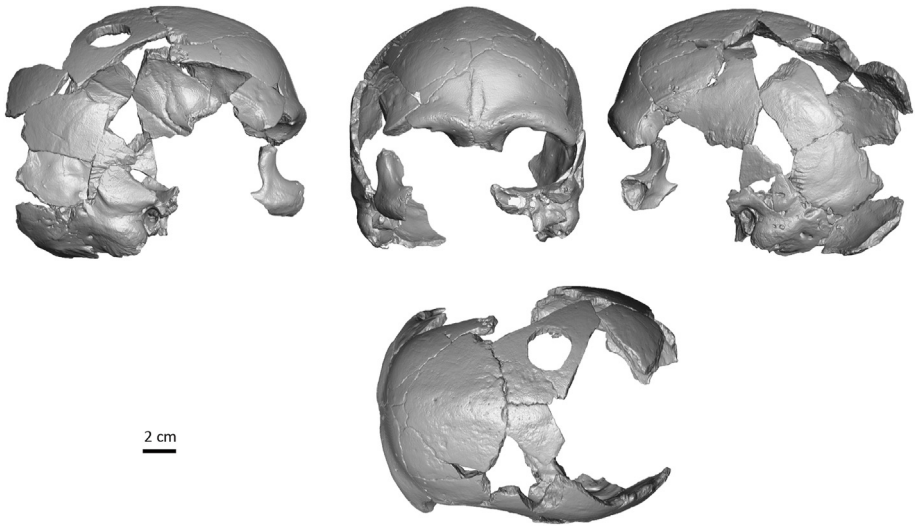

Fig. 2. Virtual rendering of the Border Cave 1 cranium in lateral right (top left), anterior (top middle), lateral left (top right) and superior (bottom) views.

of the Witwatersrand (South Africa), at a spatial resolution of 117.4 μm (isotropic voxel size). Digital data of OH 9 and Bodo were provided by the Institute of Anthropology, University of Vienna (Austria) through the Digital Archive of Fossil Hominoids project and were scanned at Innsbruck (Austria) at a resolution of 0.47x0.47 × 1 mm and of 0.49 x 0.49 × 1 mm, respectively). The cranium of Cro-Magnon 1 was scanned in Paris (France) with a resolution of 0.45x0.45 × 1 mm. The endocast of DH 1 was downloaded from MorphoSource (http://n2t.net/ark:/87602/m4/M48481).

The virtual brain endocasts were extracted from the BC 1, OH 9, Bodo and Cro-Magnon crania by using Endex software (Subsol et al., 2010; http://liris.cnrs.fr/gilles.gesquiere/wiki/doku.php?id¼endex). Sulcal and vascular imprints were automatically detected using a method for the detection of topographic variation in 3D meshes (Yoshizawa et al., 2007, 2008; Beaudet et al., 2016, 2019; de Jager et al., 2019; Dumoncel et al., 2021). The 3D surface of Border Cave 1 was also registered with the 3D surface of Cro-Magnon 1 for further comparison using the 'Align' module of Avizo v9.0 software (Visualization Sciences Group Inc.)

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

The bony labyrinth morphology was reconstructed using Avizo v9.0 software. In this study we focused primarily on the semicircular canals. Measurements were taken in Avizo v2002.3.1 (Thermo Fischer Scientific), following the protocols of Gunz et al. (2012) and Uhl et al. (2021), which consists of identifying the midpoint of the lumen in order to pinpoint landmarks defining the height and width of the labyrinth semicircular canals (Spoor, 1997; Spoor and Zonneveld, 1995). Raw measurements were transformed into shape indices, retaining variables that maximized the number of fossil samples that could be included for comparison. In total, seven indices were used, including those conveying the arc of each semicircular canal (ASCh/w, PSCh/w, and LSCh/w), the sagittal labyrinth index (SLI), and the radius of curvature of each semicircular canal relative to the total canal radii (ASC%R, PSC%R, and LSC%R). These variables were used to explore shape affinities in a Principal Component Analysis (PCA), performed using PAST software (v4.05, Hammer et al., 2011). BC 1 was treated as an unknown specimen and projected onto the PCA space comprising the comparative sample.

3. Results

3.1. Brain endocast of BC 1

3.1.1. General description

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

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

3.1.2. Sulcal imprints

The fronto-marginal sulcus makes an incision in the left orbital margin (Fig. 4A). Two furrows are detected on the dorsal surface of the left frontal lobe that might be remnants of the superior frontal sulci. Ventrally to the superior frontal sulci are two ventrodorsally-

Table 1
Comparative sample for the study of [a]brain imprints, [b]cranial vault thickness and [c]bony labyrinth.

Specimens	Sites	Dating (~ka)	Source
early *Homo*			
SK 847[c]	Swartkrans (South Africa)	2190-1800	Spoor et al. (1994)
Homo erectus s.l.			
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)
Middle Pleistocene			
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. (2011)
Abri Suard[c]	Abi Suard (France)	185-101	Spoor et al. (2003)
Neanderthal			
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. (2003)
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)
Homo naledi			
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
Homo sapiens			
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)

(*continued on next page*)

Table 1 (*continued*)

Specimens	Sites	Dating (~ka)	Source
Manot 1[a]	Manot Cave (Israel)	55	Grimaud-Hervé et al. (2021)
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]	Peştera Muierii (Romania)	30	Doboş et al. (2010)
Cioclovina[c]	Peştera Cioclovina (Romania)	29	Uhl et al. (2021)
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]	Combe Capelle (France)	8	Holloway et al. (2004)
Lothagam 4b[c]	Lothagam (Kenya)	9-6	Crevecoeur et al. (2016)

oriented furrows. The most rostral one could possibly be identified as part of the inferior frontal sulcus. The furrow that nearly connects the two vertical imprints might be part of the inferior frontal sulcus (following the pattern seen in Connolly, 1950 p. 186 Figure 132). Rostral to this series of furrows is a vertical imprint identified as the precentral sulcus. The caudal portion of the left parietal surface preserved is particularly convoluted. The most ventral sulcus, which is markedly arched, is identified as the caudal end of the middle temporal sulcus (a3 in Connolly, 1950). The furrows located ventral to the middle temporal sulcus could be part of the superior temporal sulcus (a2 in Connolly, 1950; see pattern 236 p. 226). If this identification is correct, the bulge that is visible immediately above might correspond to the angular gyrus. On the right hemisphere, remnants of sulci are detected but are difficult to identify.

The sulcal pattern in Border Cave 1 does not show any substantial differences with the extant human sulcal pattern (i.e., spatial relationships between sulci, Connolly, 1950; de Jager et al., 2019) nor with fossil human specimens for which sulcal imprints are described (e.g., the *Homo naledi* specimen DH 3, the fossil *Homo sapiens* specimen Manot 1, Holloway et al., 2018; Grimaud-Hervé et al., 2021).

3.1.3. Vascular imprints

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

In the Border Cave 1 endocast, both the anterior and posterior branches of the middle meningeal vessels are reticulated. In the left hemisphere, the middle branch derives from the anterior branch. As such, BC 1 is close to Neanderthals and modern humans in showing a more developed anterior branch from which the middle branch arises and a posterior branch nearly orthogonal to the anterior branch (Grimaud-Hervé, 1997; Guipert et al., 2011; Bruner et al., 2005), and differs from *Homo erectus* and *Homo naledi*, in which the middle branch derives from the posterior branch (Grimaud-Hervé, 1997; Guipert et al., 2011; Holloway et al., 2018), as well as from Florisbad, in which the posterior branch is more developed (Bruner and Lombard, 2020). In particular, this pattern (i.e., the fact that the middle branch derives from the anterior branch) is shared with Jebel Irhoud 1 and 2, Broken Hill 1, Salé, Omo 2, and La Ferrassie 1 (Grimaud-Hervé, 2004).

3.2. Cranial vault thickness distribution in BC 1

The colour map in Fig. 5 reveals that the frontal bone is particularly thick compared to the preserved portions of the parietal bones. In terms of thickness distribution, the maximum values are confined to the midline of the most anterior part of the frontal bone while the posterior regions show a more heterogeneous pattern with thickened areas being widely distributed. When compared to the cranial vault thickness cartographies of fossil hominins published in Balzeau (2013) and Beaudet et al. (2018), bone thickness distribution in the Border Cave 1 cranium resembles the patterns seen in Cro-Magnon 1 and Abri Pataud 1, which both share a diffuse distribution of thickened areas over the frontal region. However, it differs from the extant human condition that is characterized by a thickened area located in the bregmatic area (Balzeau, 2013; Beaudet et al., 2018).

3.3. Bony labyrinth of BC 1

3.3.1. General description

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

3.3.2. Multivariate analysis

Shape index values are reported in Fig. 7 alongside the corresponding PCA plot. Therein, Neanderthals and modern Middle Pleistocene hominins from Eurasia are largely separated from recent Holocene *Homo sapiens* and *Homo erectus* along the main axis of variation (PC 1; Fig. 7). This separation is driven in large part by measurements of the lateral canal (loadings: LSC%R = 0.63, LSCh/w = 0.44), as well as the sagittal labyrinthine index (loading: SLI = 0.24)—a derived trait in Neanderthals (Spoor et al., 2003).

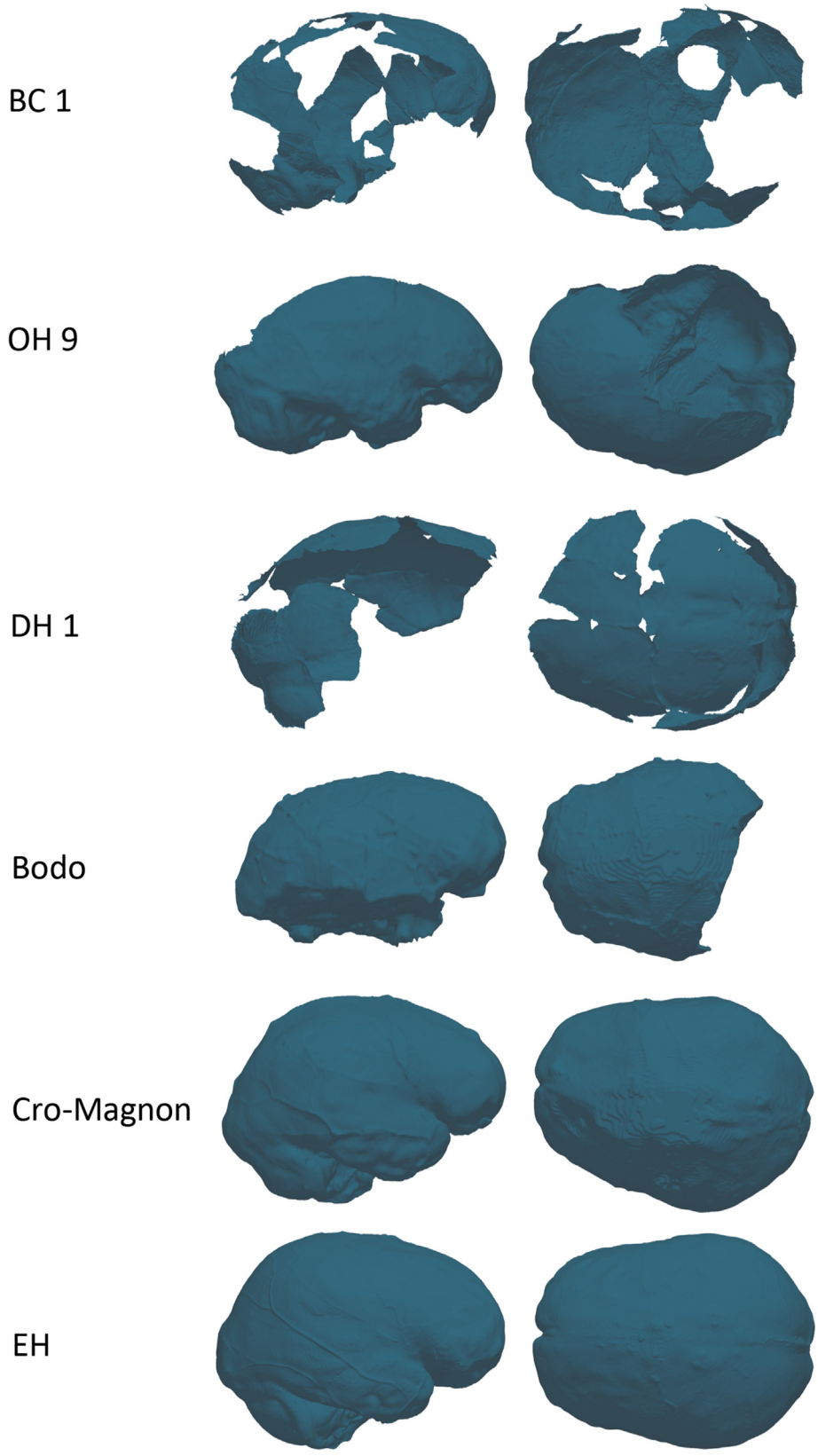

Fig. 3. The brain endocasts of Border Cave 1 (BC 1), *Homo erectus* (OH 9, left side mirrored), *Homo naledi* (DH 1), African Middle Pleistocene *Homo* (Bodo), fossil (Cro-Magnon) and extant (EH) *Homo sapiens* in lateral right and superior views. Images not to scale.

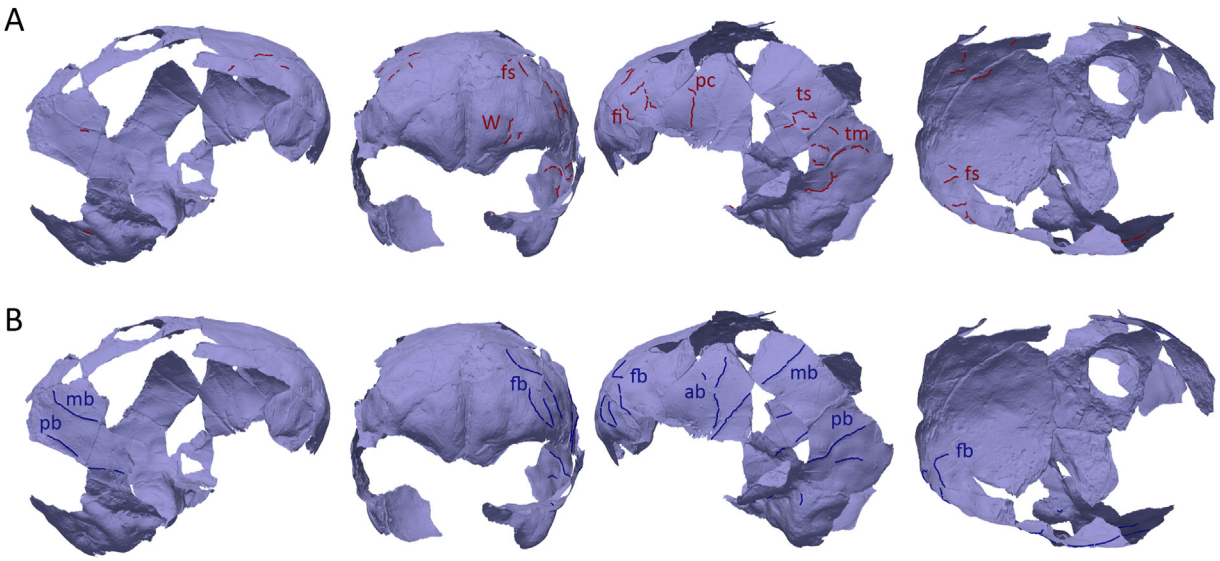

Fig. 4. The sulcal (A) and vascular (B) imprints detected and identified in the Border Cave 1 endocast in (from left to right) lateral right, anterior, lateral left and superior views. ab: anterior branch; fb: frontal branch; fi: inferior frontal sulcus; fs: superior frontal sulcus; ip: intraparietal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

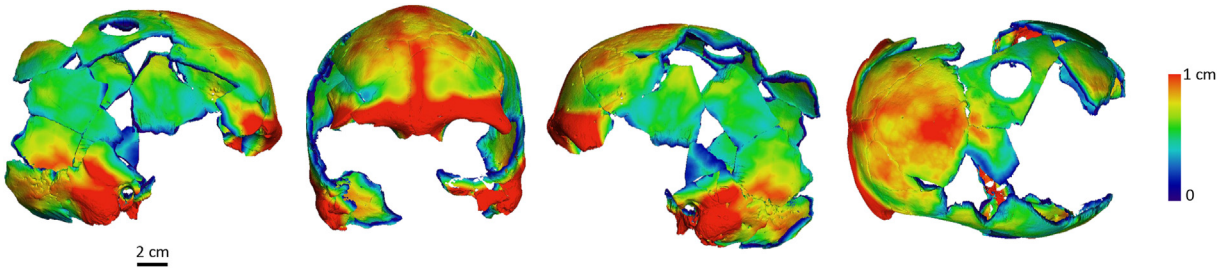

Fig. 5. Cranial vault thickness cartographies of Border Cave 1 in (from left to right) lateral right, anterior, lateral left and superior views. Topographic thickness variation is rendered by a pseudocolour scale (in cm) ranging from thinner dark blue to thicker red. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

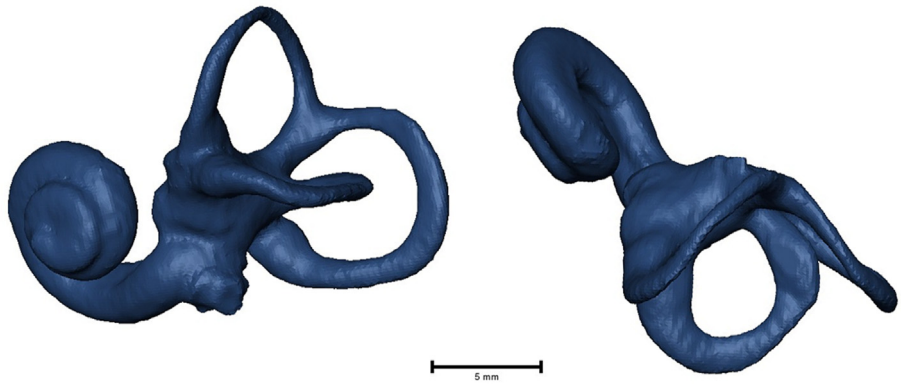

Fig. 6. Virtual rendering of the bony labyrinth endocast of Border Cave 1 in lateral (left) and superior (right) views.

While the Qafzeh-Skhūl series of early Late Pleistocene *Homo sapiens* is also largely separated from Neanderthals along PC 1, the Late Pleistocene *Homo sapiens* fossils are widely distributed. Along PC 2, the recent Holocene sample is largely separated from the *Homo erectus* specimens. When delimiting the comparative samples with convex hulls along the major axes of variation, Border Cave 1 is outside the range of all groups. It occupies a space characterizing labyrinths with relatively large, curved posterior canals (loading: PSC%R = −0.44) and is close to the OH 9 fossil from eastern Africa.

4. Discussion

Given the scarcity of fossil hominins attributed to *Homo sapiens*

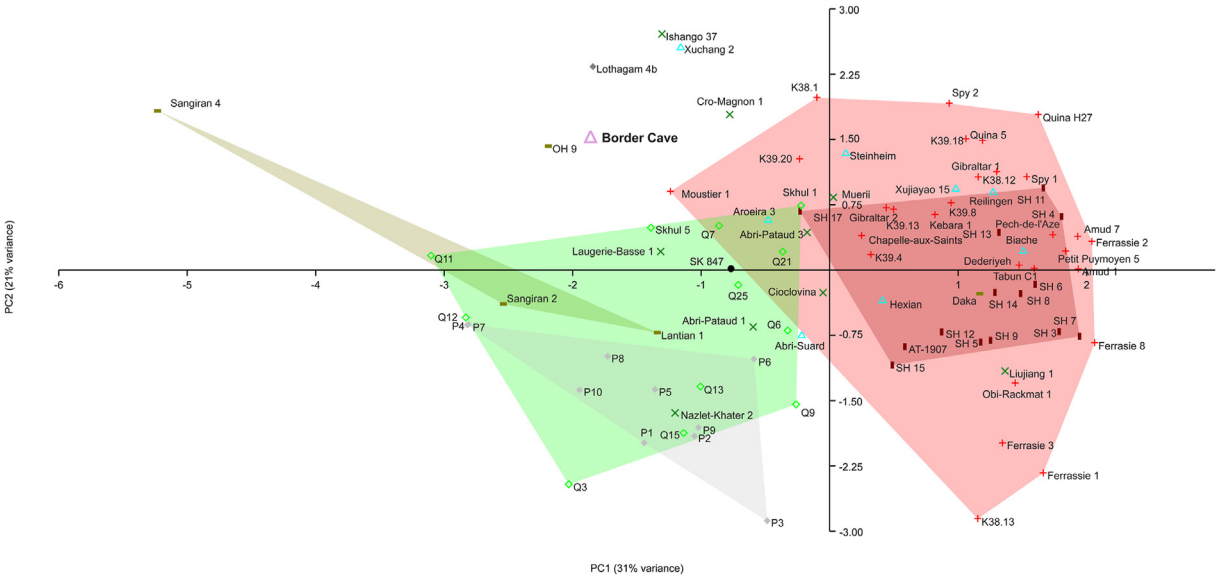

Fig. 7. Principal component analysis of seven bony labyrinth variables measuring the arc of each semicircular canal (in mm: ASCh/w = 88.3, PSCh/w = 101.1, and LSCh/w = 89.3), the sagittal labyrinth index (SLI = 43.6), and the radius of curvature of each semicircular canal relative to the total canal radii (ASC%R = 35.4, PSC%R = 37.9, and LSC%R = 26.7). Convex hulls delimited for Neanderthals (red crosses), the Middle Pleistocene Sima de los Huesos Atapuerca hominins (crimson red bars), the early Late Pleistocene *Homo sapiens* from Skhūl and Qafzeh (green diamonds), extant humans from Pretoria, South Africa (gray diamonds), and *Homo erectus s.l.* from Asia (tan bars). Acronyms: P: Pretoria; S: Skhūl; K: Krapina. Symbols: Late Pleistocene fossils: green Xs; Middle Pleistocene fossils: turquoise triangles; Border Cave 1: violet triangle. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

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

4.1. Human brain evolution

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

4.2. Human inner ear evolution

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

canal morphology, overlapping with *Homo sapiens* in the former case and with Neanderthals in the latter case. As such, further samples from the Pleistocene of Africa are necessary for understanding the diversity and evolution of the bony labyrinth in *Homo* within and outside the continent.

4.3. Behavioural and evolutionary implications

Inter-specific and diachronic changes in the brain and inner ear of fossil hominins, which are involved respectively in contributing to cognitive abilities and hearing and balance systems, may have critical behavioural implications. If we consider the hypothesis of an early emergence of the globular brain shape within the hominin lineage, and a possible relationship between brain globularization and changes in human behaviour, a derived brain shape in BC 1 raises interesting questions about potential correlations between the shape of the brain of the hominins that inhabited Border Cave and cultural innovations documented at this site, such as the systematic maintenance of bedding grass as early as 200 ka (Neubauer et al., 2018; Wadley et al., 2020). However, the polarity of the relationship between biological change and cultural innovations needs to be further explored in the future to decide if evidence from the fossil record (including from Border Cave) reflects gradual or punctuated evolutionary processes. While models of cognitive and cultural evolution tend to be dichotomized as processes of either genetic mutation and natural selection (i.e. where a sudden genetic change is responsible for key modifications in the brain and adaptive cognitive skills that contribute to cultural innovations; Klein, 2000) or gene flow and genetic drift (i.e. where ecological and demographic factors of population size, structure, and admixture are responsible for a gradual emergence of derived biocultural traits; Scerri et al., 2018), more nuanced evolutionary scenarios must also be considered (e.g. exaptations: d'Errico and Colagè, 2018; Colagè and d'Errico, 2020) alongside diverse theoretical frameworks (rev. in Sahle et al., 2018; Will et al., 2019).

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

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

5. Conclusions

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

Author contributions

A.B. and H.R.-C. designed/performed research; B.Z. provided data; A.B. and H.R.-C. analysed/interpreted data; A.B., H.R.-C, L.W., F. d'E., L.B., P. de la P., B.Z. wrote/revised the paper.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the Fossil Access Advisory Panel and the Evolutionary Studies Institute (University of the Witwatersrand) for access to Border Cave 1, and Gideon Chinamatira for X-ray microtomographic acquisitions. We sincerely thank the Digital Archive of Fossil Hominoids team (https://www.virtual-anthropology.com/) and the Rising Star team (MorphoSource project 'Rising Star' ID 00000C124) for sharing data. We are grateful to the following institutions for their financial support: Bordeaux University, Centre for Early Sapiens Behaviour, DSI-NRF Centre of Excellence in Palaeosciences (Genus) (CEOOP 2020-1), National Geographic Society (NGS-54810R-19), Grand Programme de Recherche 'Human Past' of the University of Bordeaux Initiative d'Excellence, National Research Foundation of South Africa (#129336), University of Bordeaux Programme Talents (Grant No. 191022−001), Research Council of Norway through its Centre's of Excellence funding scheme, SapienCE (Project No. 262618), and National Science Foundation (#2131940-EduceLab: Infrastructure for Next-Generation Heritage Science). We thank the Editors, Antoine Balzeau and one anonymous reviewer for their comments that contributed to improve the quality of this paper. Ethical clearance for the use of the extant human cranium was obtained from the

Main Research Ethics committee of the Faculty of Health Sciences, University of Pretoria in February 2016.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2022.107452.

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