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From fossils to mind

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Fossil endocasts record features of brains from the past: size, shape, vasculature, and gyrification. These data, alongside experimental and comparative evidence, are needed to resolve questions about brain energetics, cognitive specializations, and developmental plasticity. Through the application of interdisciplinary techniques to the fossil record, paleoneurology has been leading major innovations. Neuroimaging is shedding light on fossil brain organization and behaviors. Inferences about the development and physiology of the brains of extinct species can be experimentally investigated through brain organoids and transgenic models based on ancient DNA. Phylogenetic comparative methods integrate data across species and associate genotypes to phenotypes, and brains to behaviors. Meanwhile, fossil and archeological discoveries continuously contribute new knowledge. Through cooperation, the scientific community can accelerate knowledge acquisition. Sharing digitized museum collections improves the availability of rare fossils and artifacts. Comparative neuroanatomical data are available through online databases, along with tools for their measurement and analysis. In the context of these advances, the paleoneurological record provides ample opportunity for future research. Biomedical and ecological sciences can benefit from paleoneurology's approach to understanding the mind as well as its novel research pipelines that establish connections between neuroanatomy, genes and behavior.

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What, if anything, can fossils tell us about the mind? Paleontologists draw links between anatomical details that are preserved in the fossil record (e.g., the dimensions of a bone) and functions (e.g., locomotion). We start from the premise that "minds are simply what brains do"[1], but understanding minds through fossils has proven to be a tortuous task at the center of a very contentious topic. Brain tissue does not fossilize like teeth and bones do, so it is only possible to observe the internal cavity of the skull's braincase – called the endocranium – to understand external brain anatomy of extinct species. Endocasts – naturally occurring or artificially manufactured internal casts of the endocranium that *look* a lot like brains – only provide information about a few gross anatomical features, whereas a comprehensive understanding of brain function needs to incorporate microstructure, gene expression, connectivity, biochemistry, physiology, and behavior, among others. Furthermore, the structural and functional bases of the cognitive abilities that differentiate humans from other species are not fully understood even in present day humans and primates.

The evolutionary history of the human brain is fundamental to understanding the modern human mind. As the field of brain evolution has drawn increasingly from biomedical methods such as neuroimaging and genomic analyses, it has also become clear that the field can contribute to human health and well-being. Aspects of brain structure and function that are particular to humans may be linked to our susceptibilities to neurodegeneration and mental health disorders. Evolutionary history forms a foundation for translating animal models of human conditions.

The evolutionary history of the species we discuss is represented in a phylogenetic tree (Fig. 1). The human brain is best understood through comparisons with closely related species of primates and other mammals, and also more distantly related species, which share both ancestral and convergent features with humans. The study of birdsong, for example, has provided essential insight into the neural mechanisms of vocal learning in birds, and its convergence with human language[2]. Early amniotes, including dinosaurs (early relatives of birds) and early synapsids (early relatives of mammals), provide a broader evolutionary perspective. Our own species (*Homo sapiens*) is a member of the great ape clade, also called hominids, along with three other great ape genera: *Pan* (*Pan troglodytes* - chimpanzees and *Pan paniscus* - bonobos), *Gorilla* (*Gorilla gorilla* - Western gorillas and *Gorilla beringei* - Eastern gorillas), and *Pongo* (*Pongo pygmaeus* - Bornean orangutans and *Pongo abelii* - Sumatran orangutans). The term "humans" refers to both fossil and present day *Homo sapiens*, and where relevant it can also include closely related archaic human species who have been shown to have made recent contributions to our genome. Hominids have among the largest brains of all animal species, except for the most massive ones – proboscideans (elephants) and cetaceans (whales and dolphins)[3]. Within hominids, our closest extant relatives are the chimpanzees and bonobos, with whom we shared our most recent common ancestor approximately 7–10 million years ago (Ma)[4,5]. Hominins include *Homo sapiens* and those fossil species that are more closely related to them than to chimpanzees and bonobos. There are numerous hominin species which evolved and became extinct over the past 6-7 million years, including species of the genus *Australopithecus*, from which the genus *Homo* likely arose approximately 2.8 Ma, as well as at least one other now extinct genus called *Paranthropus*[6] (Fig. 2). In this review, we primarily focus on hominins, but also cover aspects of brain evolution in other species.

First, we review what we know about brain anatomy from the fossil record, and the state of the art in paleoneurology. Second, we discuss the gaps in our knowledge about brain evolution and highlight the need for more comparative research concerning energetics, function, and development. We seek to address big theoretical questions about what makes the modern human brain different not just from all other extant species, but even from the Neanderthals (*Homo neanderthalensis*), which are closely related archaic humans with whom *Homo sapiens* interbred for thousands of years[7,8]. These questions may have been asked for centuries, but answering them requires more comparative investigation of biological mechanisms. Third, we point to emerging directions in the field. We provide guidance to researchers to move the field forward. We indicate how mechanistic evidence from molecular and evolutionary biology can now be used to triangulate findings from studies of endocasts. We highlight the potential of new fossil and archeological discoveries and discuss how to best use neuroimaging methods to interpret anatomy from endocasts. Finally, we point to the possibilities that can arise from better data sharing and provide a link to an online list of tools and resources in neuroscience and paleontology.

Data we can obtain from endocasts

The study of brain evolution in extinct animals based on their fossil remains was made possible by the introduction of endocasting techniques in paleoneurology[9–11]. The soft tissues of the nervous system rarely fossilize (with some exceptions[12,13]). As the brain grows and expands during ontogeny, its surrounding structures leave an imprint in the cranial bone. Endocranial imprints in fossil crania can therefore provide evidence about brain size, vasculature of the meninges, and aspects of brain morphology, including overall shape, sulcal patterns, and lateralization. It is notable that adult brains do not fill the entire cranial cavity, and that the space between the brain and the braincase is filled with cerebrospinal fluid, meninges, and blood vessels.

Size. Brain size is mainly assessed indirectly through studies of endocranial volume, and thus depends on assumptions about the relationship of the brain to the braincase. Early on, greater brain size was assumed to represent higher intellectual capacities like memory or problem-solving abilities, and it was used to infer possible behaviors like sociality, complexity of the hierarchical system, the nutrient richness of the diet, and behavioral flexibility[14]. Brain size has long been a central consideration in understanding human evolution, especially because the human brain is large. The human brain is 3-4 times larger in volume than that of other hominids and appreciably larger than would be predicted by allometric scaling for a primate of similar body size[15]. Parallel to this, the archeological record provides evidence for increasing technological sophistication. However, the association between archeological artifacts and their makers is not always certain, and is constantly revised in light of new paleontological and archeological discoveries[16]. Members of the genus *Australopithecus* lived approximately 4.2–2 Ma and had adult endocranial volumes on average 20% larger than chimpanzees[17–19]. Historically, inclusion in the genus *Homo* required an arbitrary minimum brain size, as well as association with stone tools[20], but this has since been updated due to evidence for toolmaking that predates the appearance of *Homo*[21] (see discussion further on in the review). Also, two relatively recent species of *Homo*, *Homo floresiensis* and *Homo naledi*, had unexpectedly small endocranial volumes[22–24]. Trends in brain size increase have also been hypothesized in other mammalian lineages. According to Marsh[25], during the Paleogene, all mammals had a small brain and there was a gradual increase in the size of the brain over evolutionary time, yet this was not the case in all clades. Likewise, reductions in brain size have been hypothesized

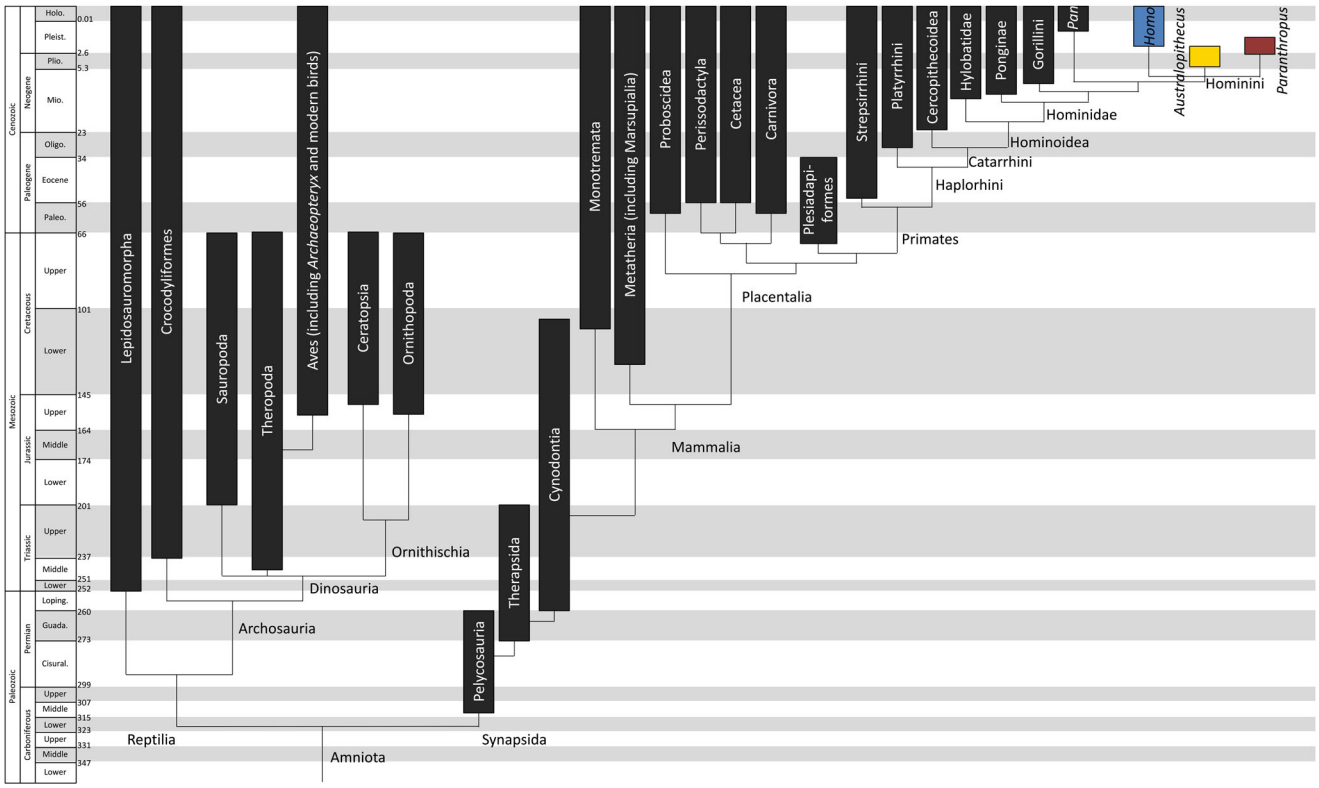


Fig. 1 Time-scaled phylogenetic tree of amniotes. Included are taxonomic groups covering species discussed in this review and the accompanying "From Fossils to Mind" edited volume[304]. The geological time scale is from Cohen et al.[305]. Phylogeny and time ranges are based on Benton[306], Kemp[307], Sues[308], and Kumar[309].

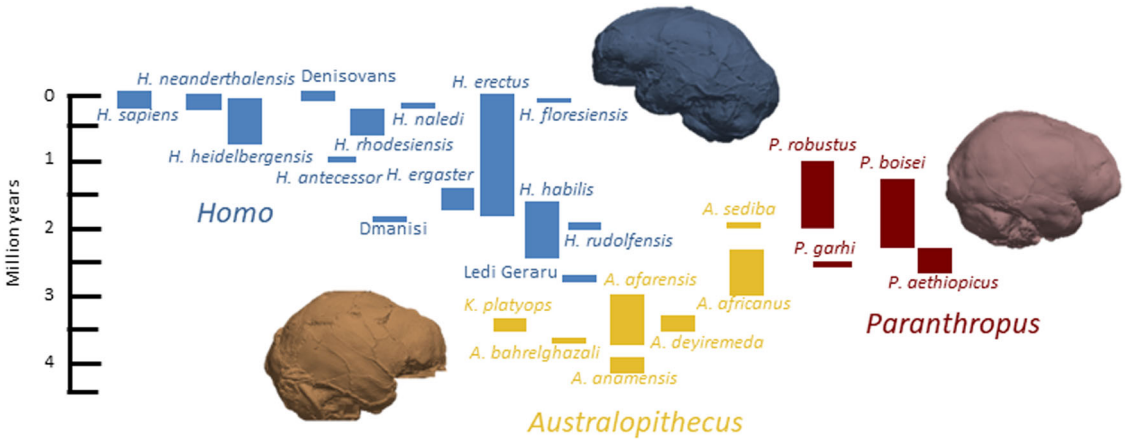


Fig. 2 Hominin species time ranges and approximate taxonomic groupings into the three major hominin genera. In order of first appearance, *Australopithecus* (yellow), *Paranthropus* (red) and *Homo* (blue) species are plotted against a time scale, after Wood et al.[310]. Virtual endocasts are featured to represent each genus.

in other vertebrate lineages. It is currently accepted that some species have smaller brains than their ancestors, including some primates[26] and sauropod dinosaurs[27]. The ratio between brain size and body size is under dynamic developmental constraint and evolves independently, in terms of direction and rate, in different vertebrate taxonomic groups[28].

As absolute brain volume was shown not to be a reliable proxy of intelligence and/or cognitive ability across animals, Jerison[29] proposed the use of an Encephalization Quotient (EQ) – the ratio between actual brain size and expected brain size (as derived from regression with body size among different reference species). The aim was to control for the allometric relationship between brain and body size, for relevant cross-species comparison of brain size variability. Comparisons between different clades have established that some groups display a mean EQ above 1, like carnivorans, cetaceans, primates, and birds. In dinosaurs, a modified measure of encephalization developed by Hurlburt[30], the Reptile Encephalization Quotient (REQ), shows disparity between various clades. Sauropod and ceratopsian dinosaurs have values under 1, whereas ornithopod and theropod dinosaurs display higher values[31].

Although relative brain size has been proposed to be an index of cognitive ability, the relationship between brain size and

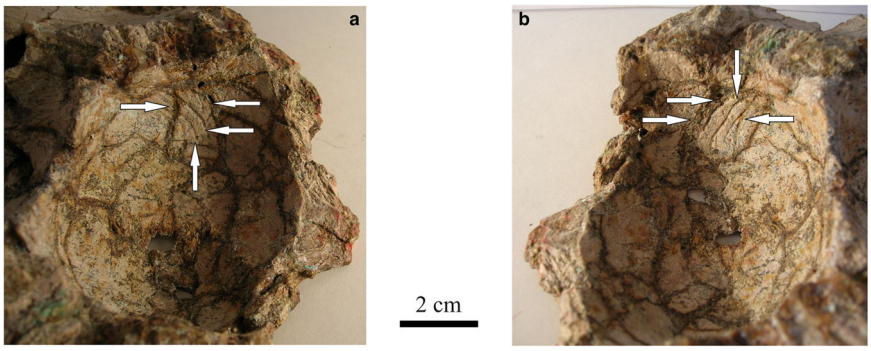


Fig. 3 Valleculae on the frontal bone of a hadrosaurid dinosaur. a, b Internal surface of the frontal bone of a hadrosaurid dinosaur (*Amurosaurus riabinini*, AEHM 1/240) viewed on the left side and right side. Arrows point to some of the valleculae. (Lauters[311], available at https://doi.org/10.5281/zenodo.7454914).

behavioral repertoire is hotly debated. Even after accounting for body size, some proboscideans and some cetaceans do have or have had brain sizes comparable to some representatives of the genus *Homo* (EQ of about 5), which should be considered when discussing the relevance of brain size to intelligence[32–34]. Furthermore, decades of research in primates have stressed a relationship between brain size and ecological factors[35,36]. However, social factors could be under explored due to greater difficulty in defining and obtaining relevant ethological data[37,38], which could have more localized effects on brain organization[39,40]. These disparities can also be seen in examples from the vertebrate paleontological record. For example, the dwarf elephant of Sicily (*Palaeoloxodon falconeri*) reached an EQ of 5 and up to 7 on a purely herbivorous (low quality) diet[33]. Thus, the use of EQ as a proxy of intelligence is contentious, and other constructs have been proposed to better represent the mechanisms linking brain size and cognition[41].

Vasculature. Cerebral blood flow is an indication of brain activity, including cognitive and other physiological processes. Blood flow to and within the brain in fossil specimens can be estimated from depressions made by blood vessels on the inner surface of the endocast, called valleculae, as well as from bony canals. Valleculae appear when the brain is in close contact with the bone surface, being more pronounced when the meninges are thin[9,42]. The observation of valleculae suggests a close apposition between brain surface and endocranial surface, indicating that the endocranium can be used to assess the size and shape of the brain in extinct vertebrate species. The space between the brain and skull is particularly noticeable in reptiles with smaller brains, including some extant lepidosauromorph reptiles such as sphenodons and iguanas. However, in most mammals and archosaurs (birds, dinosaurs, and alligators), the brain takes up a larger portion of the endocranial cavity and endocasts can serve as a reliable proxy for brain size and shape[43]. Although it had previously been assumed that dinosaur brains only occupy half of the endocranial cavity[29], the discovery of valleculae has shown that some dinosaur brains were larger than previously estimated[30,44]. Among dinosaurs, Osmólska[45] and Evans[46], and later Godefroit et al.[47] and Lauters et al.[48], showed the presence of valleculae in Oviraptoridae, Pachycephalosauridae and Hadrosauridae (Fig. 3). Within hominins, a close correspondence between brain and endocranial sizes has long been assumed[29]. However, the degree to which the brain fills the cranial cavity varies among mammalian groups, with notable exceptions such as proboscideans[32].

Vascular imprints in hominin endocasts and foramina through the cranial base have featured in discussions about taxonomy[49,50], thermoregulation[51] and blood flow rate[52]. Studies of the vascular imprints in fossil hominin endocasts identified specific patterns in early hominins, with *Paranthropus* being characterized by an enlarged occipital-marginal sinus, while the middle branch of the middle meningeal vessels cannot be found in *Australopithecus*[49,50], but see[53]. The reorganization of the vascular system in early hominins has been interpreted by some as evidence for the emergence of a thermoregulation system for cooling down the brain under conditions of hyperthermia (the "radiator" theory[51]). Indeed, thermal stress might represent a severe biological and evolutionary constraint, especially if we consider the increase in brain size within the hominin lineage and the role of brain volume in heat production. Additionally, the size of the arteries, inferred from the size of the foramina in the cranial base, gives us an idea about blood flow and brain glucose utilization, a relationship which has been examined across mammals[52,54]. A study taking advantage of this correlation to infer brain metabolism reported a disproportionate increase of blood flow rate to the brain in fossil hominins[52].

Shape. All adult vertebrate brains have three major portions: a forebrain (prosencephalon), a midbrain (mesencephalon), and a hindbrain (rhombencephalon). In recent years, comparisons between vertebrate brains have benefitted from an updated nomenclature[55] that reflects homology between structures (i.e., similarity due to evolutionary relationship). New methods, such as profiling neurons on the basis of transcriptomes, have provided new tests of homology[56]. However, differences in the relative size and shape of these portions and their components can make it difficult to directly compare the brains of distantly related species from fossils alone, since only the outer shape of the brain is preserved.

In most amniote species, such as dinosaurs, the forebrain, midbrain, and hindbrain are discernable on fossil endocasts. The cephalic and pontine flexures of the brain can be summarized as the angles between the forebrain and midbrain, and midbrain and hindbrain, respectively, and can be determined from endocranial surfaces. Such brain endocast flexure is known to vary substantially across species, but there is an overall trend toward greater flexure in small animals and less flexure in large animals[57]. This trend is also observed ontogenetically, where younger individuals have more marked flexures than mature individuals[58]. This is due to the negative allometric scaling of the brain, where smaller animals tend to have a proportionately larger brain that is more restricted by the size limits of the skull and spatial limits from other structures, such as the eyes. As a result, they tend to have increased flexures to accommodate the spatial restrictions of the skull[59].

Discernable features of mammalian endocasts are disproportionately cerebral (i.e., corresponding to the pallium of the

telencephalon). Due to the development of the neocortex in mammals, the outer surface is mainly telencephalon which covers structures of the diencephalon and midbrain, with the impressions of ventral hindbrain and cerebellum also visible in endocasts. With increased encephalization in primates, other brain parts are positioned mostly inferior to the cerebrum and contribute to a flexion at the cranial base.

In humans, the cerebrum is disproportionately even larger and more superiorly positioned, enveloping most of the brain except for the cerebellum (a structure of the hindbrain). The folding of the cerebrum into convolutions made up of sulci and gyri is partially represented on fossils. In addition, overall cerebral form can also be studied. The shape and size of the human cerebellum is also represented in endocasts[60], however its very fine folds (called folia) are not imprinted on endocasts. A striking finding of cerebral shape comparison is that, while both present day and fossil *Homo sapiens* are similar in endocranial volume to Neanderthals, they have different endocranial shapes with only present day *Homo sapiens* being characterized by a "globular"[61] endocranial shape. This globular shape is related to the emergence of taller frontal area, more bulging parietal areas, round occipital area housing a large and bulging cerebellum, and narrow and anterior-medially oriented temporal poles[62–64]. As part of this process, the basicranium became more flexed. The cranial base also flexes during the first year of life of extant humans[65]. This trait emerged relatively recently within the lineage[62,66,67] and is addressed further on in the review.

Cerebral sulci. The boundaries of cerebral cortical areas in fossil hominins are often assumed to be closely, if not exactly, associated with sulci which are sometimes evident in extant species[68–71]. Understanding the functional relevance of cerebral sulci and gyri is thus crucial for deriving as much information as possible from endocasts. It has been shown that the number of cortical areas increases with brain size across mammals[72–75] as does the complexity of sulcal morphology across species[76,77] and among humans[78]. The number of distinct cortical areas, however, does not appear to vary substantially with brain size among anthropoid primates. Homologues of human prefrontal cortex areas, for example, have been described in macaque monkeys[79]. In humans, the presence of the paracingulate sulcus as an additional fold in some subjects has been linked to subtle cytoarchitectural variation[80] as well as behavioral[81] differences (see Toro[77] for a discussion). In macaques, thalamic inputs to the primary visual cortex have been found to be involved in the development of primary visual cortex histology as well as the positioning of the lunate sulcus[82]. Computer simulations have found that convolutions may occur at cortical area borders as a mechanical consequence of cortical growth[77]. This notion of mechanical stress is congruent with research relating the development of gyri to growth factors that increase neurogenesis[83] as well as the finding that fold wavelength – the width of a fold – is conserved among primates[26] given the relatively stable cortical thickness.

While we cannot test brain function in extinct species, we are able to use key features to make inferences about various functional brain regions and their boundaries. Two regions of the cortex differ considerably in sulcal morphology between humans and nonhuman primates and are of interest to paleoneurologists: the inferior frontal gyrus, in which Broca's language area is situated, and the lunate sulcus, associated with changes in the size of the parietal association cortex relative to the occipital visual cortex[84,85]. When part of the cortex has expanded large enough to fold over and cover another one, the overhanging part is called an operculum. Developmental studies show humans have gained frontal and orbital opercula in the inferior frontal gyrus, making the morphology of the sulci more complex. Additionally, humans never develop a deep lunate sulcus covering other gyri as seen in nonhuman primates, making their sulcal boundaries more simplified in this region[86,87].

It is a matter of debate in paleoanthropology to what extent evolutionary changes in sulcal patterns are causally linked to species differences in overall brain volume. Early australopiths had sulcal patterns more similar to extant great apes in form[19,53], while later, larger-brained members of *Homo* had sulci that more closely resemble modern humans[17], but the sulcal pattern in later australopiths and early *Homo* is still debated[88]. Clarifying the timing and functional consequences of these sulcal changes requires new resources, more fossils, more comparative data from extant ape brains for reference, and innovative approaches from other disciplines.

Lateralization. Several brain functions in humans and many other vertebrates are lateralized[89], which is reflected in associated lateralized behaviors[90]. Prime examples for asymmetrically organized brain functions are lateralized vocalization systems and limb preferences in many vertebrate species[91,92]. In many nonhuman primate species, for example, there is asymmetry in hand skill and preference related to the motor demands of different actions[93]. Behavioral lateralization in humans and nonhuman primates has been linked to hemispheric asymmetry in the anatomy of various brain regions, including the primary motor cortex and inferior frontal cortex[94,95], as well as the morphology of the corpus callosum[96,97]. Indeed, it has been hypothesized that hemispheric specialization increased in hominins along with handedness, tool use and making, and language[90].

While extant primates in general exhibit lateralization in these faculties, humans are thought to stand out by showing more consistent and more robust functional lateralization patterns[89]. The human cerebral cortex displays a larger degree and greater range of leftward directional asymmetry compared to chimpanzees, particularly in the posterior perisylvian region[98]. Given that lateralization of brain functions has been suggested to be associated with maintaining rapid conduction within intrahemispheric circuits to support time-critical computational processes[99,100], this difference could be considered an important step in human evolution as language and toolmaking capacities emerged[90]. However, it is a matter of debate which aspects of brain asymmetry are uniquely human, as very little is known about brain asymmetry in great apes beyond data from chimpanzees. To fill this gap, endocranial imprints captured from computed tomography (CT) scans have been studied as proxies for brains. For example, Neubauer et al.[101] measured the magnitude and pattern of endocranial shape asymmetry in humans, gorillas, orangutans, and chimpanzees. They found that the magnitude of asymmetry was about the same in humans, gorillas, and orangutans. Chimpanzee endocasts, however, were less asymmetrical on average than those of their great ape and human relatives. These endocranial results corroborate Gómez-Robles et al.[98] findings on the differences between chimpanzee and human brains as determined from magnetic resonance imaging (MRI) scans, but the broader comparative context suggests a different evolutionary interpretation: perhaps chimpanzees are unusually symmetrical among hominids. Neubauer et al.[101] also examined the pattern of asymmetry and were able to show that not only humans, but also chimpanzees, gorillas, and orangutans exhibited the pattern of asymmetry previously described as typically human: the left occipital lobe, the right frontal lobe, and the right temporal pole and right cerebellar lobe protruded more relative to their contralateral parts. These results challenge the long-held notion that the human asymmetry pattern is unique.

Evidence of lateralization in fossils might improve our understanding of the emergence and development of complex cognitive abilities in hominins[102]. As summarized in Uomini and Ruck[103], hand preferences can be determined from behavioral evidence such as cave paintings (e.g., proportions of left and right handprints found), stone tools (e.g., direction of traces of use on stone tools) and striations on fossil teeth (when they were used in gripping an object), from directional asymmetries measured on skeletons (e.g., arm bones), and from endocranial asymmetries. For example, evidence of right-handedness at the population-level was deduced from dental striation analyses in *Homo heidelbergensis*, *Homo neanderthalensis*, and fossil and present day *Homo sapiens*[104]. Furthermore, it was found that the average spatial asymmetry pattern on endocasts is shared among extant hominids and among fossil hominins[105], but that humans show a pattern of asymmetry more variable than great apes, which may reflect increased functional and developmental modularization of the human brain[101]. Unfortunately, fossil evidence of behavioral and anatomical hemispheric asymmetries is scarce, and fossil preservation sometimes makes it difficult to observe and measure the underlying patterns of anatomical asymmetry.

Unresolved questions

Theories about brain evolution center around these questions: What are big brains for? Could an increase in brain size serve different functions in different species? Could changes in the way brains function occur independently of changes in brain size? Could the development of large brains relate to plasticity, and in particular, culture? *We need to know what big brains do*. Humans claim the largest brain size (in weight and neuron number) relative to body size, with some aspects (e.g., surface area of association cortex) being particularly pronounced. To enrich our understanding of human brain size, it is important to consider how brain size is interpreted in distantly related species. We can gain insight into how large brains work by looking at convergent mechanisms of evolution in brain weight, neuron number, neuron density, energetics, and organization. Humans belong to one of only three groups of species that have brains over 700 g, along with whales and elephants. Birds also provide opportunities to study convergent mechanisms, and have much higher neuronal densities than mammals, with total neuron numbers that fall within primate range[106]. While the hominin fossil record provides the only direct evidence about encephalization in humans, a more thorough understanding of brain size changes could come from studying other vertebrates such as large-brained mammals, neuron-dense birds and their closest relatives (dinosaurs and crocodiles), as well as early synapsids, which allow us to draw deep comparisons between these groups.

The brain's function as a "mind" depends on the whole body in which it is integrated. Sensory, motor, and physiological processes depend on the brain and the body together. Brain activity impacts the body beyond conducting mental functions, most obviously by consuming energy and producing heat. As such the paleoneurological evidence is best understood in the context of evidence from diverse research areas including comparative physiology and experimental archeology, among others.

Energetics. Average endocranial volume increased during the evolution of the genus *Homo* from approximately 600 cm^3 in *Homo habilis* to 1350 cm^3 in present day *Homo sapiens*[62,107]. However, some later species, *Homo naledi* and *Homo floresiensis,* had less than half the brain mass of *Homo sapiens*. Besides the advantages of having a larger brain with more neurons providing more processing power, increase in brain size comes at a cost. Brain tissue is one of the most energetically demanding tissues in the mammalian body[108]. For example, in *Homo sapiens*, the adult brain requires 20% of the daily energy intake, even though it makes up only about 2% of the body mass[109], and cerebral blood flow estimations based on the size of cranial foramina for some related mammalian species indicate that their brains are similarly expensive[54]. Remarkably, human children's brains, at the time of peak formation of neuronal connections, consume more than 60% of the body's resting metabolism[110]. Most of the energy funneled into the brain is claimed by its approximately 90 billion neurons, mostly for signaling processes and maintenance of resting potentials[111,112]. Notably, although roughly 80% of the human brain's neurons are located in the cerebellum, this structure consumes only about 10% of the brain's total energy. In contrast, the cerebral cortex contains roughly 20% of neurons and takes up nearly 60% of its energy[113,114]. This is due to the large, branched structure of many cortical neurons which have numerous synapses for integrating inputs and a large number of small unmyelinated axons with high conduction costs[115]. The number of synapses per neuron increases in association with brain size enlargement across primates, with humans predictably having cortical neurons with the greatest number of synapses[116]. Due to the lack of brain material from extinct hominin species, we can only speculate on neuronal numbers and associated energy costs. However, based on cranial foramen data from extant primates and fossil hominins, it has been estimated that blood flow increased steeply during the last 3 million years of human evolution, which is estimated to have seen a six-fold increase in total cerebral blood flow rate[52]. Additionally, neuron number in extant primates (including humans) scales almost linearly with brain mass, which would mean that the number of neurons might have more than doubled during evolution of the hominin lineage[111].

How could humans afford such an increase in brain size and the corresponding increase in neuronal number while meeting the required energy budget? It was recently shown that avian species with similar or even higher neuron densities than primates[106,117] show lower energy demands per neuron[118]. The modern human brain appears to achieve higher computational efficiency with a reduced energy budget due to reduction of voltage-gated potassium conductance in specific cortical neurons[119]. Direct measurements of whole-body metabolism indicate that *Homo sapiens* have a larger total energy expenditure and higher basic metabolic rates compared to other great apes, possibly indicating an overall increase of energy demands in hominin evolution[120]. This could be partly attributed to larger brains with more, and larger neurons. However, it should be noted that we are only beginning to understand how these species differ in brain cellular composition (including glia) and the molecular mechanisms that guide metabolic activity[121]. To meet the increasing energy demands of both body and brain, humans have adapted through both physiological and behavioral mechanisms to increase energetic turnover compared to great apes and this could potentially be related to brain size enlargement[120]. For example, data indicate an increase in body fat in modern humans combined with altered foraging strategies, more food sharing among individuals, and a less cost-intensive locomotion type[122]. The invention of fire, cooking, and other food preparation techniques might have made more calories available[123], but see[124]. It has been suggested that these adaptations co-evolved with the increase of brain volume, and that they influence each other – for example, the higher processing capacities of larger brains allowed for more sophisticated foraging strategies and more cooperative social interactions which made more energy available to further promote brain growth. However, large and expensive brains could potentially pay for themselves in ways other than through increases in cognitive abilities. In fact, it has been suggested that large brains with increased numbers of glial cells might have evolved for thermoregulation in whales[125,126]. As discussed above, we have much yet to learn about how brain size relates to cognitive abilities.

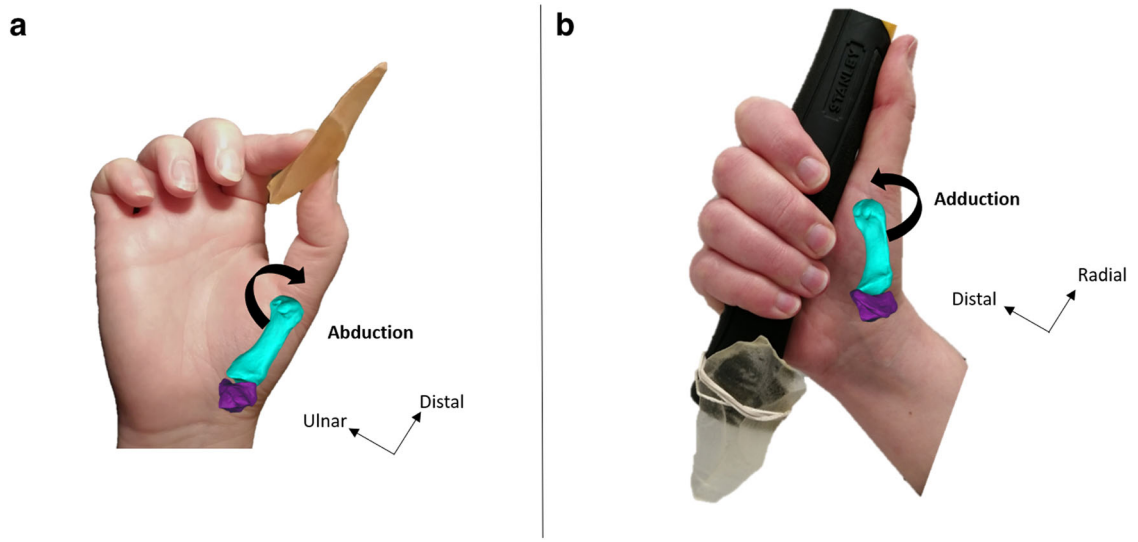


Fig. 4 Examples of the relationship between hominin fossil hand morphology and early tool use. a, b A present day human's hand demonstrating a precision grip when grasping an artifact (**a**) and a power "squeeze" grip when grasping a hafted artifact (**b**; both palmar views). Superimposed in turquoise (first metacarpal) and purple (trapezium) are the bones forming the trapeziometacarpal complex at the base of the thumb and responsible for its movements in a present day human (**a**) and a Neanderthal (Kebara 2; **b**). (Bardo[312], available at https://doi.org/10.5281/zenodo.7452329).

How do brains operate on a different budget in humans compared to other species? It has been suggested that changes in metabolic rates reflect changes in cell composition and microstructure. To answer this question, we need more information about brain energetics in different species. We need to relate evidence from the archeological and paleoecological records of fossil hominids, such as how they extracted foods, to various changes in their brains. We can triangulate that information to further model aspects of cerebral metabolism for fossil species.

Behavior and cognition. We do not have direct access to the behaviors of humans of the past, nor to the cognitive processes that underlie them, since these do not fossilize. It is, therefore, up to archeologists to infer their emergence and presence from the archeological record. The material culture of Paleolithic hominins includes tools[127–129], graphic productions such as engravings and paintings[130–138], objects of personal adornment[139–142], non-utilitarian objects transported over long-distances[143,144], and burials[145–148], among others. Neuroscientific experiments conducted on modern participants have been used to infer the neural basis of the cognitive abilities needed by Paleolithic hominins to produce the artifacts that archeologists have discovered. Although these studies are valuable and informative, they necessarily involve present-day human subjects with present-day human brains performing replications of ancient behaviors. For example, it remains unclear which brain activity patterns in a *Homo erectus* individual corresponded to the production of hand axes. Pioneering studies have used functional neuroimaging to explore the neural basis of stone toolmaking and its potential co-evolution with language[149–152]. Other research has focused on the incremental working memory requirements for the successful knapping of stone tools from successive lithic industries[153–155].

To date, we know very little about how our brains process potentially symbolic aspects of material culture such as ornaments, body paintings, and engravings which appeared in the archeological record long after the earliest stone tools. Functional MRI (fMRI) was recently used to investigate human brain activity while visually perceiving the earliest abstract engravings[156]. A follow-up study addressed the neural correlates of visually perceiving these abstract engravings when they have been attributed to a human maker[157]. Characterizing the cerebral bases of the cognitive processes implemented by modern participants to produce or perceive archeological material reveals information on the probable cognitive capacities and neural functions of earlier hominins. Nevertheless, this approach has some limitations. The strategies used by Paleolithic hominins and those used by modern participants may differ due to differences in environment and culture. To limit this bias, researchers have, for instance, controlled for the effect of using language to give task instructions[153] or included a group of archeologists who are experts in Paleolithic engravings to mimic the familiarity fossil hominins had with this type of material[157].

Paleolithic hominin brains depend on comparisons with other primate species as well. Unfortunately, there are few studies comparing functional brain organization across humans and other species using the same methods. Further, brain organization seems to differ between humans and other primates in regions relevant to understanding the neural bases of fossil hominin cognition. Thus far, it has been proposed that the early visual areas (V1, V2 and V3) show fewer differences between humans and rhesus macaques[158] compared to intraparietal association areas that integrate multisensory information and function in the representation of tool use[159–161]. It has been suggested that species differences relate to developmental timing, and that more rostral areas, and in particular the prefrontal cortex which matures later ontogenetically, differ more between humans and other primates[162,163]. Understanding brain function in *Homo sapiens* and other extant species helps us to propose hypotheses on the evolution of hominin brain organization, and how it may relate to cognition and behavior.

Fossil hominins' behavioral repertoires also depend on their postcranial anatomy. Fossil hand function is understood through the analysis of bone shape[164,165] and musculoskeletal modeling[166,167] and this is related to stone toolmaking ability through biomechanical studies[168,169]. For example, Neanderthal thumb morphology appears to be better suited for power "squeeze" grips than precision hand postures (although there is high interindividual variability[165]; Fig. 4). Experimental studies involving present-day human participants could further reveal how the brains and bodies of fossil hominins relate to the archeological record.

Are human brains specialized for toolmaking and other behaviors represented in the archeological record? How are their behavioral repertoires linked to brain organization, and are they independent of brain size? To answer this question, we need to know how brain structure relates to behavior in humans and other species. We can use that information to further model how fossil hominins could produce the artifacts they did, provided the brains they had.

Development and plasticity. One of the aims of evolutionary developmental biology (known as Evo-Devo) is identifying developmental processes that support conservation and variation in structure and behavior. Much research in the field of human brain evolution has focused on identifying developmental processes specific to humans. One insight emerging from comparisons of ontogenetic trajectories across extant and extinct species is that the human brain grows *in utero* and during the first two years of postnatal life at a rapid rate for an extended period compared to chimpanzees. The extended duration in brain growth accounts for the relative enlargement of the adult human brain[170–173]. Another insight is that the human frontal cortex grows at a faster rate during the last trimester than it does in chimpanzees, and this cortical growth may be linked to differences in frontal lobe morphology[86,87,174–176]. While ontogenetic comparisons have yielded much insight into the evolution of the human brain, the paucity of fetal and postnatal brain samples available to study human and great apes has hindered progress in identifying developmental mechanisms accounting for structural and behavioral modifications in the human lineage.

Some new strategies have been developed to overcome the issue of small samples with the goal of providing a more complete characterization of the developmental mechanisms generating variation across human and non-human primates. The integration of information across scales of organization (e.g., behavior, anatomy, gene expression) is instrumental in finding corresponding ages across the lifespan of humans and chimpanzees, as well as other species[177]. This is because the sequence in behavior and biological maturation and aging are sufficiently similar across the two species that we can translate ages across their lifespan. Age alignments are possible throughout development to the end of life in chimpanzees. Importantly, most chimpanzees do not live past their forties, which equates to fifties to sixties in humans and subsequently there is a phase of life in humans (beyond fifties) with no clear counterpart in chimpanzees. Accordingly, chimpanzees should suffer from less cognitive decline towards the end of their lives than humans, and chimpanzee offspring may not benefit from the care of aged females as is evident in humans[178]. The evolution of lifespan has a range of consequences for species-specific cognition and social structures. As already mentioned, ontogenetic series of chimpanzee and human brains are difficult to obtain and hence limited, but a direct comparison of these series indicates that certain aspects of brain development, such as neocortical myelination, are protracted in humans compared to chimpanzees[179]. Other aspects of brain development, such as the timing of neocortical synaptogenesis, are shared by both species[180].

Another way to overcome the very limited availability of ontogenetic series is by comparing patterns of variation observed in adult brains to infer certain aspects of development. For example, quantitative genetic analyses of large samples of chimpanzee and human adult brains indicate that human brain anatomy is more strongly influenced by environmental factors than chimpanzee brain anatomy, which is indicative of a higher level of developmental plasticity in humans[181,182]. While increased brain plasticity must have evolved in hominins, it is often considered to be associated with the evolution of secondary altriciality in humans[182–184]. Inferring levels of plasticity in fossil hominin species based on their patterns of anatomical variation is particularly challenging. There is, however, increasing evidence indicating that brain plasticity is influenced by genetic factors[185,186] that can be identified and traced in hominin species through paleogenetic studies[187,188]. DNA methylation is an epigenetic mark that has been reconstructed in hominin ancient DNA (aDNA) samples which is highly correlated with gene expression and heritable through multiple cell divisions[189,190]. A better understanding of the molecular mechanisms in human-specific neuroplasticity could come from fossil hominins, since humans show substantial differential DNA methylation of genes involved in neurodevelopment and synaptic plasticity in comparison to great apes[191].

Are human brains specialized for plasticity and an unusual propensity to be shaped by environmental variables? To answer this question, we need more information about brain development in different species. A better representation of neonatal fossil hominins could help us to better model how brain shape develops.

Emerging directions

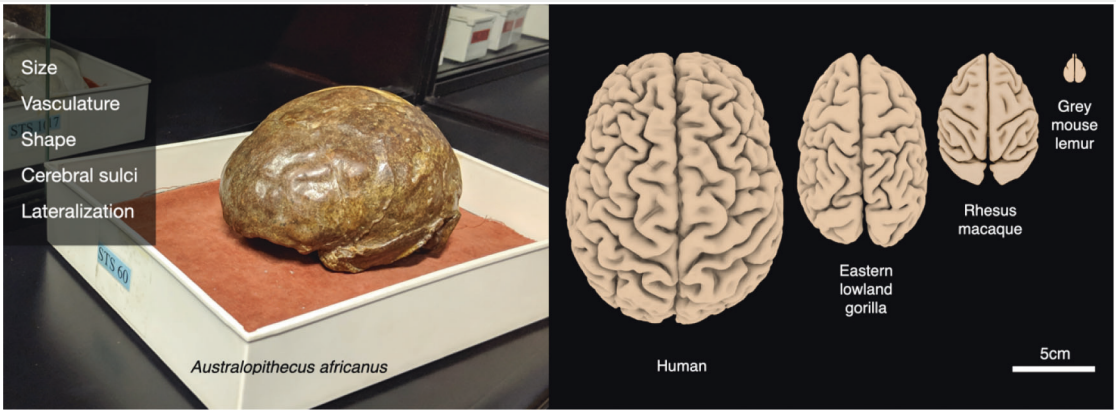
New directions are emerging for future research involving paleoneurological collections that incorporate neuroimaging, phylogenetic comparative methods, molecular biology, paleoanthropological discoveries, and sharing data and tools. These offer the potential to integrate information across different scales of organization from in vivo as well as in vitro systems to investigate biological mechanisms. New integrative frameworks allow for synergies and opportunities to answer unresolved questions about human brain evolution (Box 1).

Neuroimaging. Integrating endocast data with neuroimaging has opened an avenue to examine the evolution of the hominin brain in the context of the brain structure and function of present day humans. Neuroimaging techniques, such as MRI, are widely used to reconstruct and segment the human brain in three dimensions (3D). Combining data from neuroimaging and endocasts thus can be beneficial for examining the extent to which fossil endocast-derived features reflect aspects of brain structure. Early examples of such a combination include adapting metrics traditionally used on endocasts to MRI data[192,193]. For example, craniometric ratios of the LB1 (*Homo floresiensis*) endocast were compared to the normative distribution of the craniometric ratios of *Homo sapiens* derived from a large sample of MRI data, providing quantitative evidence of how LB1 deviates from *Homo sapiens*. In another illustrative example, Fournier et al.[194] used brain MRI data from present day humans to reconstruct both the brain hull and the endocast, where consistent asymmetry patterns were observed. These findings suggest the feasibility of using endocasts to infer the evolution of brain asymmetry patterns.

Other studies further suggest that combining endocasts with neuroimaging makes it possible to investigate more comprehensive and localized morphometric characteristics of the brain, such as gyrification[195]. A recent study used endocasts and MRI data from the same sample of extant human subjects and revealed a close relationship between MRI-derived brain sulci patterns and the endocast-derived sulcal imprints in frontal, temporoparietal, and occipital regions[196]. These findings show a great potential to study the evolutionary process of structural reorganization in these cognitive-critical regions through comparisons of endocasts across species. A major aim of comparative studies is to infer the functional consequences of evolutionary changes in the hominin brain. In an exploratory study toward this goal, Kochiyama

Box 1 | Summary of the kinds of data obtainable from the fossil record, unresolved questions about the origin of the human mind, and emerging directions that incorporate interdisciplinary research tools and innovative pipelines, making it possible to now answer those questions. Illustrating this is the natural partial endocast STS 60, from the collection at the Ditsong National Museum of Natural History, Pretoria, South Africa (photo on left) which preserves brain features that can then be compared to extant species (graphic on right; adapted from Heuer et al.[26])

DATA WE CAN OBTAIN FROM ENDOCASTS



UNRESOLVED QUESTIONS

Energetics: *How do brains operate on a different budget in humans compared to other species?*

Behavior and cognition: *Are human brains specialized for tool making and other behaviors represented in the archeological record?*

Development and plasticity: *Are human brains specialized for plasticity and an unusual ability to develop in response to environmental variability?*

EMERGING DIRECTIONS

Neuroimaging: Brain organization and connectivity can be mapped in endocasts using neuroimaging templates. Reorganization can be compared to functional neuroimaging studies in which behaviors inferred from the archeological and fossil records are re-enacted.

Phylogenetic comparative methods: Evolutionary history is a powerful tool to associate traits in multiple species, even when the fossil record is incomplete.

Molecular and cellular biology: Fossil DNA sequences are studied functionally through brain organoids, transgenic models, and fossil-genotype-to-fossil-phenotype associations within living people.

Paleoanthropological discoveries: Fossils and artifacts contribute the only direct evidence about evolutionary events.

Sharing data and tools: Online datasets of comparative brain collections and fossils from museums permit powerful investigations, which can take advantage of free online tools that improve work efficiency through collaboration, citizen science, and artificial intelligence.

et al.[197] reconstructed the Neanderthal 'brain' by deforming MRI-derived 3D human brain to the Neanderthal endocasts, to estimate the volume of distinct brain regions in both species. A prominent enlargement of the cerebellum was revealed in humans compared to Neanderthals (confirming earlier estimates using a different method[60]). They suggested that the enlarged cerebellum in *Homo sapiens* could relate to its function in cognitive abilities such as cognitive flexibility, attention, language processing, and episodic and working memory in present day humans. Cerebellar functions have been emphasized in light of

recent findings supporting structural, size, and molecular changes in the cerebellum in humans[198–202].

There are some caveats concerning the correspondence between endocasts and brains, such that information inferred from the endocast does not always parallel the organization of the brain. A recent study combining MRI and endocast data from humans and chimpanzees argued that evolutionary changes between the brains of humans and chimpanzees are disassociated with changes of neurocranial organization of the two species[203]. These findings seem to indicate that some aspects of brain organization are better reflected by endocranial anatomy than others. We thus advise verifying the examined characteristics using comparative endocast and neuroimaging data from primates before drawing a conclusion on brain evolution from the evidence of endocasts solely.

Phylogenetic comparative methods. Phylogenies are hypotheses about the evolutionary relationships between species constructed from data such as genomes and fossil morphology (Fig 1). Species are more similar when they are closely related, a concept known as phylogenetic non-independence. Phylogenetic comparative methods comprise a statistical toolset that explicitly tackles this problem and, more generally, have the potential to improve inferences when different species are compared[204]. Although widely applied in evolutionary biology, phylogenetic comparative approaches have been used to a more limited extent in the study of fossil hominins[24]. Previous use of such approaches to understand brain evolution in fossil hominins concerns mainly brain size[205] and encephalization[206], but some aspects of variation in brain shape have been explored under this framework as well[207]. These approaches have the potential to help us infer ancestral states in the evolution of the hominin brain, as well as to reveal differences in evolutionary rates for different branches of the hominin phylogeny, which has been done for some cranial[208] and dental traits[207], and for some behavioral traits[209]. Fossil species can be included in ancestral state estimations even if their evolutionary relationships are not fully resolved, and make it possible to test models of evolution[210]. The inclusion of fossil data improves ancestral state estimations, as it calibrates values at nodes[211]. Hominin paleoneurology can also gain insight from studies of brain and body size scaling[212,213] which use phylogenetic comparative methods to measure the convergence and divergence of traits across species, reconstruct ancestral states, and impute missing values. These approaches, however, are undeniably hampered by the uncertainty associated with the hominin phylogeny. Previous Bayesian analyses of the hominin phylogeny can be used to carry out these analyses[6,214], but they are not free of controversy[215,216]. This phylogenetic framework, however, is likely to be improved and refined as more fossils are found and described in the future. In addition, the uncertainty associated with particular phylogenetic scenarios can be measured and included in calculations[6,214].

Phylogenetic comparative approaches can be combined with other kinds of evidence to provide a more nuanced understanding of how traits are related. For example, quantitative methods of shape analysis (geometric morphometrics or other quantitative approaches) can provide a more nuanced description of endocranial shape variation over the hominin phylogeny[217], in a similar way as it has been done to describe the evolution of endocranial shape in platyrrhine primates[218,219]. This approach, however, is still limited to the types of information that can be obtained from the endocranial evidence. Critical aspects of the microstructural, macrostructural and biochemical organization of the brain that are not preserved in endocasts cannot be reconstructed in fossil hominins through this strategy. Nonetheless, broader mammalian comparative contexts[220], may still be useful to infer certain aspects of neurodevelopment in fossil hominins[221], as well as the level of covariation between brain size and body size[222–224], and other size- and shape-related variables[223].

For example, hypothetical fossil brain structural connectivity could potentially be modeled from endocasts, even in the absence of any direct evidence. White matter tracts were reconstructed in the 100-year-old brain of the extinct Tasmanian tiger (*Thylacinus cynocephalus*) based on comparison with one other species, the Tasmanian devil (*Sarcophilus harrisii*)[225]. Structural brain connectomes have now been investigated in 125 mammalian species in comparison to phylogenetic distances[226]. Phylogenetic comparative methods could be used to improve predictions about brain structure in extinct hominins.

Molecular and cellular biology. Inferences that have a direct genetic basis or that leave a record in individuals' proteomes, may be testable in the future as more aDNA and paleoproteomic data become available. Indeed, aDNA analyses have revealed that *Homo sapiens*, Neanderthals and Denisovans shared coding changes in the *FOXP2* gene that can be related with certain forms of brain plasticity in these species[188,227,228]. Even when aDNA is not available, it is possible to 'rebuild' fossil genomes from the genomes of extant species using phylogenetic comparative methods, as has recently been done for the hypothetical mammalian common ancestor[229]. Such analyses present testable hypotheses about ancestors against which to compare future aDNA and paleoproteomic data derived from the fossil record.

New methodological advances based on the use of mouse models and brain organoids are now allowing researchers to test the functional significance of modern human-specific gene variants, including aspects of neurodevelopment[186,230]. Organoids, which are clusters of proliferating cells[231,232], open new possibilities for comparative work across extant and extinct species, for which the primary brain tissue cannot be accessed. Organoids are generated from pluripotent stem cells (embryonic stem cells or induced pluripotent stem cells) and spun at high speed. These clusters of stem cells self-assemble into a collection of progenitor cells giving rise to various cell types[231]. Pluripotent stem cells can be induced from mature cells (e.g., skin cells) making organoids amenable for study in virtually any species. Crucially, the spatial patterns of gene expression in brain organoids are reminiscent of the brain's spatial layout, thus facilitating species comparisons. Cells from organoids also form connections[233]. Based on these observations, it has been argued that organoids bear sufficient resemblance to nervous systems that they can be used to capture cross-species differences in developmental pathways.

Organoids have been instrumental in studying extinct species and extant species. Neanderthal alleles have been inserted into human pluripotent stem cell genomes to reveal how they impact brain development, opening up new ways to study genetic variation across extinct populations[234,235]. Organoids also permit studying developmental processes in extant nonhuman primates, including the most endangered species (e.g., orangutans, gorillas). Many, but not all, of recent studies have found that brain organoid maturation is slower in humans relative to extant great apes and monkeys[236–238]. The slower speed of human organoid maturation in vitro mirrors the extended duration of human brain growth relative to chimpanzees and other great apes observed in vivo. Yet, an unresolved question is how observations made from brain organoids translate to ground truth in primary tissue of the full organism. For example, it is unclear whether the media used to amplify pluripotent stem cells into organoids can

impact observed species differences in gene expression, and rate of neuronal differentiation. We can now probe the maturation of the human brain at the single-cell level with single-cell RNA sequencing[239]. Accordingly, we know that brain organoids resemble but do not fully recapitulate the cell populations that are evident in human brain development. It is crucial to elucidate how well in vitro biological programs reflect in vivo biological programs[240]. Once those relationships are clarified, the integration of information from individuals, organoids, and scales of biological organization will provide exciting avenues to a better characterization of the mechanisms giving rise to characteristic features of the human brain.

A recent study used organoids to compare the role of the gene *Transketolase-like 1* (*TKTL1*) in corticogenesis of Neanderthals and *Homo sapiens*[241]. The findings point to differences in corticogenesis between Neanderthals and *Homo sapiens*, suggested to affect the frontal lobe, since there is high expression of the enzyme TKTL1 in the progenitors of the modern human frontal lobe. TKTL1 in *Homo sapiens* has a single amino-acid substitution (arginine) while the archaic form in Neanderthals, Denisovans, and other primates harbors a lysine[7]. TKTL1 in *Homo sapiens* specifically promotes the generation of basal radial glia progenitors that are key to primate cortical expansion via their increased capacity to generate neurons[242]. Since Neanderthals and *Homo sapiens* share similarly sized brains at adulthood, future research about development by molecular biologists, neuroscientists, and paleontologists could elucidate specific mechanisms that differ in their brain development.

New methods allow for inferences to be made about present-day human genetic variants derived from admixture with archaic humans. Such variants can be interpreted in the context of modern human brain and endocranial phenotypes. A globularity metric was established to describe the difference in endocranial globularity that has been observed based on the comparison of endocasts of *Homo sapiens* and Neanderthals[67]. The globularity metric was further examined using a large sample of MRI data from extant human subjects, suggesting a potential genotype-phenotype association of Neanderthal DNA alleles in the human genome to play a key role in variations in brain globularity. This approach to understand gene function could be extended to incorporate phenotypic data about brains, bodies, and behaviors, and potentially even take into account what we know about Neanderthal behavior from the archeological record.

Paleoanthropological discoveries. As in all the sub-disciplines of paleontology, paleoneurology will benefit from the discovery of new specimens preserving either complete crania or natural endocasts. While they are relatively scarce, from time to time such specimens are unearthed and contribute to a better understanding of brain evolution. In parallel, cutting-edge methods, for example in virtual paleontology, provide exciting new data even from older finds.

Recent fossil discoveries have been used to investigate long-standing questions about the growth, organization, and shape of fossil hominin brains. Comparing the endocranial volumes of two *Australopithecus afarensis* infants dated to around 3.3 Ma to adult endocranial volumes of the same species, Gunz et al.[19] suggested that these early hominins had a prolonged brain growth compared to chimpanzees after birth. Accordingly, the pattern of brain development that characterizes our species today may have emerged early within our lineage. Another breakthrough came from the discovery and comparative analysis of the endocasts of the earliest *Homo sapiens* including specimens from Morocco dated to 300,000 years[66,243], which revealed a recent origin of the globular shape of the human brain[62]. Indeed, only fossils dated to less than 35,000 years fall within the range of shape variation observed in present-day humans[62,66,244]. Future discoveries of fossil crania representing the early ontogenetic stages of brain development will continue to shed light on when patterns of modern human brain development arose. Additional perinatal specimens will shed light on whether cranial shape features can be attributed to prenatal development versus childbirth, and on whether cranial shape of *Homo sapiens* is a result of facial gracilization[245,246].

A recent study[88] investigated a digitized sample of *Homo* endocasts from Africa and Eurasia using geometric morphometric methods to identify which brain regions had undergone differential expansions. The new analysis suggests reorganization of the inferior frontal gyrus (where Broca's area is located) probably occurred after 1.8 Ma. Broca's area is of particular interest due to its role in language, and it is also involved in tasks requiring complex hand movements such as toolmaking[247]. Such fossil findings could be further interpreted in the context of archeological evidence for the emergence of modern human behavior. The timing of this neuroanatomical change could be compared to changes in technology, hand anatomy, and other paleobiological factors. Using the archeological record as a guide, ancient behaviors that arose around 1.8 Ma could be replicated in laboratory studies that use physiological measures of brain and postcranial activity to determine the correspondence between Broca's area and the behavior of fossil *Homo*.

The archeological record is a key marker of hominin brain and cognitive evolution. Recent archeological findings have indicated that the earliest use of stone tools was around 3.4 Ma[248], and the intentional production of stone tools occurred by 3.3 Ma[21]. There is morphological evidence of human-like manipulation dated to around 3 Ma[249]. All of these predate the appearance of the genus *Homo* by at least 200,000 years ago (*Homo sp*. remains from an unknown species have been dated to 2.8 Ma[250]). This implies that other hominins also had the ability to use and make stone tools. This includes australopiths, whose hand morphology is close to that of non-human great apes[164,166]. The recent discovery of Oldowan tools associated with *Paranthropus* remains also supports the idea that non-*Homo* hominin species may have had the cognitive abilities for using and making tools[251]. Furthermore, archeological studies that applied recently available techniques, such as microwear analysis and spatial analysis, have contributed to a new appreciation of the Neanderthals' role in the production of bone tools and symbolic structures[252,253]. Future discoveries about fossil hominin material culture, functional anatomy, and neurobiology will continue to shed light on their technological and socio-cultural abilities.

Sharing data and tools. Investigations of complex phenomena, such as brain evolution, benefit from holistic, integrative approaches that synthesize diverse data from multiple sources, allowing researchers to address questions beyond the capabilities of any one group (Fig. 5). Research consortia are one solution to this challenge. ManyPrimates is an open grassroots consortium that collects comparative experimental psychological data about diverse primate species to address questions about the origin of the human mind using phylogenetic models[254]. In completing its first study, it has built a reproducible infrastructure for conducting broad-scale collaborative comparative research[255]. Despite this success, however, such big team science approaches face funding challenges and are not always free and openly available[256].

More expansive approaches draw from open science principles[257], reproducible research[258] and FAIR data management practices[259], alongside the CARE principles for indigenous

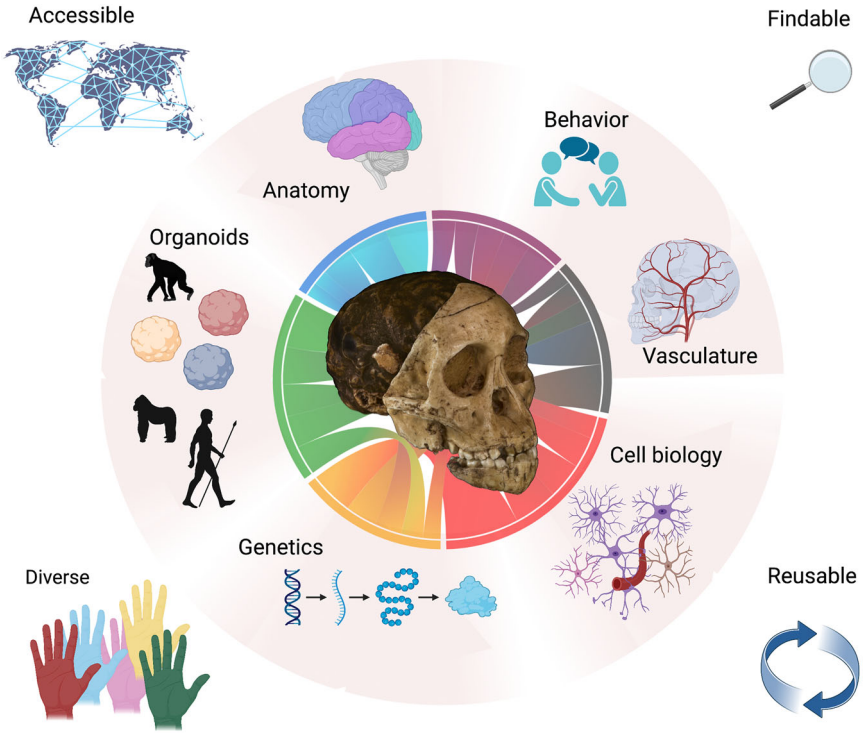


Fig. 5 The "From Fossils to Mind" framework. Endocasts provide information about brain anatomy and vasculature in extinct hominin species, and evidence for their behavior can be gleaned from the archeological record. These data can be interpreted by integrating ancient DNA with new experimental methods at multiple scales (e.g., cell biology, anatomy, genetics, and organoids). To accelerate progress, researchers should collaborate in diverse teams and make their data accessible, findable, and reusable. Created with Biorender.com. Chord diagram done with Flourish (https://app.flourish.studio). The photo of the fossil cast in the center was composited from *Australopithecus africanus* - Cast of Taung child by Didier Descouens, available under CC BY-SA 4.0 at https://commons.wikimedia.org/wiki/File:Australopithecus_africanus_-_Cast_of_taung_child.jpg.

data governance[260]. As we enter "the decade of digital brain", the neuroscientific community is developing a concept to work with data to obtain new knowledge and model the brain[261]. The COVID-19 pandemic provided a case study on the scientific success achievable through collaborative as opposed to competitive knowledge generation emphasized by open science[262]. It follows that improvements in data integration accelerate progress through greater efficiencies, and more powerful analyses with greater dimensionality.

The transition to open science and integration represents a major shift in our epistemic culture (sensu Cetina[263]) and comprises two sets of challenges. First are the difficulties posed by social, political, and economic hurdles to open sharing. Across scientific fields, researchers are often reluctant to share data in order to maintain priority in publishing and commercial pursuits[264–267]. However, new generations are bringing fresh expectations regarding information sharing. Progress can be seen in revisions to the education of researchers, where preregistration, data management planning, and information science are increasingly incorporated into basic scientific training[268,269]. Similarly, journals, funding agencies, and academic societies are shifting their policies to encourage good practice in data sharing[270,271]. The challenges facing paleoneurology are further exacerbated by the fact that much of the primary fossil, archeological and comparative primatological data are distributed across institutions and cannot physically travel because of safety concerns, intellectual property issues, as well as international regulations pertaining to the export/import of biomaterials from endangered species and cultural artifacts. The COVID–19 pandemic has forced museums to rely more heavily on technology than they previously used to and has stressed the need to create and curate digital data as well as platforms that allow for remote accessibility. Creating digital replicas or proxies for the primary data, including microCT scans of fossils and artifacts, brain MRI scans and digitized histological sections, genetic sequences, and video captures of behavior, all make data more mobile and facilitate sharing. However, curating digital data in a museum comes with advantages as well as disadvantages[272] that need to be addressed, especially if the process is to be carried on in a manner that most benefits local researchers and the custodians of the fossils in developing countries. Efforts at data sharing often run up against ethical issues emanating from the global power imbalances between developed and developing countries, imbalances that echo historic colonization and exploitation. The CARE principles provide a foundation for developing mutually beneficial systems of scientific exchange that respects the rights and authority of indigenous groups living and working with researchers in the field as well as local stakeholders such as the national museums, and cultural heritage authorities responsible for maintaining fossil and archeological collections.

The second major hurdle is technical. Once we can agree to share, how can we integrate the diverse types of data necessary for evolutionary studies of the mind, provided that the data originate from a multitude of sources, teams and domains of interest each with differing research praxes? Technical implementation of open science principles depends on a suite of interrelated best practices, standards and collaborative scientific infrastructure that provide open access to validated primary data. Data that are documented with standardized metadata and indexed can be easily located on the Web. The National Center for Biotechnology Information was established by the USA government to develop automated systems for storing molecular biology data and also provides tools to study them[273]. In another compelling example, the Global Biodiversity Information Framework, developed by the

Table 1 Directories, collections, tools, and database infrastructure described in the text. Arranged by material covered (italics).

Name	Website
DIRECTORIES / COMPILATIONS	
Awesome Public Datasets	https://github.com/awesomedata/awesome-public-datasets
European Network for Brain Evolution Research	https://sites.google.com/site/eurobrainevolnet
COLLECTIONS	
Digitized museum collections	
Royal Belgian Institute of Natural Sciences	https://virtualcollections.naturalsciences.be
Digital endocasts and models	
EndoMap	https://www.endomap.org
MorphoMuseum	https://morphomuseum.com
MorphoSource	https://www.morphosource.org
Neuroimaging	
Brain Analysis Library of Spatial maps and Atlases (BALSA)	https://balsa.wustl.edu
Brain Catalogue	https://braincatalogue.org
BrainBox: Brain Catalogue Primates	https://brainbox.pasteur.fr/project/BrainCataloguePrimates
Digital Brain Bank: Digital Brain Zoo	https://open.win.ox.ac.uk/DigitalBrainBank/#/datasets/zoo
National Chimpanzee Brain Resource	https://www.chimpanzeebrain.org
PRIMatE Data Exchange (PRIME-DE)	https://fcon_1000.projects.nitrc.org/indi/indiPRIME.html
Digitized histology	
BigBrain	https://bigbrainproject.org
BrainMaps.org	http://brainmaps.org
Comparative Mammalian Brain Collections	http://brainmuseum.org
Brains (tissue / physical specimens)	
National Chimpanzee Brain Resource	https://www.chimpanzeebrain.org
Primate Brain Bank	https://primatebrainbank.org
Gene expression	
Allen Brain Map	https://portal.brain-map.org
PsychEncode (comparative brain development)	http://www.evolution.psychencode.org
TOOLS	
Endocast annotation	
Curve-editor	https://gitlab.com/jeandumoncel/curve-editor
Endex	https://perso.liris.cnrs.fr/gilles.gesquiere/wiki/doku.php?id=endex
Neuroimaging annotation	
Brain Visa	https://brainvisa.info/web
BrainBox	https://brainbox.pasteur.fr
PRIMatE Resource Exchange (PRIME-RE)	https://prime-re.github.io
Histological annotation	
MicroDraw	https://microdraw.pasteur.fr
Developmental age comparison	
Translating Time	http://www.translatingtime.org
DATA INFRASTRUCTURE AND STANDARDS	
Darwin Core	https://dwc.tdwg.org
Global Biodiversity Information Facility (GBIF)	https://www.gbif.org
National Center for Biotechnology Information (NCBI)	https://www.ncbi.nlm.nih.gov
Paleo Core	https://paleocore.org

Note. This is not an exhaustive list. See directories / compilations above for more resources.

Organization for Economic Cooperation and Development[274,275] aggregates primary species occurrence data based largely on databases maintained by the world's museums and other research institutes. Each institution maintains its records independently, and shares them collaboratively using common data standards such as Darwin Core[276]. Similar systems are available for smaller academic research communities that can serve as model implementations for a collaborative paleoneurology community. These include efforts to systematize data collection protocols in primatology[277]. In paleoanthropology, Paleo Core maintains a data standard derived from Darwin Core, provides tools for field data collection, and an online platform for research teams to collaboratively manage their data[278–281]. Despite these examples, no overarching infrastructure exists for integrating the diverse neurobiological, molecular, anatomical, fossil, archeological, and behavioral data essential for studying the origin of the human mind. Establishing the necessary infrastructure will require better funding and resources[272,282,283].

Recently, much progress has been made in making digital resources in neuroscience and paleontology freely available to the public. Here we highlight a selection of relevant resources that could be used in paleoneurology. Although we describe these and provide their URLs (Table 1), this is not an exhaustive list, and we also refer the reader to the curated and open Awesome Public Datasets, a repository that covers topics including Neuroscience, Museums, and Biology. All of the atlases, databases, tools, brain collections, resources, and software described here are listed in the webpages of the European Network for Brain Evolution Research, which also links to a mailing list on relevant topics.

Sharing of digital endocast models is available through the digital repositories MorphoMuseum, with endocasts from extant and extinct species (e.g., humans, cercopithecoids, ungulates, cynodonts, dinosaurs, sloths, turtles), and MorphoSource (e.g., bats, rodents, primates, birds). Digitized museum collections, such as paleontological and anthropological 3D models that are available online from the Royal Belgian Institute of Natural

Sciences, not only facilitate access to resources, but also allow for new morphometric statistical approaches to be more readily applied to endocasts. In line with this, the digital recognition of sulci using mathematical curvature and automated comparison is becoming more common[23,284]. Density maps that represent the probability of finding a specific sulcus in a human endocast[285] can be viewed and downloaded from EndoMap. Endocasts can be automatically reconstructed from 3D models of dry crania using the software Endex[285] and an algorithm for labeling detected sulci is freely available online[196].

As endocasts become increasingly available in digital form, they benefit from comparison to the brains of extant species. An advantage of digital resources is that they can easily be combined in analyses, providing an opportunity for investigations to transcend disciplinary boundaries. Online brain collections allow for the comparison of structures in multiple species, and can be developed into algorithms to improve parcellations. Many of the brain collections are presented along with filters and search functions, and often include tools to annotate and measure them. Significant samples of chimpanzee, human, and other primate brain MRIs, covering the lifespan, have become available. For example, the Brain Analysis Library of Spatial maps and Atlases, an adjunct of the Human Connectome Project, includes MRI and fMRI data from humans and macaques. The National Chimpanzee Brain Resource includes a searchable directory of chimpanzee brain MRIs and physical specimens, with information about rearing, handedness, availability of cognitive test performance, and age. The Primate Data and Resource Exchange (PrimeDRE[286,287]) is a growing resource for structural, diffusion-weighted and functional MRI data from primates, mainly macaques, and tools to work with these data[288]. Many physical brain collections also feature online inventories and websites. The Primate Brain Bank provides brains for researchers. The Brain Catalogue allows users to interactively view MRI data and surface reconstructions, provides tools for collaborative segmentation, and gives open access to MRI data from a large number of vertebrate species. The Digital Brain Zoo allows users to preview and request structural MRI and diffusion MRI outputs for diverse mammalian species. The Allen Institute shares high-resolution histological and transcriptomic data from humans and mice as adults and in development. PsychENCODE provides human, macaque, and chimpanzee gene expression data in brain tissues over development.

Tools are publicly available to precisely map and measure brain structures from digital brain images. For example, BrainVisa is downloadable free software useful for functions such as mapping sulci. More recently, tools have been developed for online collaborative use. The Web app BrainBox enables researchers to collaborate in real-time on the segmentation of challenging datasets, such as developmental or cross species MRI data, to measure structures of interest and render 3D reconstructions on the fly in the browser[289]. The collection of structural MRI data from 34 primate species used to reconstruct surfaces in Heuer et al.[26] is available on the BrainBox website together with their cerebral masks for easy access and community driven projects.

Histological collections are more demanding to create than MRIs, and require more storage space at high resolutions. Still, some histological collections are available online. Flatbed scans and photos of brains from the Comparative Mammalian Brain Collections spanning over 100 different species of mammals are available online. BrainMaps has comparative neurohistology for several species at microscopic resolution. MicroDraw enables collaborative annotation of digitized histological images. It is available online and supports large histological files, thus enabling researchers to work collaboratively on labor-intensive projects to annotate brain regions of interest on the basis of cellular organization. It has recently been used to provide a layer of collaboration to the Comparative Mammalian Brain Collection[290]. MicroDraw can also be used to work with BigBrain, the first openly accessible, microscopic resolution, 3D model of the human brain. Finally, algorithms utilizing multi-omic datasets are becoming available to facilitate comparison between different species brains and behaviors, with the potential to make life history predictions for fossil species as well. Translating Time is a free Web tool that incorporates the timing of abrupt transformations to translate ages across species. It can also be used to identify biological programs that vary in their timing in humans relative to most other species, including chimpanzees[177,220,291].

Likewise, new computational techniques could address limitations in the study of endocasts. A limitation with understanding species from fossils alone is that their identifications and classifications are uncertain. Recently, artificial intelligence (AI) has been used to classify fossil specimens and develop taxonomies[292,293]. Also, labeling anatomical data is time consuming and subject to observer error. An efficient pipeline for processing large and complex anatomical image datasets currently used in the biomedical sciences is to crowdsource annotations using citizen science initiatives, and use these data to train deep learning models for human-level performance[294]. Automated taxonomic classifications and anatomical annotations could gain even more robust support from 3D geometric morphometry, and could be compared to vertebrate molecular evidence in the context of phylogeny. Reciprocally, paleoneurology can also inspire the development of AI itself by "reverse engineering" the minds of humans[295], as well as other species, by documenting the changes that occurred during their natural histories.

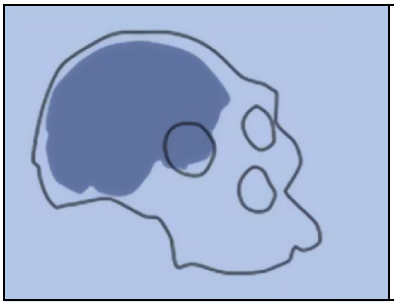
We propose a set of guidelines to move the field forward (Box 2). Progress could be made for data sharing and availability by borrowing the advantages from one repository and extending them to others[296]. We need to develop more dynamic data repositories which allow users to input data themselves. There are challenges with species uncertainty in fossil and historical collections that could benefit from more extensive annotations. Another challenge to overcome is how to manage files of very large sizes, such as microscopic resolution histological images.

Box 2 | "From Fossils to Mind" recommendations for researchers

Researchers interested in the origin of the human mind can do the following to accelerate discovery:

1. Contribute data and rich metadata in standardized formats to online databases that are open, FAIR, and CARE.
2. Where lacking, create new online databases, and provide a way for others in the community to continuously contribute relevant data.
3. Acquire long-term government and industry sponsorship for databases and large collaborations.
4. Develop comparative resources alongside applications (biomedical, and potentially ecological and cultural) to receive greater funding priority.
5. Collaborate in diverse teams to pool resources, data, and expertise about the species studied.
6. Collaborate inclusively with stakeholders, museums, local institutions, and local researchers in developed and developing countries.
7. Integrate open, FAIR, and CARE data sharing with university teaching and public outreach.

Box 3 | Image representing the "From Fossils to Mind" workshop which led to the development of this paper



Information can be found on the Southern African Neuroscience Society website[1]

[1]https://saneurosoc.co.za/fromfossilstomind

Interdisciplinary dialogues and collaborations are essential to moving the field ahead.

Outlook

Paleoneurology has conjured up new ways to study the dead from within the living. Paleogeneticists, paleoanthropologists and archeologists have developed techniques to reconstruct long extinct species' DNA, neuroanatomy, and behavioral repertoires using present day human participants. Novel methods have revealed associations between genotypes and phenotypes, and brains and behaviors, that can have a broader impact within the biomedical sciences (Fig. 5).

Although human brains share an overall similarity with the brains of other mammals, they remain an outlier in comparison to even our closest relatives in certain important parameters reviewed here. This has implications not only for human health, but also for understanding what is possible in terms of brain evolution. Regarding the former, human brain specializations make us vulnerable to brain disease. The increased size of our brain may lead to a predisposition to neurodegenerative disease[297], the metabolic demands of our brains[298] and the complex connectivity patterns[299] may lead to a predisposition to schizophrenia, and our unique neurotransmitter[300] and genetic profile[246,301] leave us vulnerable to other mental health and substance use disorders[302].

New techniques arising from the ecological, geological, and biomedical sciences provide paleontologists and archeologists with new opportunities, which in turn have the potential to inform broader applications. Fossil genomes can shed light on human disease. *Homo sapiens* – and the groups we recently admixed with – adapted to different environments around the world over time. Some of the alleles that are at present associated with human diseases such as auto-immune diseases, sickle cell disease, asthma, neuropsychiatric disorders, chronic kidney disease and obesity for example, might have previously been linked to these adaptations[301]. The study of Neanderthal-specific gene variants contained in modern human genomes in combination with endocast data from fossils provides the opportunity to glimpse into the effect that the gene variants have on phenotypic variation. Such observations from fossil endocast studies could in turn serve neuroimaging studies by defining new metrics of interest such as the globularity metric and determining new relationships between genotypes and phenotypes in modern humans. Brain organoids open a host of new possibilities for therapies and precision medicine, which can take advantage of the comparative work across extant and extinct species. Further progress can also be made by combining phenotypic and genotypic evidence in a phylogenetic framework, which adds statistical power to our understanding of how traits relate to each other beyond what is attainable from experimental studies on model systems alone[303].

The brains of vertebrates have evolved on different trajectories in the diverse range of species that have lived on our planet. The fields of paleoneurology and evolutionary neurosciences have come a long way to uncover how the brains of each species of primate are different, how they are similar and how that relates to function and behavior in each respective environment. Progress is being made towards understanding how brain size, shape, macroanatomy, microanatomy, metabolism and development differ between extant species of hominids and uncovering the molecular neurobiology of extinct species.

Altogether, the combination of phylogenetic comparative approaches across the hominin phylogeny and in broader comparative contexts, the incorporation of new aDNA datasets, the use of new experimental approaches, the use of advanced methods to analyze the endocranium and determine its correspondence to neuroimages, new fossil discoveries, the interpretation of archeological evidence, and a more efficient approach to sharing the available resources offer new avenues to explore the evolution of the brain in fossil hominins (Fig. 5). This combination of approaches will allow us to move beyond long-standing debates on the significance of endocranial traits to a more informative scenario where a phylogenetically informed hypothesis will be testable using molecular and experimental data.

The deep perspective provided by bringing 'fossils to mind' allows for an intricate understanding of how neuroanatomy relates to genes and behavior, which in turn sets the context to study the same processes in the present, and even in the future (Box 3).

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The authors declare no competing interests.

Ethics

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