Looking for the origins of the human brain: The role of South Africa in the history of palaeoneurology

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DATES:
Received: 15 May 2024
Revised: 26 Sep. 2024
Accepted: 30 Sep. 2024
Published: 07 Feb. 2025

HOW TO CITE:
Beaudet A, de Jager E, Tawane M, Billings B. Looking for the origins of the human brain: The role of South Africa in the history of palaeoneurology. S Afr J Sci. 2025;121(1/2), Art. #18604. https://doi.org/10.17159/sajs.2025/18604

ARTICLE INCLUDES:
☒ Peer review
☐ Supplementary material

DATA AVAILABILITY:
☐ Open data set
☐ All data included
☐ On request from author(s)
☐ Not available
☒ Not applicable

EDITORS:
Jemma Finch
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KEYWORDS:
Taung Child, *Australopithecus*, brain evolution, brain endocasts, ethics

FUNDING:
Centre National de la Recherche Scientifique (CPJ-Hominines)

In 1925, Raymond Arthur Dart published his description and interpretations of the 'Taung Child' in the journal *Nature*, including a description of the natural brain endocast associated with the face and mandible. Details preserved in the endocast of the Taung Child have opened critical questions and debates about how the human brain evolved, and how to identify and study evidence of brain changes from fossil hominin crania. In this paper, we review and synthesise methodological innovations (how do we study fossil hominin brains?) and critical conceptual shifts (how did the hominin brain evolve?) triggered by the discovery of the Taung Child. In particular, we detail the impact of the study of the well-preserved crania and natural endocasts from the southern African hominin-bearing sites on our understanding of brain evolution and the integration of newly developed analytical tools into research in palaeoneurology (e.g. imaging techniques, 3D modelling). Additionally, we examine how the use of digital replicas of fossil hominin endocasts and the need to study extant human brains to form a comparative platform might raise questions about research practices (e.g. study and exhibition of fossil and extant human brains) and management of such invaluable heritage resources (e.g. data sharing). We finally consider how our view of human brain evolution, and in particular the putative uniqueness of the hominin brain, has changed over the last century.

Significance:

We review and synthesise methodological innovations and critical conceptual shifts triggered by the discovery and description of the brain endocast of the 'Taung Child' by R.A. Dart in 1925. In particular, we detail the impact of the study of the well-preserved southern African hominin crania and natural endocasts on our understanding of brain evolution and the integration of newly developed analytical tools into palaeoneurology. Then, we examine how the use of digital replicas and the need to study extant human brains might raise questions about research practices and management of such invaluable heritage resources.

[Abstract in** Setswana**]

Introduction

In 1925, Raymond Arthur Dart published his description and interpretations of the 'Taung Child' in the journal *Nature*.[1] In addition to being the first tangible evidence of the African origins of the human lineage and the type specimen of a new hominin genus and species (*Australopithecus africanus*), the Taung Child preserves a natural brain endocast that initiated intense discussions about the mechanisms involved in the emergence of human neuroanatomical specificities (Figure 1A). As such, the description of the endocast by Dart, and subsequent research on the unique South African fossil hominin record by several generations of biological anthropologists, contributed to a new sub-discipline in biological anthropology dedicated to the reconstruction of the evolutionary history of the hominin brain. Consequently, the Taung Child triggered substantial methodological innovations (how do we study fossil hominin brains?) and critical conceptual shifts (how did the hominin brain evolve?). In parallel, the use of digital replicas of fossil hominin endocasts, as well as the need to study extant human brains to form a comparative platform raises questions about research practices (e.g. the study and exhibition of fossil and extant human brains) and management of such invaluable heritage resources (e.g. data sharing).

The impact of the discovery of the 'Taung Child'

How South African fossils changed the way we study brain evolution

In the absence of brain tissues, palaeoanthropologists have to rely on brain imprints preserved on the inner surface of the braincase (endocasts) to reconstruct the hominin brain evolutionary history (Figure 1). The interest of palaeoanthropologists in fossil hominin brains was likely sparked by successive major innovations in neurosciences revealing the intimate relationship between brain areas and functions. For instance, the identification of the role of Broca's and Wernicke's areas in language would probably have opened new perspectives on how to relate fossil crania with behaviours.[2,3] As such, the end of the 19th century and the beginning of the 20th century was marked by the publication of the first observations of fossil hominin endocasts (*Pithecanthropus erectus*[4]; Neanderthal[5]). Those landmark descriptions simultaneously started a long-standing debate about whether the information that palaeontologists derive from the study of endocasts is reliable.[6,7] Within this context, the discovery of the natural endocast of the Taung Child revived the debate about the reliability of the endocast and initiated key comparisons of the internal aspect of the crania with the associated brains in extant chimpanzees that support the presence of major sulcal imprints in the endocasts.[8] Far from being resolved, the debate persists, and South African researchers and institutions have recently played a central role in the discussion by using imaging techniques applied to living humans to quantitatively and directly compare, for the first time, the shape and organisation of the endocast and the corresponding brain[9], although previous direct observations of primate brain and braincase should be acknowledged[10,11].

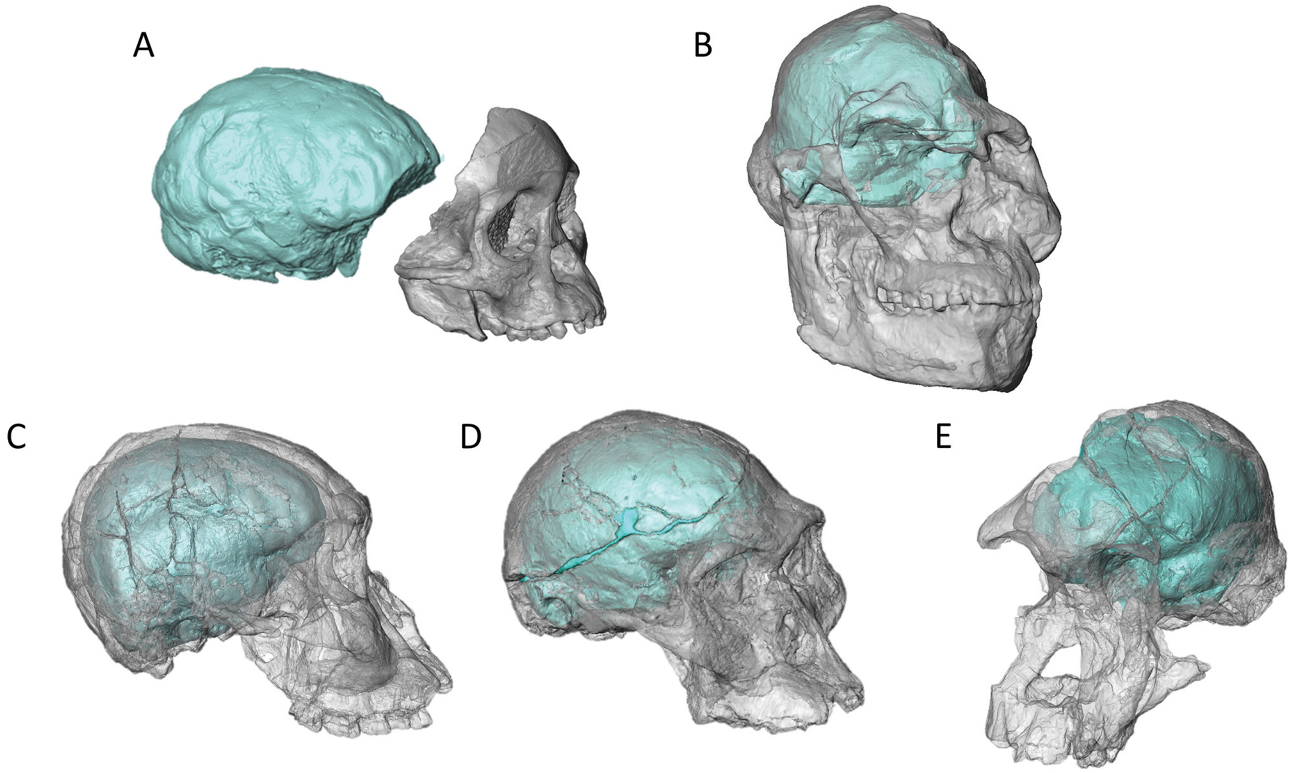


Figure 1: The endocasts of the 'Taung Child' (A) and of some of the most complete southern African *Australopithecus* crania (B: StW 573, C: Sts 71; D: Sts 5; E: StW 505). 3D models derive from surface scanning ('Taung Child') and microtomography.

South Africa has been a leader in the field of virtual biological anthropology since the very beginning of the use of X-rays in palaeontological studies. Early studies using computed tomography were applied to fossil material from the Cradle of Humankind (e.g. MLD 37-38, Sts 71, StW 505; Figure 1) to look at inner features, such as endocranial capacity and vascularisation.[12-14] Additionally, the very first scanning experiment using neutrons in palaeoanthropology was performed on the iconic *Australopithecus* specimen Sts 5 ('Mrs Ples'; Figure 1) at the South African Nuclear Energy Corporation (Necsa)[15], paving the way for future analyses of dense fossil specimens for which X-ray tomography failed to reveal an appropriate contrast between the bone and surrounding matrix[16,17]. Similarly, imaging South African *Australopithecus* crania with X-ray synchrotron radiation was fundamental for observing the fine organisation of the frontal lobe of *Australopithecus*[18] and the intimate details of the braincase[19].

In addition to imaging techniques, the study of South African hominin endocasts contributed to major analytical development. Because the endocast is a complex 3D object, accurately measuring variation in the respective organisation of the lobes and, more locally, brain areas, represents a challenging task (reviewed in [20]). As such, the use of landmarks and semi-landmarks[20], landmark-free surface-based comparisons[21-24] and automated detection of brain imprints[25,26] revealed previously unknown details of South African hominin brains. For instance, surface analysis of the best-preserved South African *Australopithecus* (Sts 5 and Sts 60) and *Paranthropus* (SK 1585) endocasts supported the hypothesis of a more derived brain shape in *Australopithecus* and identified local neuroanatomical specificities in the brain of *Paranthropus*.[24,25] At the same time, computer-assisted analysis of the well-preserved imprints in StW 573, StW 505 and MLD 3a emphasised the necessity of developing new methods for accurately identifying key features, such as the lunate sulcus.[25,26]

The contribution of South Africa to our understanding of human brain evolution

Details preserved in the endocast of the Taung Child have been crucial for opening new discussions about the chronology and processes involved in the emergence of derived neuroanatomical traits in the hominin lineage. Our brain is characterised by a complex structural organisation (i.e. sulcal and gyral pattern) and a prolonged maturation (reviewed in [27]). Interestingly, both aspects could be examined in the endocast from Taung and in the South African fossil hominin assemblage as a whole.

By comparing the endocast of the Taung Child with the brain of living humans and brain imprints in other fossil hominins, Dart identified significant differences used as evidence that *Australopithecus africanus* was a "man-like ape" contrary to early "ape-like man" descriptions of the more recent "Java Man".[1,28] In particular, he noticed that "[…] the sulcus lunatus has been thrust backwards towards the occipital pole by a pronounced general bulging of the parieto-temporo-occipital association areas"[1(p.197-198)]. A human-like posteriorly placed lunate sulcus in the Taung Child would have had substantial evolutionary implications as it would indicate an early reorganisation of the hominin brain. As a consequence, Dart's identification has been intensely discussed in the literature and the possibility of a more "primitive" (i.e. ape-like) configuration of the lunate sulcus and surrounding brain areas has been considered.[29-34] Interestingly, Dart himself corrected his own observations and identifications of brain imprints in the 'Taung Child' (reviewed in [31]), which is a vivid example of the complexity of "reading" brain endocasts.

Following the description of the endocast of the Taung Child, a very detailed description of the endocasts of South African fossil hominins eventually emerged, generating previously unknown knowledge of the neuroanatomical features characterising the brain of extinct species. One of the earliest and most comprehensive descriptions of fossil hominin brain imprints (sulcal and vascular), but also overall dimensions (linear measurements) and shape analysis (superimpositions of contours), focused on the natural and artificial endocasts from Taung, Sterkfontein and Kromdraai.[35] Similarly, pioneer descriptions of the middle meningeal vessels of early hominins were based on specimens from Taung, Sterkfontein and Swartkrans[36], including a previously unrecognised enlarged occipital/marginal sinus system in the Taung Child[37]. Sulcal imprints of iconic specimens in South Africa were further studied in great detail and fuelled critical discussions over the mosaic-like versus concerted evolution of brain areas[29-34,38,39] (Taung, StW 505, SK1585). Knowledge gained thanks to the exceptional quality of the South African fossil record was applied by palaeoanthropologists to the study of eastern African endocasts[40,41], and greatly improved our appreciation of regional and interspecific variation[39,42].

Besides the exceptional degree of preservation of the brain imprints in the Taung Child, the discovery of an immature *Australopithecus* represents a unique opportunity to learn more about fossil hominin brain growth and development. For instance, the interpretation of a possible remnant of the anterior fontanelle in the Taung Child as evidence of late fusion of the metopic suture, and thus prolonged postnatal brain growth, was actively discussed in the literature.[43,44] The comparative analysis of the size of the endocast of the 'Dikika child', found in 2000–2003 in Ethiopia[45], further supported the possibility that a derived pattern of brain growth (i.e. prolonged) might have emerged within *Australopithecus*, although they identified a lunate sulcus in an ape-like rostral location[46].

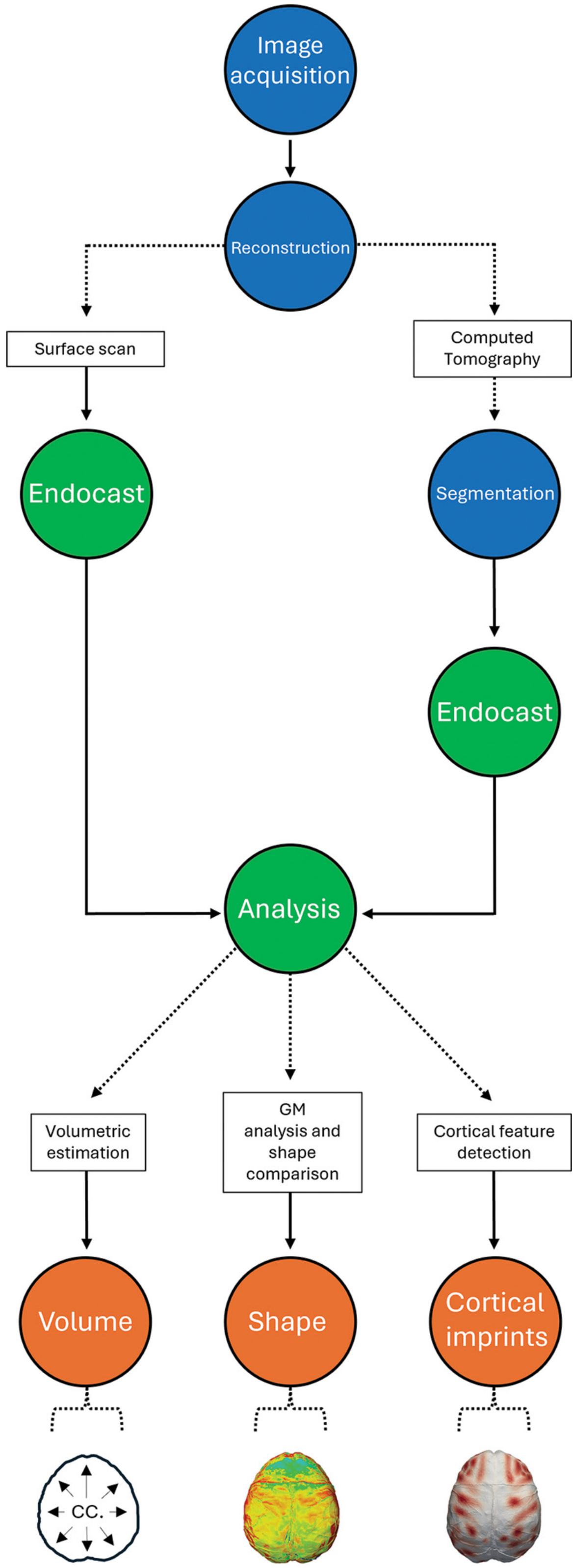
The impact of the discovery of the Taung Child is not limited to the understanding of *Australopithecus* neuroanatomy but is also reflected in the interest of palaeoanthropologists in brain endocasts and their potential in the search for human origins. For instance, the study of the endocast of the small-brained hominin *Homo naledi* found in Rising Star supported the presence of *Homo* species with a brain size similar to *Australopithecus* combined with a derived cortical organisation and rejected allometry as the only factor explaining the human brain specificities.[42,47,48] As such, (re-)analysis of the specimens attributed to *Homo* from South Africa could contribute to the unresolved question of when and how the derived human brain emerged. In particular, conundrums persist regarding the reorganisation of key brain areas, which the examination of South African specimens could help to elucidate. Recent studies of *Homo* specimens dated to 2.03–0.07 Ma from eastern Africa and Eurasia highlight the difficulty of identifying a pattern or evolutionary trends in a highly variable sample, including in crucial brain areas such as Broca's area.[49,50] Although the taxonomic status of some of these specimens is debated, partly due to their fragmentary nature, cranial remains found at Sterkfontein, Swartkrans and Drimolen attributed to *Homo*[51-53] (e.g. StW 53, SK 27, DNH 134) could therefore contribute to the clarification of the chronology of critical changes that affected Broca's area in the human lineage, with potential functional and behavioural implications.

Palaeoneurology today in South Africa

New technologies in palaeoneurology

As previously mentioned, the study of hominin brain evolutionary history is almost completely reliant on cranial endocasts which are replicas of the inner surface of the cranial vault. There are typically two types of endocasts that palaeoneurologists use to study brain morphology in the fossil record. The first type is a natural endocast, such as the endocast of the Taung Child, which is created when fine sediments infiltrate the cranial cavity shortly after death through the cranial foramina and solidify over time.[1] Alternatively, synthetic endocasts are typically created using moulding materials such as liquid latex and Plaster of Paris that are applied to the cranial area of interest.[39] These physical endocasts were analysed using predominantly qualitative methods and provided a platform for controversial debates in part due to the fragmentary nature of data inherent to endocasts, causing observational biases, and in extreme cases a scientific validation for scientific racism.[54] Besides their troubled past, endocasts are the best window into the living brain of our fossilised hominin ancestors and their hominid relatives.[55]

More recently, the introduction of imaging methods into palaeosiences provided palaeoneurology with an improved quantitative empirical approach for studying endocasts and brain evolution in the fossil record (Figure 2). The introduction of computed tomography (CT), 3D laser scanning[56], and, to a lesser extent, magnetic resonance imaging (often used in comparative studies[57]), allows scientists to analyse information quantitatively on a micro level of accuracy and encourages more collaboration as a result of digital data being easily shared through various platforms[58] (e.g. Morphosource). Additionally, CT imaging offers the opportunity to extract endocranial information from some of the most distorted and sediment-filled fossil crania using advanced reconstruction and segmentation techniques. For example, CT imaging enables us to extract the inner surface of the cranial vault through segmentation, where different materials are defined based on their grey values (determined by tissue densities[59]). Two segmentation techniques are widely used to extract virtual endocasts from fossil crania. The first is manual segmentation, which is more commonly used when fossil crania are



GM, geometric morphometrics

Figure 2: The typical workflow to analyse endocasts using modern techniques consists of image acquisition using computed tomography or 3D surface scanning to obtain or extract an endocast; following the derivation of an endocast, various analyses can be performed to obtain results.

filled with sediments (e.g. frontal bone of Taung Child); these sediments are removed to expose the internal table of the cranial vault. Manual segmentation tools are widely available through commercial software such as Avizo (Thermo Fisher Scientific Inc.) or open-source software such as 3D Slicer (www.slicer.rog) to name a few. Alternatively, an automatic segmentation tool can be used to extract the endocast directly from the manually cleaned cranium or from crania that are not filled with sediment. Some specialised open-source segmentation methods are readily available, such as Endex software[60] or, more recently, the R package Endomaker[61]. Both have their advantages and disadvantages, depending on the condition of the cranium.

Following the segmentation and extraction of the virtual endocast, the cranial capacity can be easily calculated, and various analytical methods can be applied in order to calculate shape differences between endocasts using registration techniques or, alternatively, the thin-plate spline (TPS) method[62,63], and surface morphs[64]. Both latter methods are dependent on geometric morphometrics.[63] Additionally, landmark-free surface-based comparisons within which surface deformations between different objects are mathematically modelled as diffeomorphisms were applied to fossil specimens with the objective of quantifying shape differences.[22-24]

In addition to calculating shape differences between endocasts, extensive efforts are being invested in finding ways to automatically detect the imprints of sulci and gyri that the brain imprints on the inner table of the cranial vault. The study of imprints on the surface of the endocasts has extensively improved since the incorporation of 3D imaging techniques. Although visual methods to define sulcal imprints are still used, in some studies, more innovative methods are applied to illuminate sulcal imprints on endocasts. For instance, for the *Australopithecus afarensis* endocast of DIK 1-1 from Ethiopia, the authors used the TPS method to warp a segmented brain of a chimpanzee onto the endocast of DIK 1-1 for comparison. They were able to successfully confirm the rostral ape-like position of the lunate sulcus on the DIK 1-1 endocast using this method.[46] Another method that can be used is the Curvature module in Avizo and various other imaging software to highlight topographical changes on the endocast surface[47]; however, this can be misleading as it still relies on visual observations and does not give quantifiable data on sulcal imprints. More recently, feature detection techniques have been introduced to automatically detect cortical relief on endocasts using a crest line detection method.[65] This method has proven successful in accurately detecting cortical imprints on both fossil and extant human endocasts.[25,50,66] Additionally, this method allows for further analysis of variation of sulcal imprints within species using methods that are typically used in neuroscience.[67]

Methods for studying hominin endocasts have significantly advanced since the discovery of the Taung Child. The rapid advancement of computational methods for analysing imaging data, coupled with ongoing progress in machine learning and artificial intelligence, as well as the expertise on fossil brains developed in South Africa, promise to unveil intriguing mysteries around the evolutionary history of the hominin brain in the immediate future and assist with the subjective nature of the process of identifying brain imprints.[68]

Curation, heritage policy, ethics and dissemination

As detailed in the previous section, fossil hominin endocasts can be studied by palaeoanthropologists as physical or virtual objects. As with any other fossil remains, accessing natural fossil hominin endocasts stored in South African curating institutions (e.g. Ditsong National Museum of Natural History) requires following the procedure established by the *National Heritage Resources Act* (NHRA). The main objective of the act is to conserve, protect, and offer guidance on the management of heritage resources. As such, an application has to be submitted, and access is granted only after careful consideration of the merits of the study and the lack of any detriments that could befall the specimen during the study. However, curating fossil hominin digital endocasts comes with more complexities. Indeed, the situation is dire with regard to digital data[69] and, because of a lack of appropriate infrastructure, records management in most government entities (inclusive of museums as curating institutions) is on the brink of collapse. This lack of infrastructure has created a situation in which the fossil digital data of some museums resides with third parties, because the curating institution is not capable of hosting and managing their own data. Digital data can be passed along to a group of researchers, without due process being followed, as is expected by the curating institutions. Transparency, disclosure and honesty are at times lacking when researchers share digital data.[58] There is still a gap in the legislative frameworks to govern the management of digital data, with the National Policy on the Digitisation of Heritage Resources[70] still in a draft format. Access (open or otherwise) to these digital data/repositories is also yet to be determined by the laws of the country. Open access is believed to have the capacity to address the fragmentary manner in which access to journals and information systems was set up in the past by the apartheid government, which favoured a select few. The belief is that research information and access to data should be set up on a platform that gives equal opportunity to South African scholars and students.[71] Ironically, some of the best-preserved brain endocasts are not subjected to the same extreme scrutiny as most of the well-known preserved hominins in these curating institutions are.

Socially, especially in a South African context, the brain, as a human body organ, is regarded as sacred, and is to be treated with the utmost respect, whether it is fossilised or fresh. When one speaks to the Taung communities about the brain endocast of the Taung Child, one is met with shock, because their traditional and cultural beliefs are that human remains are to be buried, not to be displayed for all to see. The explanation of deep time and accurate scientific information is at odds in this case with the subject of handling and prodding human bodies, which is regarded as taboo, as is donating one's body for research and teaching.[72] In parallel, understanding brain evolution also requires a solid knowledge of the extant human brain through physical or digital (medical imaging) dissection. Contemporary human brains are a requirement for comparative analysis with fossil endocasts, to understand the neuroanatomical underpinnings and associated functional correlates used to inform the narratives about brain evolution. These human brains are sourced from South African health sciences institutions through different modes of consent, which include bequeathal, next of kin and unclaimed. Unclaimed individuals include decedents that have not been claimed by family members; as such, no consent has been provisioned and, in these instances, the inspector of anatomy may "donate" these remains to institutions according to the *South African National Health Act*.[73] Whilst this method of acquiring bodies and brains is legal, it is considered unethical due to the lack of informed consent. However, many institutions in South Africa have made concerted efforts in leading ethical body sourcing in Africa[72]; the School of Anatomical Sciences at the University of the Witwatersrand has been at the forefront of this ethical transition[74]. Good ethical practice, which has not always been a central feature of South African scientific research, is becoming more focused and prominent, evidenced by the inclusion of oversight committees, improved curatorial policies and legislative changes. These interventions garner trust from communities, ensuring their inclusion and donation to the academic programme. Accordingly, it is of the outmost importance that the scientific community is transparent about their research by sharing the findings with a broad public audience, explaining the scientific process and why it requires the use of sensitive material, such as fossils and fresh human brains.

South African scientists invariably contribute to making evolutionary science more visible and understandable to a lay audience. Besides being one of the main tourist attractions in the Cradle of Humankind, the Maropeng Visitor Centre plays an active part in disseminating scientific knowledge and offering educational resources on human origins. Human brain evolution, from Taung to extant humans, represents a key component of the "What makes us human" exhibition and featured in successful exhibits, such as the one entitled "Face to Face: Reconstructing Hominins from the Cradle of Humankind" launched in 2022 and coordinated by Kimberleigh Tommy[75] (Figure 3). Brain evolution being put forward as a major factor shaping human evolution in such popular exhibitions, can likely be considered the result of 100 years of intense research on hominin brains in South Africa, triggered by the exceptional discovery of the Taung Child. This is of particular importance to South Africans due to the fact that the discovery of the Taung Child corroborated to the world that the origins of humankind

Source: Courtesy of EndoMap (reproduced with permission).

Figure 3: Photograph of the exhibit "Face to Face: Reconstructing Hominins from the Cradle of Humankind" launched in 2022 at Maropeng.

were in Africa. In addition, certain studies during apartheid tried to use the human brain as a tool to demonstrate a hierarchy of the endowment of intelligence interracially, which was consequently debunked.[76] Further to which, an accurate understanding of how the brain functions and evolved allowed for the abandonment of earlier egregious ideologies centred on discrimination such as the eugenics movement.

Perspectives

The study of brain endocasts, and the popularity of research on what is considered the most unique and complex organ in extant humans, have certainly contributed to reinforcing the disproportionate interest of palaeoanthropologists in cranial remains over postcranial remains (see Schroeder et al.[77] in this issue) and bias our view on what makes us so special. While the role of the brain in human biological and cultural evolution cannot be denied, the putative exceptional nature of the human brain specificities (i.e. large brain, complex organisation, delayed maturation) is regularly questioned and the uniqueness of humankind reconsidered. For instance, the frontal lobes often feature in research looking for human-specific neuroanatomical traits with behavioural implications, such as the organisation of Broca's area and language (reviewed in [78]). However, studies on extant great apes have demonstrated that humans do not have particularly large frontal lobes[79] and that this region did not evolve faster than others within our lineage[80]. Moreover, hypotheses suggesting a coincidental emergence of some of the most intriguing characters of the human brain are gaining support (e.g. exaptation of the Broca's area for language, primary role of the braincase over the brain[81,82]) and question our mechanistic view of human brain evolution while raising new interesting questions (e.g. can we explain human brain evolution?). On a similar note, moving away from the traditional anthropocentric approach, the comparative study of non-related taxa, such as birds, has opened new avenues of research and possibilities to test long-standing evolutionary hypotheses (reviewed in [58]). After 100 years of research on hominin brain evolution, an exciting new journey has begun that will benefit from the development of new technologies (e.g. AI[83]).

Acknowledgements

We sincerely thank the editors for their invitation to contribute to this special issue.

Funding

The support of the French National Centre for Scientific Research (CNRS) towards this research is hereby acknowledged (CPJ-Hominines).

Data availability

There are no data pertaining to this study/article.

Declarations

We have no competing interests to declare. We have no AI or LLM use to declare.

Authors' contributions

A.B.: Conceptualisation, writing – initial draft, writing – revisions. E.d.J.: Conceptualisation, writing – initial draft, writing – revisions. M.T.: Conceptualisation, writing – initial draft, writing – revisions. B.B.: Conceptualisation, writing – initial draft, writing – revisions. All authors read and approved the final manuscript.

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