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The Multivariate Basis of Human Brain Evolution: The Prerequisites of Fire Control and Cooking

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ABSTRACT

This study investigates the evolutionary origins of the human brain, focusing on the trend of increasing size in hominins, while also addressing exceptions such as *Homo naledi*, *Homo floresiensis*, and the recent reduction observed in *Homo sapiens*. It examines hypotheses related to brain enlargement, challenging the Social Brain and Ecological Hypotheses by suggesting that the increase in brain size was not an inevitable response to social complexity or ecological pressures. While the Cooking Hypothesis is considered, it is not identified as the primary driver of brain expansion. Instead, fire control and cooking are proposed as prerequisites for sustaining brain size increases by meeting the energetic demands of larger brains. Additionally, we examine mutations that influenced brain size and complexity and contributed to the genetic variability that was pivotal to brain evolution, particularly in Africa during its final phase.

1 | Introduction

Scientists from different disciplines have long sought to understand the evolutionary causes underlying the complexity and size of the human (*Homo sapiens*) brain. Brain size has consistently been a focal point in discussions about human evolution, particularly due to the so-called remarkable size of the human brain. However, brain size alone is not what matters, as the brains of whales and elephants are twice the size of the human brain but have lower neuronal densities and fewer neurons than those of a chimpanzee [1]. The human brain contains a significantly higher number of neurons compared to other primates [2]. It has approximately 86 billion neurons, a striking contrast to the 28 billion neurons in chimpanzees and 33 billion in gorillas [3]. Thus, while gorillas can match or exceed human body size, their brains are roughly three times smaller than those of humans. This discrepancy may not indicate an oversized human brain but rather an evolutionary divergence in body size among great apes that did not occur in the *Homo* lineage. It has been proposed that the human brain likely contains the expected number of neurons and nonneuronal cells for a primate brain of its size [1]. Therefore, it may not represent a truly remarkable size as previously suggested.

Beyond the total number of neurons, the human brain surpasses other primates in additional metrics, such as the volume and surface area of the neocortex, a part of the cortex (see Box 1), which are considerably larger than in other primates [4–6]. Cytoarchitectonic and comparative neuroimaging studies consistently highlight the substantial expansion of transmodal association cortices (see Box 1) in humans. These regions, responsible for integrating sensory information from unimodal cortices for higher-order processing [7], are notably larger in humans than in other primates [8–12]. This expansion deviates from the expected patterns of allometric scaling seen in primate brains [8, 13]. In this sense, the human brain is undeniably remarkable [14].

The expansion of cortical regions, predominantly corresponding to transmodal association cortices, was accompanied by distinct metabolic challenges. These areas exhibit lower oxygen tension

BOX 1 | Brain Glossary

Cerebral organoids

They are three-dimensional cell cultures that mimic aspects of the developing human brain (Figure 4). They are derived from human pluripotent stem cells and can self-organize into structures resembling different brain regions. Cerebral organoids provide a valuable model for studying brain development, disease mechanisms, and drug responses in a more physiologically relevant context compared to traditional cell cultures. They offer insights into neurodevelopmental disorders, such as microcephaly and autism spectrum disorders, and hold promise for personalized medicine approaches. Additionally, cerebral organoids enable researchers to explore the complexity of the human brain's cellular interactions and circuitry, advancing our understanding of brain function and pathology.

Cortex

The cortex is the outer brain layer in vertebrates, composed of gray matter with neurons, dendrites, and glial cells. It processes sensory information, coordinates voluntary movement, and supports higher functions like memory, reasoning, and decision-making. It is divided into:

1. *Cerebral Cortex*: Includes the neocortex (for complex functions like perception and abstract thought) and allocortex (for primitive functions like emotions and olfaction).
2. *Cerebellar Cortex*: Covers the cerebellum, responsible for motor coordination and balance.

The cerebral cortex has folds (gyri) and grooves (sulci) that increase surface area and is divided into hemispheres and lobes with specialized functions.

Dendritic trees

Dendritic trees are complex, branched structures extending from a neuron's soma, serving as the primary sites for receiving synaptic inputs. Their branching allows a neuron to integrate information from thousands of connections.

Key characteristics include:

1. *Branching Patterns*: Dendritic shape and extent vary by neuron type, influencing connectivity and function.
2. *Spines*: Small protrusions on dendrites, especially in excitatory neurons, are critical for synaptic input, learning, and memory.
3. *Signal integration*: Dendrites integrate excitatory and inhibitory signals to determine the neuron's output.

Encephalization

The evolutionary increase in the relative size of the brain compared to the body within a species or lineage. Measured by brain-to-body ratio or encephalization quotient (EQ).

Endocast

It is a replica of a fossilized skull's inner surface (see Figure 2), representing the shape and structure of the brain cavity. It provides insights into the brain size and morphology of extinct species, aiding in the study of their cognitive abilities and evolutionary history in paleontology and anthropology.

Endocranial volume (ECV)

The endocranial volume refers to the capacity within the cranial cavity that houses the brain.

Interneurons

Interneurons are a diverse group of neurons that mediate communication within the central nervous system (CNS). Unlike sensory or motor neurons, they form local circuits in the brain and spinal cord, playing a crucial role in processing, integrating, and modulating signals. They contribute to functions such as reflexes, learning, memory, and sensory perception. Interneurons are classified by morphology, neurochemical markers, or function, with key types including GABAergic interneurons (inhibitory) and glutamatergic interneurons (excitatory).

Neocortex

The neocortex is the largest and most advanced part of the cerebral cortex in mammals, with a six-layered structure unique to this group. It is vital for higher brain functions like sensory perception, motor control, spatial reasoning, conscious thought, and language. In humans, it makes up the majority of the brain's surface area, supporting complex cognitive and behavioral abilities. Organized into horizontal layers and vertical columns, the neocortex integrates sensory input and generates outputs for voluntary movements and cognition. It is divided into functional regions, including sensory, motor, and association areas, which work together for sensory processing, motor control, and abstract reasoning.

Neuroepithelial cells

They are specialized cells found in the early neural tube during embryonic development. They give rise to various types of neurons and glial cells, playing a crucial role in the formation of the nervous system.

Neurogenic radial glial cells

They are specialized progenitor cells in the developing nervous system, responsible for generating neurons and glial cells. They serve as a scaffold for migrating neurons during brain development.

Prefrontal cortex

It is a crucial brain region in higher-order cognitive functions, encompasses areas like Broca's area for speech formation, frontal eye fields for gaze, dorsolateral prefrontal cortex for working memory, and the ventromedial prefrontal cortex for risk processing. Its fundamental role lies in coordinating thoughts and actions according to internal goals. This region, covering the frontal lobe's front part, is implicated in executive functions such as planning, decision-making, and personality expression. Additionally, it moderates social behavior, controls speech and language, and supports rule learning. Authors have emphasized its integral connection with a person's will to live and personality, underscoring its significance in cognitive processing and behavioral regulation.

Pyramidal neurons

They are a type of neuron found in the cerebral cortex, hippocampus, and amygdala, characterized by their pyramid-shaped cell bodies and long dendrites extending from the apex and multiple branching points. They play a fundamental role in information processing, integrating and transmitting signals within the brain's neural circuits.

Radial glial cell

Radial glial cells are specialized glial cells that act as key progenitors in the development of the central nervous system (CNS). Their elongated shape extends from the ventricular zone to the brain's outer surface. They serve two main roles: providing scaffolding for neuron migration and acting as neural stem cells, producing neurons, astrocytes, and oligodendrocytes. These cells are crucial for proper cortical organization and CNS development. After development, most radial glial cells differentiate into astrocytes, though some remain in areas like the retina.

Oligodendrocytes

They are a type of glial cell found in the central nervous system (CNS) responsible for the formation and maintenance of myelin sheaths around axons. Myelin is a lipid-rich substance that insulates axons, enabling rapid transmission of electrical signals and efficient communication between neurons. Oligodendrocytes arise from oligodendrocyte precursor cells (OPCs) during development and remain involved in myelin repair and regeneration in response to injury or disease. Dysfunction or loss of oligodendrocytes is associated with demyelinating diseases.

Transmodal Association Cortices

They are regions in the human brain where information from multiple sensory modalities converges, enabling higher-order cognitive processing such as integration, abstraction, and complex decision-making. These cortices, including areas like the prefrontal and posterior parietal cortices, are greatly expanded in humans compared to other primates. Their development is an evolutionary hallmark associated with advanced cognitive functions. In contrast, unimodal association cortices are dedicated to processing information from a single sensory modality, such as visual or auditory stimuli, before transferring the processed data to transmodal regions. Together, unimodal and transmodal areas form a hierarchical network critical for sensory processing and cognition.

than primary sensory and motor cortices, likely because their growth outpaced vascular efficiency during evolution. As these expanded regions consume all available oxygen, they cannot rely solely on oxidative phosphorylation for energy production from glucose. Instead, they partially depend on glucose fermentation into lactate to meet their metabolic demands [12, 15, 16]. This metabolic adaptation reflects the expansion of the neocortex beyond what would be expected from allometric scaling, necessitating alternative pathways to support its energy-intensive functions [14].

Hence, a key constraint on brain size is the energy required to sustain its neuronal structure. Its energy demands correspond to its neuron count [1]. The specific metabolic rate of the brain (resting energy expenditure per unit weight) is the third highest among organs, following the heart and kidneys [17]. In humans, the brain represents approximately 2% of total body mass but consumes an extraordinary 20%–25% of total energy. In contrast, other primates allocate about 8%–10% of their metabolic energy to brain activity, while most other mammals use only 3%–5% of their energy for the brain [18–21]. In children, particularly around the middle of the first decade of life, the brain consumes a larger portion of total energy, accounting for up to 50% [22]. This high energy consumption in childhood is particularly striking given that at birth, the human brain is only 28% of its adult size. For comparison, in chimpanzees, the brain size at birth is already 40% of the adult size [23].

Therefore, any increase in brain size during the evolution of hominins (see Box 2), primates, or other animals would have been selectively disadvantageous without adequate energy supplies. Nevertheless, a trend toward increasing brain size, which enabled our species and other *Homo* species to develop large brains, is evident. This trend is supported by the data presented in Table S1 and visually represented in Figure 1, a simplified depiction of the phylogenetic tree (see Box 2) of hominins. These sources provide a comprehensive record of brain sizes derived from fossil skulls or their endocasts [24] (see Figure 2 and Box 1), along with their corresponding ages throughout hominin evolution. Research on the evolution of the human brain also relies on evidence derived from morphological, physiological, and behavioral comparisons between humans and closely related extant (see Box 2) primates, such as chimpanzees. Comparing living primates offers valuable insights into how the gross and microscopic organization of the brain correlates with various behaviors. While these correlations allow for hypotheses regarding the anatomical basis of certain behaviors, we acknowledge the limitations in making definitive functional inferences about brain evolution due to the complex interplay of genetic, developmental, and environmental factors.

In this review, we aim to provide a thorough explanation of how and when this trend occurred, despite its energetic challenges. Additionally, we will highlight two notable exceptions to this general trend: *H. naledi* and *H. floresiensis*. We will also examine the more recent and unexpected phenomenon of brain size reduction in *H. sapiens*, which challenges the long-standing assumption of a continuous increase throughout our evolutionary history.

2 | Current Theories on the Origins of Brain Expansion

The main hypotheses explaining brain size evolution (Table 1), with the exception of the Cooking Hypothesis, share a critical assumption: that any proposed cause must exert a selection pressure sufficiently strong to offset the increased energy demands of the brain. In essence, this selection pressure arises from traits that benefited from the enhanced cognitive abilities provided by a larger brain.

2.1 | The Social Hypotheses

Social hypotheses propose that social factors, such as living in large groups, have been the primary drivers of human brain evolution. The emphasis on social explanations for primate cognition arises from the observation that complex social interactions are a defining feature of wild primates. For instance, certain prosimians, such as social lemurs, have developed complex social structures and capacities for social learning despite lacking the object manipulation skills seen in monkeys [32]. Thus, monkey social structures likely predate primate intelligence, having been established and shaped much earlier. Chimpanzees display social behaviors similar to those of humans, including engaging in warfare [33]. Experimental research has also shown that many monkeys, such as baboons, exhibit complex social cognition [34].

Several social forces are believed to have driven the evolution of larger and more complex brains. According to the Cooperative Breeding Hypothesis [35], a pivotal factor for humans may have been the emergence of alloparental care, where individuals other than the parents assist in raising offspring (e.g., provisioning young by helpers). This hypothesis posits that many uniquely human cognitive abilities, such as cumulative culture and language, originate from shared intentionality. In cooperatively breeding primates, shared intentionality arises from a prosocial tendency fundamentally absent in chimpanzees. This suggests that while chimpanzees (and possibly all great apes) possess many cognitive prerequisites for human-like mental abilities, they lack the motivational drivers necessary for such behaviors. The hypothesis further proposes that in humans, the cognitive component inherited from ape ancestry merged with a motivational component, illustrating convergent evolution observed in many cooperative breeders.

Chimpanzees also engage in political maneuvering [36]. This behavior occurs within the framework of dominance relationships, where victors may withhold reconciliation until their status is acknowledged. It also includes individuals exerting influence beyond their social rank and the formation of more stable female relationships compared to those among males. Furthermore, chimpanzees form coalitions and exchange social favors.

The Machiavellian intelligence hypothesis [37], building on de Waal's work [36], posits that the ability to manipulate others within social groups was a critical challenge for early humans,

BOX 2 | Taxonomy and Phylogeny Definitions

Clade

A clade refers to a group of organisms that includes a common ancestor and all its descendants. Clades are characterized by shared derived characteristics, or synapomorphies, that distinguish them from other groups. This helps in understanding the patterns of evolutionary change, speciation events, and the origins of biodiversity.

Extant

Any group of organisms with living members.

Extinct

Any group of organisms with no living members.

Hominin

Hominini (hominins) form a taxonomic tribe within the subfamily Homininae (hominines). This tribe includes two extant genera: *Homo* (humans) and *Pan* (subtribe Panina: chimpanzees and bonobos), while excluding the genus *Gorilla* (gorillas), which is classified separately within the tribe Gorillini of the same subfamily. Hominini also encompasses extinct species of *Homo* and ancestral genera, including *Paranthropus*, *Australopithecus*, *Ardipithecus*, *Kenyanthropus*, and *Sahelanthropus*. Members of Hominini are characterized by bipedalism and generally larger brains compared to other primates. The subfamily Homininae, along with Ponginae (*Pongo*, orangutans), constitutes the family Hominidae (great apes). Together, the families Hominidae and Hylobatidae (gibbons) form the superfamily Hominoidea.

Homo georgicus

The taxonomic status of *H. georgicus* is still in debate, as the five skulls found at Dmanisi (Georgia) are quite different. Moreover, the skull we selected as an example from this Western European site (Skull 1, D2280, the largest of the five: ECV 780 cc; Table S1), together with skulls 2–4, likely represent a more generalized ‘early hominin’ category rather than fitting neatly into either *H. erectus* or *H. ergaster* [25]. Additionally, Skull 5 is completely distinct from all other specimens found at Dmanisi, and its mandible would be appropriately considered the holotype of *H. georgicus* [25].

Lower Paleolithic

The earliest subdivision of the Paleolithic period, characterized by the earliest stone tool industries, such as the Oldowan and Acheulean, spanning from about 2.5 million to 300,000 years ago.

Outgroup

In phylogenetic trees, an “outgroup” refers to a species or group of species closely related to the ingroup (the group of primary interest) but not part of it. The outgroup is used to root the tree and infer the polarity (direction) of characters.

Phylogenetic tree

It is a branching diagram depicting the evolutionary relationships among organisms. It illustrates their common ancestry and the divergence of taxa over time.

driving the evolution of intelligence. According to this theory, intense social competition fostered the development of sophisticated “Machiavellian” strategies, ultimately leading to larger brains and the emergence of distinct cognitive abilities essential for social and reproductive success.

All these theories propose a more sophisticated social structure than that observed in monkeys but fail to explain how humans developed such complexity. The Social Brain Hypothesis (SBH) [38–40] suggests that the complexity of primate social life was the primary driver of brain expansion. According to this hypothesis, the evolutionary pressure for a large, energy-intensive brain arose from the challenges posed by social complexity.

From this perspective, the expansion of cortical regions, along with the increase in hominin brain size, provides additional support for their position [41]. More recently, they reinforced

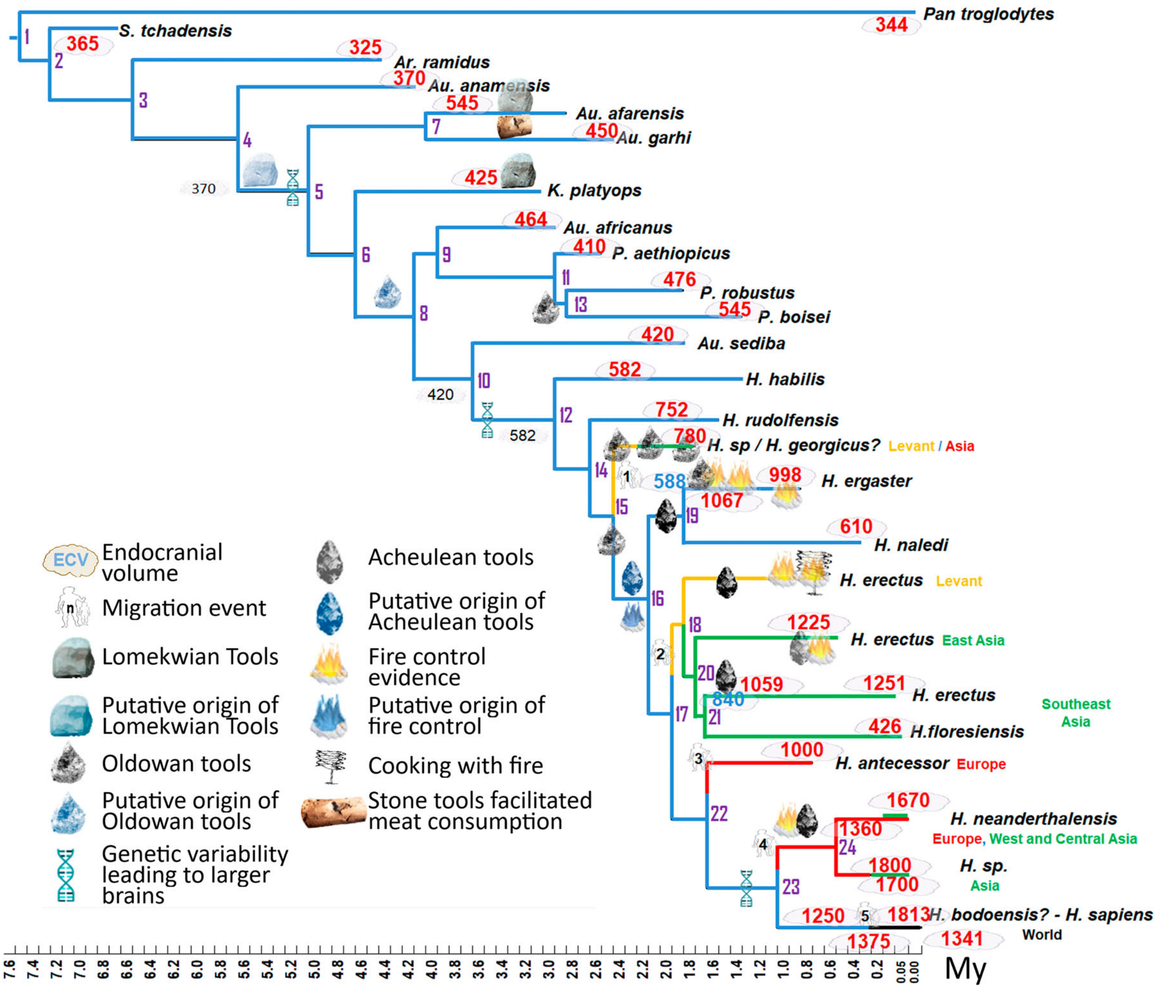

FIGURE 1 | *Simplified Hominin phylogenetic tree: brain sizes and cultural landmarks*. The tree presents a streamlined model illustrating the evolutionary progression of the Hominini tribe, with the genus *Pan* (chimpanzees, subtribe *Panina*) as the outgroup (see Box 2) for the subtribe *Hominina* (all other species in the tree). The general topology, divergence times, and species time spans are primarily derived from the works of Püschel et al. [26] and Diniz-Filho et al. [27]. Nodes are numbered for reference within the text. The placement of *Au. sediba* as the sister group to the genus *Homo* (node 10) follows the work of Mongle et al. [28]. The divergence time at node 19 is based on the 'naledi' hypothesis proposed by Püschel et al. [26]. Node 17 is supported by Zhu et al. [29], who documented the presence of *H. erectus* in China 2.1 Mya (Million years ago). The estimate for node 18 is informed by Barash et al. [30]. Nodes 22 and 23 are based on Roksandic et al. [31]. Brain volumes and corrections to divergence times and species time spans are informed by the fossil record, as detailed in Table S1. Genera: *Ar.*: *Ardipithecus; Au.*: *Australopithecus*; *H.*: *Homo*; *K.*: *Kenyanthropus*; *P.*: *Paranthropus; S.*: *Sahelanthropus*. Geographic locations are indicated by colored lines: Africa (blue), Asia (green), Europe (red), Levant (yellow), and World (black). My: Millon years.

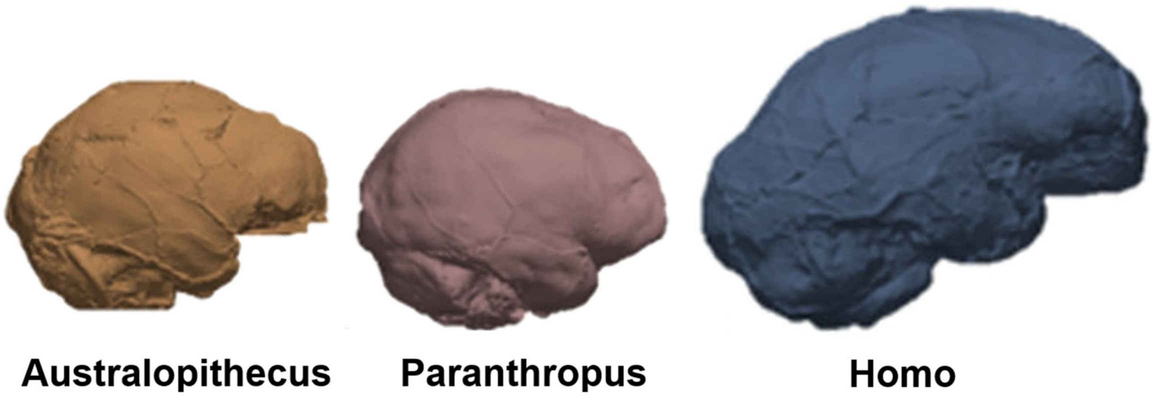

FIGURE 2 | *Virtual endocasts.* Examples of virtual endocasts (See Box 1). Reprinted with permission from de Sousa et al. [24] Figure 2.

TABLE 1 | Hypotheses related to human brain size increase.

Social	
• Basic social behavior in prosimians	[32]
• Complex social behavior in monkeys	[33, 34, 98]
• Machiavellian intelligence in monkeys	[36]
• Machiavellian intelligence in hominids	[37]
• Cooperative breeding in hominids	[35]
• Social brain hypothesis	[38, 39, 99]
Ecological	
• Diet	[49, 50, 100]
• Home range size and food distribution complexity	[49]
• Extractive foraging technics	[52, 53]
• Foraging behavior	[51]
Brain energy cost	
• Expensive-tissue	[57, 58]
• Expensive brain	[60]
Mixed brain energy cost—ecological	
• Cooking	[61–63]

their argument by proposing a sequence of evolutionary events for primates [42]: "...there is clear evidence that social foraging is an earlier evolutionary response than sophisticated foraging. This suggests that the first option would thus seem to provide a more coherent sequence: living in large groups is a solution to the problem of occupying predator-risky habitats, with large brains the solution for the cognitive skills needed to maintain the cohesion and coherence of large groups, while enhanced foraging skills are necessary to maintain these calorie-hungry brains." Therefore, they present a compelling explanation for the emergence of complex societies.

However, the proposed sequence of events raises certain concerns. The SBH explicitly outlines a chronological sequence of interconnected evolutionary events, each emerging as a necessary evolutionary outcome of its predecessor:

1. Populations occupy predator-risky habitats, presenting an evolutionary challenge.
2. A possible solution to this problem is living in large groups, but this comes with its own set of challenges. Large groups face evolutionary disadvantages, as noted in the proposal itself, such as the need to "maintain the cohesion and coherence of large groups." This arises because relational complexity increases with group size [43], along with greater direct competition for resources, wider group dispersion, longer daily travel distances, and expanded home ranges [44–46].
3. In response to the complexities of living in large groups, populations may evolve larger brains. However, this adaptation has immediate evolutionary costs, as larger brains require more energy, as discussed earlier.
4. The challenges posed by larger brains could be mitigated by the very increase in brain size, which would enhance foraging skills and help compensate for the additional energy demands.

The fundamental issue is that "event" 3 (and thus "event" 4) is unnecessary if large group size has a neutral or positive net effect on fitness (see Box 3) [48], as the scenario itself proposes it as the "solution". In this case, there would be nothing else to compensate for. It is unclear whether the mutations enabling larger groups arose and spread before or during encounters with predator-risky habitats (an "evolutionary race"). Regardless of the underlying population genetics (see Box 3), the situation eventually resulted in a neutral or positive net effect on fitness, favoring large groups despite predation threats, without further compensation.

Most importantly, if enhanced foraging skills ("event" 4) compensate for larger brains, the issue is resolved ecologically (see Box 5), as foraging skills are part of the "Ecological Hypotheses" (see below), without the need for social explanations.

2.2 | The Ecological Hypotheses

Ecological intelligence theory focuses on dietary characteristics such as the complex distribution of resources across space and time, the use of sophisticated foraging methods, and adaptations to environmental changes. These hypotheses emphasize the challenges of the nonsocial environment—locating, storing, and digesting food—essentially highlighting the difficulties presented by nature. Beyond reservations about the link between brain size and the Social Brain Hypothesis (SBH), several recent studies argue that ecological variables offer a more compelling explanation for human brain evolution, stressing the significance of the nonsocial environment.

Ecological intelligence theory highlights several factors that may have driven human brain expansion, including diet [49], with frugivores generally having larger brains than folivores [50]. Also considered are factors such as home range size, food distribution complexity [49], foraging behavior [51], and sophisticated foraging techniques [52, 53]. Interestingly, even the Social Brain Hypothesis (SBH), which emphasizes social pressures, acknowledges an ecological element, proposing that the initial driver of brain enlargement was survival in predator-rich environments—an ecological driver within the SBH itself.

Another study [54] employed a complex quantitative method to estimate the relative influence of various selection pressures on brain size evolution. While acknowledging the difficulty of establishing causal relationships, the authors categorized these pressures as ecological (finding, storing, or processing food) and social (cooperation, manipulation, alliances). The study found that ecological pressures were a stronger driver of brain size increase (60%) compared to social pressures (30%), with the remaining 10% attributed to competition between groups. In contrast to the SBH, this finding suggests that ecological pressures, rather than social ones, were the primary driver of brain size increase. However, this conclusion implies that all animals exposed to similar ecological conditions—not just

Cis- and transregulatory genes

They are crucial for genetic regulation. Cis-regulatory elements control gene expression by interacting directly with the gene's machinery on the same DNA molecule, while transregulatory elements, encoded separately, regulate expression from a distance. They form complex networks governing gene expression, cell differentiation, and development, vital for understanding genetic regulation's intricacies.

Epigenetics

It refers to the study of heritable changes in gene expression that do not involve alterations in the underlying DNA sequence. These changes regulate how genes are turned on or off and are influenced by environmental factors, developmental cues, and cellular processes.

Key mechanisms include:

1. *DNA Methylation*: Addition of methyl groups to DNA, typically suppressing gene activity.
2. *Histone Modification*: Chemical changes to histone proteins affecting chromatin structure and gene accessibility.
3. *Noncoding RNAs*: See Noncoding regulatory DNA and RNA in this Box

Epigenetic changes are reversible and play crucial roles in development, cell differentiation, and responses to environmental stimuli. They are also implicated in aging, diseases such as cancer, and transgenerational inheritance.

Fitness

In the context of evolutionary biology, fitness measures the reproductive success of an organism, genotype, or phenotype relative to others in its population. It encompasses the ability to survive, grow, and reproduce, ultimately contributing to the gene pool of the next generation. Fitness is dynamic and influenced by environmental conditions.

FOXP2 gene

This gene encodes a transcription factor critical for regulating the expression of other genes involved in neural development and plasticity. It is particularly significant in the context of speech and language, often referred to as the “language gene.”

Key roles and characteristics:

1. *Neural development*: FOXP2 is essential for the development and function of neural circuits, especially in brain regions like the basal ganglia and cortex, which are involved in motor control and cognition.
2. *Speech and language*: Mutations in FOXP2 are linked to speech and language disorders, including deficits in articulation and grammatical processing.

Gene flow

It is the movement of genes between populations through migration or mating. It leads to the exchange of genetic material, homogenizing allele frequencies between populations. It can counteract genetic drift and promote genetic diversity within a species. It is a crucial factor in evolution, shaping population structure and adaptation.

Genetic drift

It is the random fluctuation of allele frequencies within a population due to chance events. It can lead to the loss of genetic variation over time, even if it is selectively advantageous, particularly in small populations. It can also lead the fixation of neutral or even somehow harmful alleles. Genetic drift is a key evolutionary mechanism that influences the genetic composition of populations and can result in genetic divergence.

Interbreeding

It refers to the act of breeding or reproducing between individuals or populations that belong to different genetic groups, species, or subspecies.

Human accelerated regions

HARs are genomic segments that evolved rapidly in humans compared to other primates, playing a role in traits like brain development and cognitive function.

Key features:

1. *Rapid evolution*: HARs evolved faster in humans, contributing to human-specific traits.
2. *Brain development*: Many HARs influence brain growth, neural networks, and cognitive abilities.
3. *Functional significance*: HARs regulate genes involved in neural development and synaptic plasticity.
4. *Evolutionary insights*: HARs help explain genetic differences related to brain evolution in *Homo sapiens*.

MEF2 (Myocyte Enhancer Factor 2) transcription factor

MEF2 proteins regulate gene expression during development, differentiation, and cellular function, with roles in the brain, heart, and muscles.

Key roles:

1. *Neuronal development*: MEF2 controls gene expression in neurons, influencing synapse development, pruning, and plasticity for learning and memory.
2. *Muscle differentiation*: MEF2 regulates genes critical for muscle formation and function.
3. *Signal integration*: MEF2 is modulated by pathways like calcium/calmodulin and MAPK, linking signals to gene expression.

MEF2 proteins are key in connecting environmental signals to gene regulation, essential for development and tissue homeostasis.

Net effect on fitness

It refers to the overall impact of various traits on an individual's or population's reproductive success, integrating all components of fitness such as survival, growth, and reproduction. This concept is crucial because it emphasizes that analyzing individual components of fitness (vital rates) in isolation can be misleading due to demographic trade-offs. For example, a trait that negatively affects survival may positively impact growth or reproduction. Therefore, the net effect on fitness provides a comprehensive measure by considering how traits collectively influence the fitness of an individual or the population fitness, balancing the contributions of all vital rates.

Nonaptation

Within the framework of “taxonomic fitness” of Gould and Vrba [47], mutations leading to increased brain size fall, for us, under the category of “nonaptations.” According to their terminology, aptations are features that provide a benefit and enhance fitness. When shaped by natural selection, these are termed adaptations. However, Gould and Vrba coined the term “exaptations” for mutations whose emergence did not rely on previous adaptive processes. Essentially, exaptations improve fitness but were not originally designed for that role by natural selection. They might have been selected for another function initially (like bird feathers for insulation) and later co-opted for a new purpose, or they could have appeared without a prior function and then been co-opted for a specific role like improved cognition, as seen in mutations that led to larger brains.

Noncoding regulatory DNA and RNA

Noncoding regulatory DNA and RNA elements do not code for proteins but regulate gene expression, playing essential roles in cellular processes and development.

Noncoding regulatory DNA

1. *Enhancers*: DNA sequences that boost gene transcription, often acting at a distance.
2. *Promoters*: Near gene starts, these provide binding sites for RNA polymerase and transcription factors.
3. *Silencers*: DNA sequences that suppress gene transcription by recruiting repressive proteins.
4. *Human accelerated regions (HARs)*: See definition in this box.

Noncoding regulatory RNA

1. *MicroRNAs (miRNAs):* Small RNA molecules that inhibit gene expression by targeting mRNA for degradation or translation inhibition.
2. *Long noncoding RNAs (lncRNAs):* Regulate gene expression through chromatin remodeling or transcriptional interference.
3. *Small interfering RNAs (siRNAs):* Guide mRNA degradation, silencing specific genes.
4. *Circular RNAs (circRNAs):* Closed RNA molecules that regulate gene expression, often acting as miRNA sponges.

Functional roles

- *Gene regulation*: Fine-tune gene expression for precise cellular responses.
- *Epigenetic control*: See definition in this box.
- *Evolutionary innovation*: Noncoding elements drive species-specific traits by altering gene expression.

Population genetics

Population genetics is the study of genetic variation within populations and the evolutionary forces that shape this variation over time. By examining how alleles (different versions of a gene) are distributed and change across generations, population genetics provides insights into the mechanisms of evolution, adaptation, and speciation.

Population fitness

It is the finite rate of increase of a population. It is a measure of the overall reproductive success of a population and is calculated as the average fitness of all individuals within the population. In essence, it reflects the population's ability to grow and persist over time. It can be quantified directly for a single time step as the ratio of the population size at the next time step (Nt+1) to the population size at the current time step (Nt).

SRGAP2C gene

The SRGAP2C gene encodes a protein involved in neuronal development, particularly in synapse and dendrite formation.

Key roles

1. *Neuronal development*: Regulates dendritic spine formation and actin dynamics for synaptic plasticity.
2. *Cognitive function*: Linked to learning and memory, contributing to neural circuit complexity.
3. *Evolutionary significance:* Arises from gene duplication, aiding human brain complexity, especially in cognitive areas.
4. *Impact on brain evolution*: SRGAP2C's duplication is thought to contribute to advanced brain traits and larger brains.

Syngameon

It refers to groups of species that share a common gene pool and are capable of interbreeding to produce viable offspring. They are also defined as a group of semispecies sympatric (see Box 4), or at least only marginally allopatric (see Box 4), which can occasionally interbreed. This term is often used in evolutionary biology to describe populations or species that are closely related and can hybridize with one another. Syngameons play a significant role in understanding speciation processes and genetic diversity within populations.

primates—should have experienced brain enlargement relative to body size. Acknowledging this issue ("Therefore, our results highlight the fundamental question of why ecological challenges would have favored substantial brain expansion in humans but less so in other taxa"), the authors proposed a supplementary explanation. Central to their model is the concept of individual energy extraction efficiency (EEE), which is influenced by skill levels, the skill levels of social partners, and encountered challenges. Within this model, EEE quantifies the proficiency of individuals in utilizing their skillset to extract energy from the surrounding environment. It serves as a metric to assess the net energy gain—the difference between the energy obtained and the energy expended—when confronting ecological or social challenges. While ecological pressures drove the evolution of larger brains in humans for enhanced problem-solving and skill acquisition, this posed a serious challenge. A larger brain consumes a substantial amount of energy, potentially negating the benefits of increased cognitive abilities. The authors assumed that the proportion of large brains relative to body size observed in *H. sapiens*—an assumption challenged in our Introduction—could only be replicated in their mathematical model under what they defined as a weakly decelerating EEE. This occurs when young individuals can maintain a substantial rate of increase in their efficiency of energy extraction as they acquire skills. For this to be achievable, the authors proposed that cultural learning, particularly cumulative culture, teaching, and language, might be the key factor enabling weakly decelerating EEE. Learning from the accumulated pool of skills in the population allows individuals to maintain a high rate of increase in EEE as their skill levels increase in youth. This rapid learning boost early in life could then justify the larger brain size in humans compared to other animals facing similar ecological challenges. In our view, this *ad hoc* explanation is contradictory. The central and initial conclusion was that the main driver was ecological, not social. However, to make the ecological explanation unique for humans, the authors resorted to a social-based explanation, which was likely not present in the early stages of brain enlargement. This is the inverted, but analogous, problem of the SBH, which ultimately resorts to an ecological explanation

A regression-based study investigated the interplay of brain size, social structure, ecology, and life history in shaping human brain evolution [55]. To explore these relationships, researchers compiled a comprehensive data set encompassing these variables across diverse primate and carnivore species. To account for the phylogenetic relatedness of species, the study employed phylogenetic generalized least squares (PGLS) regression [56]. This statistical method incorporates phylogenetic relationships to estimate covariance in cross-species data, assuming that closely related species share more similar traits due to common ancestry. By doing so, PGLS adjusts regression estimates to account for interspecific autocorrelation. In primates, diet and ecological variables emerged as the strongest predictors of brain size, particularly the proportion of fruit in the diet. While social factors also played a role, they were less significant than ecological ones. In carnivores, ecological variables, such as home range size, were significant predictors of brain size, whereas social factors had minimal impact. Life-history traits, including extended developmental periods and maximum lifespan, were important for counterbalancing the metabolic costs associated with larger brains in both groups. The study concluded that ecological pressures are more consistent predictors of brain size across primates and carnivores, while social factors have a variable influence but only in primates. As discussed previously, social factors might have mechanistic limitations when considered alone. Despite identifying key correlations, the study does not propose an explanation or underlying mechanism by which these factors have promoted brain growth in primates but not in carnivores.

2.3 | Brain Energy Cost Hypotheses

The Expensive Tissue Hypothesis (ETH), proposed by Aiello and Wheeler [57], posits that the metabolic costs of large brains in humans are offset by reductions in the size of another metabolically expensive organ—we add, unless compensated by immediate reproductive advantages correlated with the size change. Specifically, they identified the gastrointestinal tract as a key trade-off, noting that its size is only 60% of what would be expected for a primate of similar body size. Supporting this hypothesis, other researchers have found a positive correlation between diet quality and brain mass in primates, suggesting that improved nutrition facilitated a reduction in gut size, thereby reallocating resources to brain growth [58]. While additional factors may have played a role, this study emphasizes diet quality as a primary driver of brain size evolution. More recently, the ETH has gained further support through causal modeling techniques [59]. A related framework, the Expensive Brain Hypothesis [60], extends this idea by proposing that increases in brain size must be offset either by raising the overall energy budget of the species or by reallocating energy from other maintenance processes, such as digestion, reproduction, or offspring production.

Like the Social Brain Hypothesis, mutations that reduced gastrointestinal tract size must have arisen rapidly or in parallel; otherwise, the detrimental effects of increased brain size would have been subject to negative selection. Conversely, if the reduction in gastrointestinal tract size—an inherently disadvantageous trait—occurred first, it would have required compensatory mutations that increased brain size to emerge. These compensatory mutations would have conferred a selective advantage by enhancing cognitive capacity in nutritionally compromised individuals.

2.4 | Mixed Brain Energy Cost—Ecological: The Cooking Hypothesis

The "Cooking Hypothesis" by R. Wrangham [61–63] offers a comprehensive and well-supported explanation—though not widely accepted (opposing arguments are discussed in a later section)—of how the energetic cost of brain size increase could have been accommodated. This hypothesis posits that cooking food, whether through fermentation [64] or primarily using controlled fire, correlates with an increase in brain size. Cooking made it possible to acquire the additional energy required to sustain larger brains. Wrangham proposed that the control of fire was achieved by our predecessor *Homo erectus* (*H. ergaster*) at least 1.5 Mya (see Table 2 and Figure 1). Moreover, the advent of controlled fire and the cooking of plant foods coincided with—and potentially explains—tooth reduction and other gastrointestinal adaptations in this species. For the remainder of this paper, we distinguish between African *H. erectus* populations, referred to here as *H. ergaster* [65], and Asian populations, which we continue to call *H. erectus*. This distinction is made without implying any definitive conclusion about their species status.

As a result, fire control and cooking represent essential human-created ecological factors. Within this artificial environment, mutations promoting an increase in brain size—mutations that would otherwise have been detrimental—became selectively neutral and eventually advantageous. In the models described in the previous sections, either strong selection pressures were required to favor increased brain size, inherently outweighing its negative energetic effects, or natural selection would have driven brain enlargement across all animals under similar conditions.

From our perspective, brain size increase represents a case of sustained and accumulated "use" of "nonaptations," that is, previously nonfunctional traits (see Box 3). Recently,

BOX 4 | Speciation types

Speciation

Speciation is the evolutionary process by which a single species splits into two or more distinct species and can be classified into several types based on the original geographical distribution of the divergent populations.

Allopatric

Allopatry refers to the geographical separation of populations of a species. It is a fundamental concept in evolutionary biology. Allopatry can result from various factors such as geographic barriers or dispersal events. Driven by geographic isolation, allopatric speciation is a mode of speciation where a population becomes separated from the main ancestral group due to physical barriers like mountain ranges, new bodies of water, or climate change. This isolation sets the stage for the evolution of new species. Over time, the separated populations experience different selection pressures and genetic drift, leading to the accumulation of genetic differences. These differences can eventually become so significant that the isolated populations can no longer interbreed, even if they come back into contact. Interestingly, the size of the isolated population can vary in allopatric speciation, and the process itself may take a long time.

Peripatric

Peripatry refers to the geographic isolation of a small group of individuals from the larger population of a species. Peripatric speciation is a subtype of allopatric speciation, focusing on the isolation of small, peripheral populations from the main ancestral group. Geographic isolation, a key factor in allopatric speciation, is still required here. However, the differentiating element lies in the population size. Due to their smaller numbers, these peripheral populations experience stronger founder effects and genetic drift compared to larger populations isolated in allopatric speciation. This increased genetic drift, coupled with potentially different selection pressures faced by the smaller group, can lead to more rapid evolution and the formation of a new species. Though geographically isolated, the distance between the new and ancestral populations might be relatively small in peripatric speciation.

Sympatric

Sympatry refers to species or population occurring in the same geographic area without geographical barriers. Sympatric speciation occurs when new species evolve from a common ancestral species within the same geographical area. Unlike allopatric speciation, where geographic isolation plays a key role in reproductive isolation, sympatric speciation involves reproductive barriers emerging within a single population. This process can occur through various mechanisms, such as ecological niche differentiation, disruptive selection, polyploidy, or other chromosomal variants.

BOX 5 | General definitions

Deep learning

This technology, inspired by the structure of the brain, utilizes complex algorithms to learn from vast data sets. It can be applied to analyze the exposure of flint artifacts to heat, identifying patterns invisible to traditional methods.

Ecological

Apply to the interaction and interdependence between organisms and their surrounding environment.

Fourier-transform infrared spectroscopy

A technique that analyzes a material by shining infrared light through it. Different molecules absorb specific infrared wavelengths, creating a unique fingerprint.

Micromorphology

Study of the fine-scale structure of materials using microscopy.

Popperian perspective

Emphasizes falsifiability over verification in hypothesis testing. Hypotheses gain credibility by surviving attempts at falsification rather than confirmation.

Raman spectroscopy

Analyzes a material by shining laser light on it. Scattered light reveals information about the sample's molecular structure.

Thermoluminescence

A property of some materials that emit light when heated.

researchers have questioned whether cognitive skills initially evolved to manage social complexity and later facilitated more efficient foraging, or vice versa [66]. In our view, brain enlargement resulted from successive and likely parallel nonaptations, made nondetrimental by cooking. Subsequent selection processes then shaped these traits in response to social and/or environmental challenges, aligning with recent findings that both factors influenced brain size evolution in primates [67].

Therefore, our view diverges from the 18 different ways brain size, group size, and diet might be causally related, as proposed by Dunbar and Shultz [68]. We argue that an increase in brain size was not directly caused by either social or environmental variables. In other words, brain enlargement was not the result of complex social behavior or elaborate foraging strategies but rather emerged as a nonaptation, which subsequently facilitated the development of these features.

3 | The Cooking Hypothesis under Fire: The Indirect Evidence for Early Fire Control and Cooking

Fire control and cooking have played crucial roles in hominin and human evolution. The Cooking Hypothesis proposes that fire and cooking were initially utilized by a prehuman species, plausibly the ancestors of *H. ergaster* [69]. However, a key challenge of this hypothesis is determining the timeframe during which fire and cooking began to influence hominin or human evolution.

Based on numerous publications by R. Wrangham, as cited elsewhere in this paper, there are four primary reasons to suggest that these technologies emerged before to the advent of *H. sapiens* and possibly even predated *H. ergaster*:

1. As previously discussed, the human brain accounts for approximately 20%–25% of the body's energy consumption while constituting only 2% of its mass [18–21]. Moreover, 80%–90% of this energy is devoted to its spontaneous activity, measured in the resting state without specific task demands [70]. Consequently, the evolution of larger brains required higher energy demands, which could be met through the adoption of cooking [71]. Cooking significantly enhances energy extraction from food compared to consuming it raw, even when the food is meat. Studies indicate that individuals adhering to raw diets, regardless of meat consumption, often experience low Body Mass Index (BMI, a measure of body fat based on weight and height) and reproductive challenges, while vegetarians consuming cooked diets show higher BMI and good ovarian function [72, 73]. This suggests that cooking itself, rather than the type of food, is crucial for optimizing energy intake. Research on mice has demonstrated that those fed cooked diets maintain their weight better than those consuming raw diets, including raw meat [74, 75]. The increased digestibility and energy gain from cooked food underscore its importance in meeting the net energy required for sustaining larger brain sizes and their associated higher metabolic demands.
2. *H. ergaster* exhibited reduction in masticatory structures, including a smaller mouth and blunt molars, and has been depicted with a smaller gut compared to earlier hominin forms. These anatomical features suggest that *H. ergaster* lacked the physical capacity to efficiently digest raw plants high in structural fiber, implying that the evolutionary changes leading to this species occurred over an extended period. However, alternative explanations exist for the reduced masticatory features besides cooking. For instance, these traits have been attributed to the significant role of meat in the diet, likely obtained primarily through scavenging [76–78]. Nevertheless, pronounced buccal scratch densities observed in *H. ergaster* specimens contradict the notion of a specialized carnivorous diet, instead suggesting the consumption of a diverse array of abrasive foods [79].

   Experiments with adult humans demonstrated that incorporating meat as one-third of the diet could result in nearly 2 million fewer chewing cycles annually—a 13% decrease—along with a 15% reduction in the overall masticatory force required [80]. Moreover, slicing meat and processing underground storage organs (USOs) improved the ability to break meat into smaller pieces by 41%, further reducing the annual number of chews by 5% and lowering the masticatory force needed by an additional 12%. However, unprocessed meat posed significant challenges for participants in reducing particle size through mastication. Even after 40 chews, meat typically remained as a single large particle, limiting the efficiency of energy extraction. This finding suggests that, despite requiring fewer chews and less force per calorie compared to USOs, the inability of hominin teeth to effectively break down raw, unprocessed meat likely diminished its net energy benefits, restricting the advantages of consuming large quantities of unprocessed muscle tissue. The study also highlighted the substantial benefits of cooking in reducing masticatory effort. Roasting USOs decreased muscle recruitment per chew by 14.1% and per sample by 22.0%, while allowing for the swallowing of larger particle sizes. This reduction in effort likely contributed to the evolutionary trend toward smaller teeth. Additionally, while roasted meat required greater muscular effort per chew, it resulted in smaller, more easily swallowed particles, underscoring the critical role of cooking in improving chewing efficiency and reducing the need for large masticatory structures.
3. Evidence of meat and marrow consumption (Table 2 and Figure 1) dates back to 2.5–3.3 Mya [81], though some authors dispute this [82]. However, large-animal butchering has been documented from 1.8 Mya [83]. This suggests that *H. ergaster*, which is thought to have relied heavily on animal-based foods (potentially one-third of its diet, as noted earlier), may have been scavenging at a high risk of disease from pathogens, given that carrion rapidly becomes contaminated with bacteria [84]. It is plausible that they focused on consuming marrow or brain tissue, which have lower bacterial loads due to their protection within bones [85]. However, cut marks on fossils indicate that edible meat portions were also frequently removed, suggesting that they likely practiced careful selection of carrion to minimize pathogen exposure. Another potential method for mitigating contamination risk was roasting (cooking) the meat, which would have effectively eliminated surface pathogens.
4. Unlike its tree-climbing ancestors, *H. ergaster* was poorly adapted for climbing, suggesting that it likely slept on the ground and relied on fire for protection against nocturnal predators [61].

The primary limitation of these arguments lies in their indirect nature. Direct evidence of fire management by early *H. ergaster* or even earlier hominins would provide much stronger support. Traditionally, fire identification in archaeological sites has relied on visual inspection of altered sediments, lithics, and bones. The absence of such evidence is often cited by those who reject the cooking hypothesis. Some researchers, noting the increased presence of direct fire evidence after 500,000 years ago, argue that fire control was not achieved until that time [80]. This reasoning essentially follows the principle that "absence of evidence is evidence of absence" [61]. Nevertheless, independent studies, such as those examining metabolic needs, support the idea that cooking was essential for brain development in the early stages of our genus, dating back to *H. ergaster* [86].

The arguments against the cooking hypothesis face two main difficulties. First, they fail to present compelling alternative explanations that consistently and comprehensively account for the four core pillars of the cooking hypothesis. As previously discussed, the Social Brain Hypothesis (SBH), Ecological Theories (ET), and other alternative models do not fully explain brain size evolution and may even contain inherent inconsistencies.

The second issue with arguments opposing the "Cooking Hypothesis" is epistemological. Critics rely on a simplistic reasoning: the absence of "hard" archaeological evidence of fire is taken as a lack of proof for fire use and, by extension, for cooking. This perspective fails to recognize the role of inference and deduction in studying phenomena that are distant in space or time, where direct observation is not possible. In science, "direct observation" or "hard proof" is always contextualized within an explanatory framework. For instance, in astronomy, the existence of exoplanets—too distant to be observed directly—is inferred from their effects on the brightness of their stars or from gravitational waves [87, 88]. Similarly, in particle physics, evidence confirming the existence of the Higgs boson was indirect, relying on statistical analysis. It emerged from an "excess" of events aligning with theoretical predictions, observed with exceptionally high statistical significance [89]. These discoveries face no objections regarding their empirical, theoretical, or epistemological validity.

The epistemological basis for scientific evidence—whether concerning exoplanets, subatomic particles, or early hominin behaviors such as fire use and cooking—remains consistent. Evolutionary theory, for instance, serves as a working framework that explains the continuity of the fossil record. However, by its nature, it deals with past events that cannot be directly replicated through experimentation. From a Popperian perspective (see Box 5), this makes definitively testing evolutionary hypotheses challenging. While artificial selection and direct observations of allele frequency changes in natural populations provide some avenues for testing, these approaches have limitations.

The appearance of fossil specimens without immediately apparent close relatives in the paleontological record has never invalidated core evolutionary theory. Darwin's model of gradualism proposed that evolution progresses in small, incremental steps. However, such "sudden" appearances led to alternative explanations, including allopatric and peripatric speciation models based on genetic revolution [90] and the theory of punctuated equilibrium [91]. Punctuated equilibrium suggests that most genetic changes occur during speciation events, concentrated in relatively short periods through numerous small variations rather than large-scale transformations. These rapid changes are difficult to detect in the fossil record. Yet, the absence of direct fossil evidence for these events has not prevented the theory's acceptance. Observations of rapid genetic and phenotypic changes in bacteria and viruses provide analogies for the mechanisms underlying punctuated equilibrium. Ultimately, this remains an interpretation of the past based on present observations, inherently requiring some degree of initial acceptance of the hypothesis. No one has ever directly observed a speciation event in vivo or experimentally, yet the occurrence of speciation in the past is widely accepted.

4 | Direct Evidence for Fire Control and Cooking

New analytical techniques are being employed to assess the exposure of flint artifacts to heat, independent of visual indicators such as magnetic susceptibility or color changes. These methods include Fourier-transform infrared spectroscopy, thermoluminescence, micromorphology, Raman spectroscopy, and deep learning algorithms (see Box 5 for definitions of these terms).

Compelling evidence for fire control at the open-air site of Evron Quarry in Israel has emerged from a recent study [92], which dates the site to between 1.0 and 0.8 Mya. This study utilized a combination of spectroscopic techniques capable of detecting signs of burnt fauna and lithics even in the absence of visible fire residues (Table 2, Figure 1). The authors propose that other Lower Paleolithic sites lacking visual evidence of fire should be re-evaluated using these advanced methods to gain new insights into early hominin behavior and fire use. Beyond Evron Quarry, additional evidence suggests hominin associations with fire (Table 2 and references therein; Figure 1): *H. ergaster* in Africa around 1.6 Mya, *H. erectus* in Asia around 1 Mya, and *H. neanderthalensis* in Europe by 0.98 Mya. Furthermore, the site of Gesher Benot Ya'aqov not only provides evidence of human-controlled fire but also the earliest known evidence of hominin cooking (Table 2, Figure 1), dating back to approximately 780,000 years ago [93]. This study demonstrates that fish recovered from the site had been cooked and consumed there.

Advances in physical and chemical analysis techniques are redefining what constitutes "observable" or "direct" evidence of fire associated with human activity. These innovations are pushing the timeline for fire detection in the archaeological record beyond one million years ago (Mya).

5 | Hominin Phylogeny: Brain Size Evolution, Stone Tools, and Fire Control

The first branching event depicted in the phylogenetic tree of Figure 1 occurs between our closest living relative, the chimpanzee (Figure 1 node 1), with an average brain size (endocranial volume or ECV; see Box 1) of 344 cc. This split took place around 7–7.5 Mya [26, 94]. Following this divergence, three hominin species from different genera emerged, all with relatively small brains. These species include *Sahelanthropus tchadensis* (ECV 365 cc; Figure 1 node 2), *Ardipithecus ramidus* (ECV 325 cc; Figure 1 node 3), and *Australopithecus anamensis* (ECV 370 cc; Figure 1 node 4). The first two genera, *Sahelanthropus* and *Ardipithecus*, became extinct relatively early. In contrast, *Australopithecus* persisted and diversified into several new lineages. One of these lineages included *Au. afarensis* (ECV 545 cc) and *Au. garhi* (ECV

450 cc; Figure 1 node 7), while another led to *Kenyanthropus platyops* (ECV 425 cc; Figure 1 node 6). *Australopithecus* further diversified into two major evolutionary branches (Figure 1 node 8). One branch included *Au. africanus* (ECV 464 cc) and the genus *Paranthropus* (Figure 1 node 9). *Paranthropus*, which emerged from *Australopithecus*, encompassed three species (Figure 1 nodes 11 and 13): *P. aethiopicus* (ECV 410 cc), *P. robustus* (ECV 476 cc), and *P. boisei* (ECV 545 cc). The other major branch included *Au. sediba* (ECV 420 cc) and the genus *Homo* (Figure 1 node 10). The period around 1.9 Mya, based on fossil evidence (Table S1), witnessed the remarkable coexistence of several hominin genera and early *Homo* species. These included *Australopithecus* (node 10), *Paranthropus* (node 11), *H. habilis* (ECV 582 cc; node 12), *H. rudolfensis* (ECV 752 cc; node 14), *H. georgicus* (ECV 780 cc; node 15, see Box 2), *H. ergaster* (ECV~1000 cc; see Table S1), and *H. naledi* (ECV~610 cc; node 19), and possibly *H. erectus* (ECV~1200 cc; node 18). The dating of node 19, representing the divergence between *H. ergaster* and *H. naledi*, has a wide margin of error, ranging from 1.58 to 2.35 Mya [26]. For *H. naledi*, there is only one known dating, based on the sole site where its fossil remains were found, making the exact timing of its appearance and extinction uncertain [95, 96].

Stone tools (see Box 6) provide unequivocal evidence of technological advancement in hominins. The earliest known stone tool industry, Lomekwian technology (see Box 6; Figure 3), dates to 3.3 Mya and was discovered at Lomekwi 3, Turkana, Kenya (Table 2; Figure 1). This technology has been tentatively attributed to *K. platyops* [97]. The reasons why this species may have been the first to develop stone tools remain unclear. However, it represents the earliest known hominin lineage with an ECV exceeding 400 cc. Additionally, evidence of cut marks on bones, possibly made by *Au. afarensis* (Table 2; Figure 1, node 8), was discovered near Dikika, Ethiopia, dating to approximately 3.4 Mya [81]. Although the specific tools used at Dikika remain unknown, the close dating suggests they were also likely of Lomekwian technology.

What could explain the presence of the same behavior in two populations, species, or even genera? In this case, why do two distinct genera, *Kenyanthropus* and *Australopithecus*, exhibit *Lomekwian* technology? Recent research has investigated the neurological foundations required for the development of stone tools—specifically, both hammerstone nut-cracking and flake-cutting types [66]. Their empirical findings suggest that certain fundamental brain changes during early hominin evolution may have been associated with the capacity for precise stone tool use. Following this rationale—which links neurological structures to the capacity for specific behaviors—the following alternative hypotheses might explain this shared feature (Lomekwian technology), while taking into account the challenges involved in analyzing behavioral traits [101]:

1. The neurological basis for the behavior was present in their common ancestor (homology):

a. The common ancestor also developed the behavior and transmitted it culturally to all descendant lineages.
b. The common ancestor did not develop the behavior, and it arose independently in all descendant lineages.
c. The behavior emerged in one descendant lineage and was transmitted to the others through horizontal (inter-species) cultural transmission, provided that geographical and temporal conditions allowed it.

2. The neurological basis for the behavior evolved independently in all lineages (homoplasy):

a. The behavior was also developed independently in all lineages.
b. The behavior arose in one lineage and was transmitted to the others via horizontal cultural transmission, if geographically and temporally feasible.

The geographic proximity of these species in Central East Africa suggests that all of these scenarios are plausible. However, if hypothesis 1a is correct, then Lomekwian tools may have been developed as early as ~5 Mya (Figure 1, node 5).

The next generation of stone tools, Oldowan technology (see Box 6; Figure 3), dates to approximately 3.03 Mya in Kenya and has been attributed to the genus *Paranthropus* [102]. It is likely a continuation of the same cultural development as Lomekwian technology [103]. This technology was also used by the genus *Homo* in Africa (Algeria, 2.4 Mya; Kenya, 1.7 Mya) and Asia (Jordan, 2.48 Mya; China, 2.1 Mya). This raises the possibility that *Homo* acquired this technology from *Paranthropus* through cultural transmission in Africa and later introduced it to Asia. The presence of Oldowan tools at Longgupo Cave (Sichuan Province, China) 2.1 Mya suggests that early hominins migrating out of Africa already possessed and employed this technological knowledge in West Asia [104, 105]. These West Asian hominins associated with Oldowan tools share few traits with Asian *H. erectus* but exhibit strong affinities with East African *H. ergaster* or *H. habilis* [104]. This study concludes that the first hominin to arrive in Asia belonged to a species distinct from *H. erectus*, one that possessed stone tool technology. This implies an earlier migration event across the Levant around 2.5 Mya [25, 106, 107], possibly involving *H. georgicus* (node 15, migration event 1; see Box 2), a species also associated with Oldowan tools [25, 107, 108]. It has been suggested that *H. georgicus* (1.7 Mya) resulted from a migration back to the Caucasus following an earlier colonization of China around 2.1 Mya [25].

Recent estimates using optimal linear estimation models suggest that the Oldowan tool industry likely emerged between 2.622 and 3.436 Mya, with an upper limit of 4.573 Mya. These findings increase the likelihood that *Australopithecus* was responsible for the earliest Oldowan occurrences [109]. If so, its origin could be traced back to the last common ancestor of *Paranthropus* and *Homo* around 4.1 Mya (Figure 1, node 8). If *Au. sediba* is the sister clade (see Box 2) of the *Homo* lineage [28], then the common ancestor at node 8 would also belong to the genus *Australopithecus*. This would be equivalent to hypothesis 1a, as described for Lomekwian technology, where both the neurological basis for the behavior and the behavior itself (Oldowan technology) were present in the *Australopithecus–Paranthropus/Homo* common ancestor. In this case, both the neurobiological capacity and the derived behavior could be ascribed to *Australopithecus*.

BOX 6 | Stone tools

Stone tools

They are implements crafted from stone and used by early humans for various tasks such as cutting, hunting, and crafting, representing an essential technological milestone in human cultural and technological evolution. The early technologies included (Figure 3):

Lomekwian technology

Unveiling the oldest known tool industry (3.3 Mya) at Lake Turkana, Kenya, Lomekwian technology rewrites human history. Over 150 artifacts (anvils, cores, flakes)—some remarkably large—hint at advanced tool-making by early hominids. A matched core and flake suggest deliberate creation, with analysis hinting at production techniques. Despite unclear purpose, their presence significantly pushes back the timeline for stone tools.

Oldowan technology

Dating back 2.6 million years, it is the earliest widespread stone tool industry. Simple cores and flakes were knapped (broken) from larger stones. These sharp flakes likely served for cutting, scraping, or piercing, while cores might have been used for heavier tasks. This invention, a major leap in human evolution, laid the groundwork for later, more complex toolkits. Found across Africa, Europe, and Asia.

Acheulean technology

Emerging around 1.6 million years ago, it represents a significant advancement over Oldowan tools. This industry is characterized by the production of bifacial cores, also known as handaxes. These were large stones meticulously flaked on both sides, resulting in a symmetrical and powerful cutting edge. While handaxes were the most valued tools, flakes produced during their creation were likely used for various tasks like scraping, chopping, or piercing. Compared to the simpler Oldowan tools, Acheulean technology demonstrates increased complexity in its production techniques and a greater degree of standardization, particularly in handaxe shapes. This shift marks a turning point in human technological development, showcasing a move towards more sophisticated toolkits with a global impact—evidence of Acheulean tools has been found across Africa, Europe, and Asia.

The latest known stone tool technology, the Acheulean (see Box 6; Figure 3), was first dated to 2 Mya in Ethiopia (Table 2; Figure 1, node 19) and is associated with *H. ergaster* [110]. Acheulean tools have also been found in Asia: in India at 1.51 Mya [111] and in China at 0.83 Mya [112, 113], both associated with *H. erectus* (Table 2; Figure 1, node 18). In Europe, Acheulean artifacts have been discovered in Spain, dated to 0.98 Mya [114, 115], and are most likely linked to *H. neanderthalensis* (Table 2; Figure 1, node 22), following the recent proposed reassignment of all *H. heidelbergensis* fossils to that species [31]. The Asian clade originating at node 18 (migration event 2) is the sister group of the clade originating at node 22, both connected by node 17 (Figure 1). The estimated divergence time of nodes 17 and 19 (node 16) is 2.19 Mya [26]. This second migration event to Asia likely occurred via the Levant region (Table 2; Figure 1, node 18), a hypothesis supported by the presence of Acheulean tools and *Homo* fossils at Ubeidiya, Israel [30, 116].

To determine when Acheulean technology originated, we will evaluate which of the alternative hypotheses proposed for the case of Lomekwian technology is most plausible in this context. Those relying on horizontal transmission of culture or behavior (hypotheses 1c and 2b) can be reasonably ruled out due to the significant geographic separation between the species that developed Acheulean tools (e.g., Africa and Asia). In contrast, all other hypotheses remain viable.

The earliest known Acheulean technology, dated to 2 Mya in Ethiopia, predates the divergence between *H. ergaster* and *H. naledi* (node 19). This date closely aligns with the estimated divergence time at node 16 (2.19 Mya), which separates these species from other clades that also used Acheulean tools—those in Asia (beginning at node 18) and Europe (beginning at node 22). While independent invention of this technology in Africa, Asia, and Europe cannot be ruled out (hypotheses 1b and 2a), the close temporal proximity between the earliest Acheulean record and the estimated divergence of the common ancestor of all these lineages makes hypothesis 1a the most parsimonious explanation. That is, a single origin around 2.19 Mya, attributable to an as-yet unidentified African *Homo* species represented by the common ancestor at node 16.

As previously described, substantial but sporadic evidence (Table 2, Figure 1) indicates fire use in Africa (Kenya, ~1.6, 1.55, and 1.49 Mya; Ethiopia, 1.45 Mya; South Africa, 1.05 and 1.0 Mya). Outside Africa, fire use has been dated to 1 Mya in Israel, 0.78 Mya in China (Asia), and 0.98 Mya in Spain (Europe). The widespread geographic distribution of these instances, paralleling that of Acheulean technology, suggests that horizontal technological transfer is unlikely, thus ruling out hypotheses 1c and 2b mentioned earlier. This leaves three remaining possibilities:

1a—Both the neurobiological basis and fire control were present in the common ancestor at node 16;

1b—The neurobiological basis was present in the common ancestor at node 16, but fire control was independently discovered at node 19 in Africa, node 18 in Asia, and node 22 in Europe;

2a—Both the neurobiological basis and fire control were independently acquired and developed in each of those three lineages.

If the scarcity of early evidence for fire use is primarily due to detection challenges (see previous section), then the hypothesis of recent fire control is weakened, and all three scenarios

FIGURE 3 | *Stone tool technologies*. Examples of three key stone tool technologies from the Lower and Middle Paleolithic periods: Lomekwian, Oldowan, and Acheulean (See Box 6).

remain plausible. Among them, hypothesis 2a appears less likely, as it would require multiple independent inventions of fire, each involving both the development of the neurological basis and the mastering of fire in the three lineages.

Between the two remaining hypotheses (1a and 1b), both propose that the neurobiological basis for fire control was already present in the common ancestor at node 16. With the available evidence, it is not possible to determine whether fire control was culturally transmitted from this African ancestor to the Asian and European lineages (hypothesis 1a), or whether all three lineages independently discovered how to control fire (hypothesis 1b). The latter is certainly plausible, as numerous examples exist of complex inventions or ideas being developed independently in different times and places [134–136].

Nevertheless, fire control was firmly established by at least 1.6 Mya (Table 2), and potentially as early as 2.19 Mya (hypothesis 1a). This lends support to Wrangham's original proposal that fire was used frequently for cooking by 1.8 Mya, regardless of whether it was independently discovered in different regions.

The reviewed evidence indicates that hominins controlled and regularly used fire well before 350,000 years ago [137]. This is further supported by evidence of much earlier fire use for cooking fish [93]. Controlled cooking with fire likely played an early role in brain size evolution, alongside the possibility of even earlier, sporadic exploitation of natural hot water sources water [138].

6 | How Fire and Cooking Technologies Were Possible Without a Large Brain?

We support the proposal that cooking played a fundamental role in the evolution of larger human brains [62, 63] and was a key factor in our unique cognitive capabilities. However, evidence indicates that fire and cooking technologies, along with stone tools, were mastered to some extent before the significant increase in brain size (Table 2 and S1; Figure 1). If fire and cooking technologies were indeed crucial for brain expansion, early hominins—despite their smaller brains—must have possessed the necessary intelligence to master them. This emerging and exceptional intelligence may be reflected, for example, in the development of Acheulean technology. The earliest Acheulean tools, associated with *H. ergaster* in Africa, date to approximately 2 Mya (Tables S1 and 2) and coincide with a skull of this species exhibiting a cranial capacity of only 588 cc. This form of intelligence, associated with small brain size, must have been rooted in neurological features absent in other primates and animals. By 1.6 Mya—that is, 400,000 years later—a skull of *H. ergaster* with a cranial capacity of 1067 cc was also found in Africa (Tables S1 and 2), a value within the lower range of modern *H. sapiens* brains [139].

As previously described, incorporating meat into the diet—and more specifically, slicing meat and processing USOs—could have helped conserve energy by reducing the overall masticatory force required to eat. This energy-saving mechanism may have created favorable conditions for the viability of mutations that increased brain size. Notably, the 1.6 Mya date coincides with the earliest evidence of fire use. It is therefore plausible that fire control existed before this evidence, and that both technologies enabled the first significant increases in brain size. As we have previously proposed, fire-handling skills could have been present as early as 2.1 Mya, coinciding with the emergence of the Acheulean tradition.

What brain differences, potentially originating in primates and later evolving in hominins and humans, could account for enhanced cognition independent of brain size? Cerebral complexity, for instance, has been shown to precede brain enlargement in Old World monkeys, as evidenced by the highly gyrified brain and presence of sulcal patterns such as the arcuate sulcus in *Victoriapithecus* [140]. A study examining the central sulcus in humans and great apes identified differences in brain region organization, with significant variations in its shape and structure, particularly in the hand motor area [141]. Although anatomically modern humans (*H. sapiens*) and orangutans (*Pongo spp.*) exhibit notably similar and complex central sulcus morphologies, these resemblances are likely the result of convergent evolutionary processes associated with distinct locomotor adaptations. Importantly, humans uniquely

TABLE 2 | Registered cultural landmarks during early hominin evolution.

Event	Region	Age (My)	Site	Species	Details	References
Tools	Africa					
	Ethiopia	3.39	Dikika	*Au. afarensis*	Evidence of (unknown) stone tools assisted consumption of meat and marrow from ungulates	[81]
	Kenya	3.30	Lomekwi 3, Turkana	*K. platyops*	Lomekwian tools	[97]
	Kenya	3.03	Nyayanga	*Paranthropus*	Oldowan tools	[102]
	Algeria	2.40	Ain Boucherit	*H.?*	Oldowan tools	[117]
	Ethiopia	2.00	Garba	*H. ergaster*	Acheulean tools	[110]
	Kenya	1.70	Sare-Abururu	*H. ergaster*	Oldowan tools	[118]
	Asia					
	Jordan	2.48	Zarqa Valley	*H.?*	Oldowan tools	[106]
	China	2.10	Loess Plateau Shangchen	*H.?*	Oldowan? tools	[29]
	India	1.51	Attirampakkam	*H. erectus*	Acheulean tools	[111]
	Israel	1.50	Ubeidiya	*H. erectus*	Acheulean tools	[116]
	China	0.82	Nalai	*H. erectus*	Acheulean tools	[112, 113]
	Europe					
	Spain	0.98	Cueva Negra	*H. neanderthalensis?*	Acheulean tools	[114]
Fire	Africa					
	Kenya/ Tanzania	1.60	Olduvai and Turkana basins	*H. ergaster*	Siliceous stone tools exposured to intense heat	[119]
	Kenya	1.55	FxJj20, Koobi Fora	*H. ergaster*	Burned material associated with nonburned material	[120]
	Kenya	1.49	Chesowanja	*H. ergaster*	Burnt clay	[121]
	Ethiopia	1.45	Gadeb	*H. ergaster*	Heated artifacts	[122]
	South Africa	1.05	Swartkrans, Member 3	*H. ergaster*	Burnt bones.	[123, 124]
	South Africa	1.00	Wonderwerk Cave	*H. ergaster*	Burnt bones. Plant ashes	[125, 126]
	Asia					
	Israel	1.00	Evron Quarry, open air	*H. erectus*	Burnt fauna and lithics	[92]
	Israel	0.79	Gesher Benot Ya'aqov	*H. erectus*	Burnt wood and seeds (cooked). Flints	[127, 128]
	China	0.78	Zhoukoudian, Locality 1	*H. erectus*	Burned and unburned bones are present in the same layer with stone tools	[129–131]

(Continues)

possess a second ventral motor knob—a morphological feature absent in other primates—highlighting species-specific evolutionary developments in motor cortex organization. This structural adaptation may be linked to the advanced manual dexterity and tool-use capabilities characteristic of humans [141]

Furthermore, comparative analyses of hippocampal organization between humans and macaques reveal significant functional divergences despite conserved macro- and microstructural features. While the overarching hippocampal architecture, including anterior-posterior and subfield-related organizational axes, is preserved across these primates, humans exhibit a marked reconfiguration in functional connectivity. This reorganization reflects an enhanced integration of the hippocampus within heteromodal association networks, particularly the default mode network (DMN)—a large-scale brain network comprising regions such as the medial prefrontal cortex, posterior cingulate cortex, precuneus, and angular gyrus, which is active during internally directed cognitive processes like autobiographical memory, self-referential thought, and envisioning the future. The strengthened coupling between the hippocampus and the DMN in humans underscores substantial evolutionary modifications in neural network embedding and cognitive function [142].

Additional aspects of neuronal complexity are evident in human prefrontal cortex (PFC; see Box 1) neurons. Not only are they larger than those found in macaques and marmosets, but their dendrites also exhibit increased branching [143]. Similarly, human cortical pyramidal neurons (PNs; see Box 1) demonstrate greater total dendritic length, branching, and mean segment length compared to chimpanzees. Other studies have shown that these are not simply scaled-up PNs but have evolved more complex dendritic structures [144]. These authors also identified additional neuronal specializations in humans, including the diversity of glial cells.

At the biochemical level, a comparative analysis revealed significant differences in the expression of neuromodulatory systems between species. Histological and functional analyses, including the study of rare subpallial-derived interneurons (see Box 1) expressing dopamine biosynthesis genes, demonstrated distinct patterns. These genes are enriched in the human striatum and neocortex but absent in the neocortex of African apes [145].

A valid question is whether this enhanced neurobiological basis—referring to the neural mechanisms underlying advanced cognitive functions such as tool use and fire control—necessitated greater energetic demands, considering our proposal that increased brain size required the energetic benefits of fire control and cooking. Notably, the average metabolic cost per neuron remains relatively stable across species, with small variations that are not correlated with neuronal density or brain size [146]. This constancy implies that the total metabolic cost of a brain is a linear function of its total number of neurons, each constrained to a fixed energy budget per neuron, regardless of brain size. While rodent brain structures increase in size by gaining neurons whose average size grows, primate brain structures expand by adding a larger number of neurons whose

TABLE 2 | (Continued)

Event	Region	Age (My)	Site	Species	Details	References
	Europe					
	Spain	0.98	Cueva Negra	*H. neanderthalensis?*	Heat-fractured chert. Calcined bone. Charred and/or calcined micromammal specimens	[132]
Cook	**Asia**					
	Israel	0.78	Gesher Benot Ya'aqov	*H. erectus*	Evidence for the cooking of fish	[93]
Art	**Asia**					
	Indonesia	0.64	Java	*H. erectus*	Shell tools. A shell with a geometric engraving	[133]

Abbreviations: *Au., Australopitheus; H., Homo; K., Kenyanthropus.*

average size remains constant [6, 147, 148]. Therefore, an enhanced neurobiological basis within a smaller primate brain would not necessarily have resulted in higher energetic costs. However, if such costs did arise, they could have been mitigated by dietary innovations that preceded the control of fire and cooking. As previously described, incorporating sliced meat and processed USOs into the diet would have increased foraging efficiency and caloric availability. These practices could have enabled small-brained hominins to achieve the cognitive capabilities necessary for mastering fire and cooking without facing significant energetic constraints.

Observational studies of savanna-dwelling chimpanzees suggest that early hominins may have had preadaptations for interacting with fire—what has been termed “our pyrophilic beginnings” [149]. At Fongoli, Senegal, chimpanzees have been observed remaining calm in the presence of wildfires and foraging for roasted seeds in recently burned areas [150]. Further research indicates that these chimpanzees can anticipate the movement of fires and adjust their behavior accordingly, demonstrating a level of understanding of fire dynamics [151]. Herzog et al. [149] observed that chimpanzees at Fongoli frequently engage with fire-altered landscapes during the dry season. In these environments, they often encounter food resources more readily and adjust their foraging behavior accordingly. This pattern implies that fire-modified habitats may offer enhanced foraging opportunities, providing insights into how early hominins could have similarly exploited such environments. Furthermore, experiments indicate that chimpanzees possess basic cooking-related abilities. Nine studies on chimpanzees [152] demonstrated several relevant cognitive capacities, including preferences for cooked over raw food, an understanding of food transformation, a willingness to invest effort in obtaining cooked food, self-control, planning abilities, and the capacity to save food for future cooking. These behaviors provide a framework for understanding how early hominins might have initially interacted with fire, setting the stage for the eventual development of controlled fire use.

In addition, recent research has documented naturally occurring pyrocognitive behavior in wild bonnet macaques (*Macaca radiata*) inhabiting a temple site in India [153]. Researchers recorded numerous instances of macaques attempting to extinguish fires in offering lamps containing food rewards such as sesame seeds, rice flour, or coconut. The study found significant age-related variation: adult macaques achieved higher foraging success rates compared to subadults. Moreover, among adults, there was a positive correlation between the number of lamp manipulations and foraging success, indicating that adults may develop an understanding of the causal relationship between extinguishing the fire and obtaining the food reward. These findings imply that pyrocognitive abilities in bonnet macaques emerge gradually with age, are consistent across sexes, and offer valuable insights into the evolutionary development of fire-related cognition in primates.

The observed behaviors in chimpanzees and bonnet macaques—such as calmness around fire, exploitation of fire-altered environments, and preference for cooked food—indicate that certain cognitive traits related to fire interaction may have been present in our shared primate lineage. Although chimpanzees lack the ability to control fire, their capacity to exploit natural fires and their understanding of food transformation point to a potential evolutionary pathway for the emergence of cooking in early hominins. Considering these behaviors in our closest living relatives, chimpanzees—specifically their calm behavior around fire and preference for cooked food—indicates that a predisposition relevant to the development of cooking was present in our shared primate lineage around 7–7.5 Mya [26, 94], a trait not observed in other animals. Furthermore, the observation of pyrocognitive behaviors in bonnet macaques, as documented by Victor et al. [153], indicates that such fire-related cognitive traits may have an even more ancient origin within the primate lineage. Given that the divergence between the lineages leading to macaques and those leading to humans and chimpanzees occurred approximately 23 Mya [154], it is plausible that the foundational cognitive abilities related to fire interaction were present in a common ancestor predating this split. This implies that the evolutionary roots of pyrocognition extend deeper into primate history than previously recognized, highlighting a more ancient and widespread emergence of fire-related cognitive traits among primates.

7 | Genetics of Brain Size Increase and Complexity

Recent findings indicate that, in catarrhine primates, brain size and gyrification (cerebral cortex folding) are regulated by distinct genes. This suggests that brain size increase and cerebral complexity might evolve independently [155]. Primate brain evolution exhibits a positive correlation between brain volume and gyrification. However, humans and baboons diverge from this pattern, indicating a complex interplay between these traits. While increased brain size often correlates with greater gyrification, selective pressures may have independently influenced these traits in different primate lineages. A similar conclusion was reached in a study of the extinct genus *Victoriapithecus*, which displayed a modern cercopithecoid sulcal pattern but strepsirrhine-like ECV and olfactory bulb size. This challenges the idea that increased brain size drives cerebral complexity in anthropoids and suggests independent evolution of brain complexity, size, and changes in visual and olfactory systems under different selective pressures [140].

The gradual evolution of the hominin brain toward larger sizes and more complex substructures has been driven largely by mutations in regulatory genes, as most genetic differences between humans and other great apes are found in non-protein-coding regions of the genome, with only a small portion of these variations affecting amino acid sequences within proteins [156]. Recent findings [157] demonstrate that brain evolution, particularly cortical evolution, is primarily influenced by changes in noncoding DNA and RNA, such as promoters, enhancers, and other regulatory elements (see Box 3).

Genetic changes in human evolution have resulted in a developmental pattern characterized by neoteny, evident in prolonged timelines across nearly all stages of brain maturation, particularly in progenitor cell proliferation and neuronal growth [158]. While “neoteny” commonly describes the retention of juvenile traits in adult humans relative to other apes, its broader application to developmental delays introduces conceptual ambiguity. For instance, nonhuman primates exhibit longer developmental periods than rodents or lagomorphs, yet they do not retain juvenile features into adulthood. In contrast, humans show delays spanning both embryonic and postnatal stages, extending beyond the simple persistence of preadult characteristics. To clarify these distinct processes, "bradychrony" has been introduced to denote the uniquely slowed developmental tempo observed in humans compared to other primates [159]. Whereas neoteny emphasizes morphological outcomes, bradychrony focuses on the underlying temporal dynamics, offering a more precise framework for understanding the evolutionary extension of human ontogeny.

For instance, a study assessing the morphological features of 5- to 10-day-old cerebral organoids (see Box 1; Figure 4) found that 10-day-old human organoids were larger compared to those of gorillas and chimpanzees [160]. In vivo, neuroepithelial cells (NECs; see Box 1) in the developing neocortex proliferate exponentially before transitioning to a neurogenic radial glial cell (RGC) phenotype (see Box 1). This transition is delayed in human cerebral organoids compared to chimpanzee and gorilla organoids, resulting in significantly more neuronal precursors and larger organoid volumes. The authors identified a previously unreported morphological state of NECs, which they termed transitioning NECs (tNECs). This morphological change occurred earlier in ape-derived organoids than in human-derived ones. They found that the cell morphogenesis factor ZEB2 promotes this neuroepithelial transition, with species-specific differences in ZEB2 expression accounting for the observed differences in organoid development. Overexpression of ZEB2 in human organoids induced a premature transition, replicating nonhuman ape architecture, while its suppression delayed the transition, emphasizing the critical role of the NEC–RGC shift in human brain expansion [160].

DNA methylation, a key epigenetic modification (see Box 3), plays a crucial role in establishing and maintaining cellular identity, including in the human cortex [161]. Comparative studies of DNA methylation patterns across primate species have revealed distinct differences between humans and other primates, particularly in the types of cytosine bases modified. While CG methylation (where C is followed by G) is reduced in humans compared to other primates (a phenomenon known as hypomethylation), a corresponding increase is observed in the methylation of cytosines followed by other nucleotides (CH methylation), referred to as hypermethylation. These methylation patterns vary across different cell types, with neurons exhibiting distinct profiles compared to oligodendrocytes (see Box 1), suggesting a complex interplay between cell identity and epigenetic regulation in shaping the human brain.

Other regulatory elements influencing brain development include Human Accelerated Regions (HARs; see Box 3) [162, 163]. These genomic sequences exhibit rapid evolutionary changes in humans compared to other primates. Acting as regulatory elements, HARs are linked to genes involved in brain development, indicating their crucial role in shaping human cognitive abilities.

MicroRNAs (see Box 3), another class of regulatory molecules, play a significant role in brain development by influencing gene expression at the posttranscriptional level [164]. Studies have shown that specific microRNAs are differentially expressed in the human brain, with some directly impacting neuronal proliferation, differentiation, and the expansion of neural progenitor pools—processes fundamental to primate brain evolution [164].

The distinct regulation of neuritogenesis (the growth of neurites) and synaptogenesis (the formation of synapses) in humans—processes crucial for circuit formation and connectivity—plays a key role in the advanced functionalities of our brain, as largely elucidated through research using humanized mouse models [165]. These models have been instrumental in identifying critical genetic adaptations and regulatory mechanisms that shape the unique characteristics of human neural circuits.

Genes such as FOXP2 (see Box 3), which has undergone human-specific evolutionary adaptations, play pivotal roles in the development of speech and vocalization by modulating dendritic length and synaptic plasticity [166, 167]. The human-specific gene SRGAP2C (see Box 3), when expressed in embryonic mice, prolongs neuronal maturation and increases

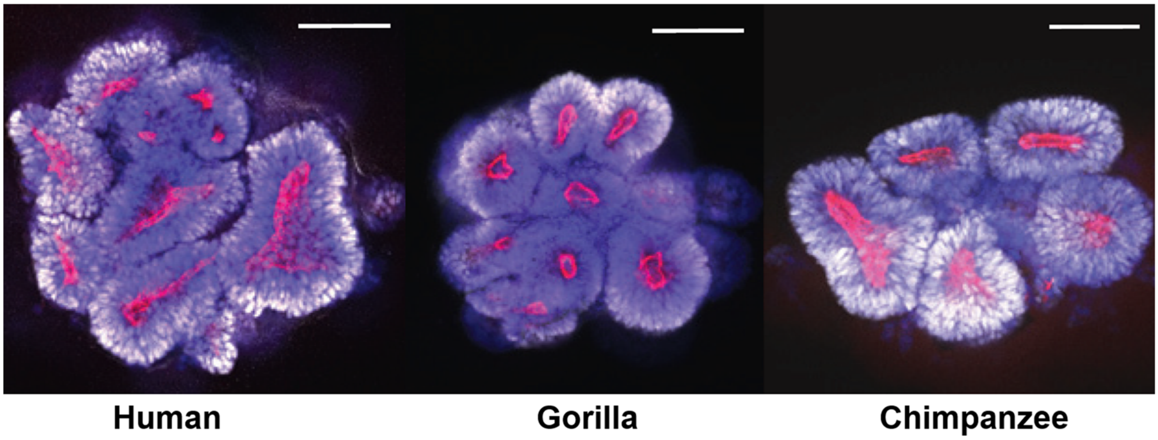

FIGURE 4 | *Primate brain organoids.* Immunofluorescence images of the center of human, gorilla, and chimpanzee organoids (See Box 1). Scale bar 100 µm. Reprinted with permission from Benito-Kwiecinski et al. [160] Figure 1E.

synaptic density and connectivity in pyramidal neurons [168]. Furthermore, osteocrin, a protein originally adapted for skeletal function, has been evolutionarily repurposed in primates to modulate dendritic growth in the brain. Its interaction with the transcription factor MEF2 (see Box 3) has facilitated the expansion of neural networks, contributing to the distinctive features of primate cognition [169].

Another important example is the interaction between cis- and transregulatory genes (see Box 3) in the prefrontal cortex (PFC) structure [170, 171]. In humans, PFC neurons form more synaptic connections than neurons in other cortical areas, a process influenced by retinoic acid signaling. Genes regulated by retinoic acid in the neocortex have been identified in mice, macaques, and humans. Retinoic acid is expressed in a gradient, with highest levels in the PFC—where humans exhibit the highest levels compared to mice and macaques—and decreasing levels toward posterior regions. Interestingly, genetically engineered mice lacking the enzyme that degrades retinoic acid develop more projections between the medial thalamus and the PFC. Shibata and colleagues [170, 171] also studied the CBLN2 gene, which encodes the synapse-organizing protein cerebellin 2 and is highly expressed in the PFC, finding that a greater variety of neuronal types express this gene in humans compared to macaques and mice. They observed that CBLN2 expression is upregulated by retinoic acid signaling and identified an enhancer near the gene that is active during early PFC development and contains several binding sites for retinoic acid receptors, thus increasing CBLN2 expression in response to retinoic acid.

There are numerous examples of genetic variations influencing human brain evolution beyond those described here [156, 158, 159, 165]. As noted in the previous section, genes involved in dopamine biosynthesis are enriched in the human striatum and neocortex but are absent in nonhuman African apes [145]. Furthermore, multivariate analysis has identified genes strongly correlated with brain [172], and the heritability of complex interindividual traits, such as brain activity and structure, appears to be governed by numerous small-effect loci, each accounting for 0.1%–1% of the phenotypic variance [165].

Therefore, mutations such as those described that contributed to larger brains during evolution may have been selectively influenced by the energy resources required and available for these changes. These mutations, which might have otherwise been deleterious, were favored in populations with the ability to cook, wherever they emerged.

8 | Population Genetics of Brain Size Increase and Intelligence

Under the described conditions, the increase in brain size underwent selection but not necessarily selection pressure. Mutations promoting brain size increases could have arisen randomly at any time and place. Given the availability of more efficient energy extraction from foods such as meat and underground storage organs—first through mechanical processing with stone tools (cutting, pounding, etc.), and later greatly enhanced by cooking—mutations favoring increased brain size could have persisted despite their higher energetic demands. These mutations could still have been lost or fixed by genetic drift (see Box 3) if neutral, or rapidly fixed if they conferred advantages under specific social or ecological conditions. However, if the genetic changes underlying brain size (and complexity) were controlled by several small-effect loci, as discussed in the previous section [165], the changes were likely very subtle, and any selective advantage (whether social or ecological) was not immediate. This suggests that these mutations may have behaved as neutral or nearly neutral, and their fate was largely shaped by genetic drift [173].

This perspective is further supported by recent findings showing that less-constrained, neutrally evolving traits were the most prevalent pattern observed across the studied brain regions [172]. Fixation of such mutations may have been facilitated in small populations, from which they spread to neighboring groups. Consistent with this, an analysis of two ancient human DNA datasets revealed that gene flow (see Box 3) and genetic drift, rather than natural selection, have been the primary drivers of recent changes in genome-wide allele frequencies [174].

Additional support for this hypothesis comes from a proposed population structure for early humans [175], suggesting that they originated and diversified within strongly subdivided populations across Africa, connected by sporadic gene flow. This model aligns with the extraordinary morphological diversity and broad geographical distribution evident in early human fossils, as well as recent archaeological and genetic evidence [175].

Recent research suggests that brain evolution may have been modular, with different regions evolving independently [100], challenging the notion of a tightly controlled, conserved developmental program driving neuroanatomical changes in response to selection. For instance, it has been proposed that the evolution of anterior and posterior cortical association areas occurred simultaneously or in tandem rather than sequentially [176]. This perspective further supports the idea of parallel evolution of nonaptations facilitated by rapid hybridization, aligning with the proposed mosaic model of brain evolution [177].

The feasibility of the proposed hybridization is a key question. Archaeological remains, even with DNA sequencing, cannot definitively determine the presence or absence of reproductive barriers, a central tenet of Ernst Mayr's Biological Species Concept [178]. Morphological differences do not necessarily imply reproductive isolation. On the other hand, populations with the same morphology and even identical DNA sequences can still be reproductively isolated, for instance, through chromosomal speciation [179]. However, while gene flow between our species and Neanderthals is well-documented [180, 181], this precedent suggests that gene flow was likely also present in earlier hominin evolution. As Pääbo noted [182], "Analyses of the genomes of our closest evolutionary relatives suggest that our ancestors were part of a network of now-extinct populations connected by limited but intermittent, or sometimes even persistent, gene flow."

The reviewed information suggests a scenario in which brain size increased through patchwork evolution, occurring in random steps across diverse geographical locations. Brain size increases may have resulted from sporadic mutations that were either neutral or later co-opted to enhance cognition—a selectively advantageous trait. Furthermore, different mutations of this kind might have occurred concurrently in different locations and later merged into the same genome through gene flow (hybridization), which may have synergized and contributed to an accelerated trajectory of brain evolution.

9 | Brain Size Increase When, Where, and Why

Genetic variability is crucial for brain evolution, including increases in brain size, as it provides the basis for selection. A key question is not just when genetic variants associated with increased brain size first appeared—which could have occurred at any point in hominin evolution—but when they became viable from an energetic standpoint. Specifically, when did such mutations stop being negatively selected due to the high energetic demands of a larger brain? As previously discussed, this likely required cultural innovations that improved dietary energy extraction, such as the use of stone tools or the control of fire. Another question is whether brain enlargement in different hominin lineages—regardless of proposed interbreeding—shared a common genetic basis or arose independently.

Brain sizes exceeding an estimated cranial volume (ECV) of 400 cc appeared in certain species of *Australopithecus* (*A. afarensis* and *A. garhi*) and in the genus *Kenyanthropus*. All of these hominins are associated with Lomekwian tool technology, and *A. afarensis* has also been linked to stone tool-assisted consumption of meat and marrow from ungulates (Table 2; Figure 1). We previously proposed, as alternative hypotheses, that Lomekwian technology may have been present in their common ancestor (node 5, Figure 1) and subsequently inherited, culturally transmitted between species, or even invented independently. In any of these cases, basic tool use—even before fire control—could have enhanced energetic efficiency through practices such as slicing meat and processing USOs and grains. Such behaviors might have supported increases in brain size beyond 400 cc, reaching an estimated ECV of ~545 cc, as observed in *A. afarensis* and the more derived *P. boisei*. Node 5 in Figure 1 proposes an ancestral brain size of 370 cc (the observed state in the sister group *Au. anamensis*) and the possible emergence of genetic variability conducive to brain expansion. Whether such genetic variability existed in earlier nodes (2, 3, and 4) remains uncertain. If it did, it may not have been retained due to insufficient energetic resources to sustain larger brains—unlike in later nodes, where tool use may have provided such support—or because the relevant genetic mutations had not yet emerged in those lineages.

According to our previous proposal, the Oldowan tool technology was present by 4.3 Mya (node 8, Figure 1). This innovation had no effect on brain size except in the *Homo* lineage (node 12, Figure 1), where brain sizes (Table S1, Figure 1) exceeded 545 cc. For example, *H. habilis* had an ECV of 582 cc, *H. rudolfensis* 752 cc, and *H. georgicus* 780 cc. In other words, although the technology for more efficient energy extraction existed, we suggest the genetic variability for further brain size increase appeared only in *Homo* between nodes 10 and 12 (Figure 1). The ancestral brain volume at node 10 may correspond to *Au. sediba* (ECV 420 cc), while brain volume of node 12 could be similar to that of *H. habilis* (ECV 582 cc), as seen early in the lineage at node 16 (Drimolen skull, ECV 588 cc; Table S1). Given this similarity, node 12's proposed ancestral state could extend to nodes 14-19, implying independent brain size increase trends from these nodes.

From node 16, dated to 2.3 Mya (Figure 1), three clades derive: a purely African clade (node 19); an Asian clade (node 18), originating from a second migration through the Levant; and a clade including our species (node 21), which originated in Africa and underwent several subsequent migrations to Europe, Asia, and the rest of the world.

The first clade, exclusively African, originates at node 19 (Figure 1) and represents the common ancestor of *H. ergaster* and *H. naledi*. Within this lineage, as previously described, a *H. ergaster* skull with an estimated adult cranial capacity of 588 cc, dated to 2.04 Mya, was discovered at Drimolen, South Africa. Additionally, at Rising Star Cave (also in South Africa), a *H. naledi* specimen with an ECV of 610 cc was found, dated to 0.335 Mya (Table S1, Figure 1). Notably, the Drimolen skull predates the estimated divergence time between *H. ergaster* and *H. naledi*, which has been placed at 1.9 Mya (node 19, Figure 1) [26]. This suggests that the brain size of *H. naledi* may not represent a drastic reduction in volume, but rather a condition close to the ancestral state of node 19. Conversely, *H. ergaster* skulls with ECVs near or exceeding 1000 cc have been discovered (Table S1; Figure 1), marking a significant advancement toward larger brains. An alternative proposal regarding the relationship between *H. naledi* and other hominins, based on relative tooth size and Bayesian inference, suggests that this species is the sister group to *H. habilis* [183]. If this is the case, the ancestral node between *H. habilis* and *H. naledi* would be node 12, for which we proposed an ECV of 582 cc. Therefore, in both alternative phylogenetic tree topologies, the brain size of *H. naledi* closely approximates that of its ancestral node and would not represent a reduction in volume.

In the Asian clade at node 20 (Figure 1), originating from a second migration through the Levant (node 18), the earliest skull is the *H. erectus* “Mojokerto Child” (Indonesia, Southeast Asia), with an ECV of 630 cc and dated to 1.49 Mya (Table S1, Figure 1). The estimated adult cranial capacity for this skull ranges between 840 and 1245 cc [184]. In Southeast Asia, the *H. erectus* lineage shows a clear trend of increasing brain size, with ECVs of 1059 cc (1.3 Mya) and 1251 cc (0.117 Mya) (Table S1, Figure 1). An *H. erectus* skull (ECV 1225 cc, 0.780 Mya) found at Zhoukoudian (China) confirms this trend in East Asia (Table S1, Figure 1).

However, in the Southeast Asian insular region, this trend appears to reverse. The skull of LB1, belonging to *H. floresiensis*, a diminutive hominin species approximately 1 meter tall [185], was discovered in Liang Bua (Island of Flores), Indonesia. This species, known from the Late Pleistocene and surviving until relatively recently (0.05 Mya), has an ECV of 426 cc (Table S1, Figure 1, node 21). This is not the only example of insular body size reduction. Another small-bodied *Homo*, *H. luzonensis*, was discovered in Luzon (Philippines) and also dates to the Late Pleistocene [186]. While some have suggested evolutionary links between *H. floresiensis* and more ancestral hominins, such as *H. habilis* [187], more recent research indicates it most likely evolved from early Asian *H. erectus* [188], as shown in Figure 1. The estimated divergence time between *H. ergaster* and *H. floresiensis* is 1.73 Mya [26], consistent with the early presence of hominins on Flores around 1 Mya [189].

While the reasons for this brain size reduction are debated, it has been suggested that scaling accounts for no more than 50% of the reduction, with the observation that insular mammals often exhibit reduced relative brain size due to energetic constraints. Such reductions are typically accompanied by compromises in neural functions related to sensory, motor, social, and/or intellectual activities. In insular environments with limited food resources and the absence of predators, selective pressures often favor minimizing brain size [190]. Despite this, *H. floresiensis* demonstrates no apparent regression in technological complexity, particularly in stone tool production, when compared with earlier hominins either on Flores or elsewhere in island Southeast Asia [191, 192].

The smallest skull from African node 22 is *H. antecessor* from Sierra de Atapuerca, Spain (the third migration; Figure 1), with a cranial capacity exceeding 1000 cc (0.9 Mya) (Table S1). The lineages derived from African node 23 have the largest brains, with the genetic variability for these sizes likely emerging in Africa between nodes 22 and 23 (Figure 1). The lineages originating at node 22 first migrated to Europe (migration event 4, Figure 1) and subsequently to Asia, giving rise to large-brained species, including *H. neanderthalensis* (estimated cranial volume [ECV] of 1360 cc) and specimens exhibiting some of the largest known brain volumes (ECV ranging from 1700 to 1800 cc). These specimens have recently been assigned to *H. juluensis* [193]. However, this taxonomic assignment remains provisional and controversial, as some researchers argue that the morphological similarities among these fossils may not warrant designation as a distinct species without supporting genetic data [194].

Finally, our species, also originating from node 23 (Table S1; Figure 1), has a current average ECV of 1341 cc [195]. Evidence of larger brains exists within this lineage both in Africa (Morocco), where an ECV of 1375 cc is dated to 0.315 Mya (Table S1), and in Europe (France), where the Cro-Magnon 3 skull, dated to 0.031 Mya, has an ECV of 1813 cc [196]. Our species evolved from an early African Middle Pleistocene (Chibanian) species that undertook the fifth and final out-of-Africa migration around 0.21 Mya [197], ultimately populating the globe and becoming the only extant *Homo* species. This African Chibanian species has recently been proposed to be named *H. bodoensis* [31]. However, this proposal has sparked considerable debate regarding its validity, with both critical [198, 199] and supportive [200, 201] responses.

According to the reticulated model of evolution for our species [202], the successful genetic composition and arrangement present in modern humans was likely achieved around 0.35 Mya. We propose that new genetic variants emerged earlier in Africa, sometime between nodes 22 and 23 (Figure 1), enabling higher brain volumes than those observed in populations derived from node 18 in Asia. In other words, an additional degree of novel genetic variability was necessary for the final phase of brain evolution, beyond the subsequent hybridization with *H. neanderthalensis* in Europe. Even today, the highest genetic variability in humans is found in Africa [203, 204].

10 | Reduction in Brain Size in *H. Sapiens*: Timing, Magnitude, and Hypotheses

Multiple studies have documented a significant reduction in brain size in *H. sapiens* over the past several tens of thousands of years. Fossil and archaeological evidence suggest that this reduction began either in the Late Pleistocene ~35 ka (thousand years ago) or more markedly during the Holocene (~10–3 ka), with some analyses indicating a continuous decrease in endocranial volume since the origin of the species (~300 ka). One interpretation of the available data emphasizes that the linear fit of the full data set suggests this reduction is not confined to the last 3–5 ka, but has been ongoing since at least the Late Pleistocene, and possibly since the earliest known fossils of the species. Estimates vary, but average reductions range from approximately 5% to 17%, or 100–150 cc in cranial capacity, depending on the population and region examined [195, 205–208].

Morphologically, this reduction has been accompanied by nonallometric changes in brain organization. Balzeau et al. [209] observed a relative decrease in the anteroposterior length and surface of the frontal and occipital lobes, while parietal lobes elongated, and parietotemporal areas remained stable, suggesting structural reorganization rather than uniform shrinkage. These findings highlight the plasticity of the *H. sapiens* brain, and the difficulty in directly linking brain size reduction to cognitive capacity, which appears to have remained stable.

11 | Discussion and Conclusions

In this study, we have examined various aspects of human brain evolution. Most significant among these are the challenging energetic demands of larger brains, which have prompted several explanatory hypotheses. These include the Social Brain, Ecological, Expensive-Tissue, and Cooking hypotheses. The first two propose that their respective underlying factors (social complexity or environmental challenges) drove brain enlargement.

We highlight that brain enlargement was not a necessary adaptation to the demands of social complexity. This remains true even if social complexity evolved as an adaptation to predator-risky habitats, where the challenges of increased social complexity were balanced by a positive population net effect on fitness (see Box 3). If this equilibrium was not maintained—if the drawbacks of social complexity outweighed reproductive success—then proposing brain enlargement as a solution becomes problematic, as it would be inherently disadvantageous.

One negative trait cannot compensate for another. The ecological explanation also faces a challenge: if the same ecological pressures influenced humans, their ancestors, and other animals (including primates), then those species should have similarly evolved larger brains, given the advantages observed in humans.

The Expensive-Tissue and Cooking hypotheses share the common feature that neither is proposed as the primary driver of brain expansion. The former can be understood as a mitigating factor for the adverse effects imposed by larger brains on individuals. However, since it is also inherently disadvantageous, it faces the same logical challenge as the Social Brain hypothesis: one deleterious trait cannot be offset by another detrimental characteristic.

For us, fire control and cooking are not considered driving forces behind brain enlargement but rather prerequisites for the persistence of this nonadaptive trait (“nonaptation”). Under this hypothesis, the previously detrimental energetic demands cease to be disadvantageous, as cooking compensates for them. Furthermore, this perspective suggests that the adoption of cooking technology preceded the evolutionary trend toward larger brains, or at least the emergence of the largest brain sizes. Consequently, early hominins uniquely manipulated their natural environments, distinguishing them from other primates and paving the way for continued modifications in brain size favoring enhanced cognition.

The core assertions of the Cooking Hypothesis primarily rely on indirect evidence, particularly anatomical traits observed in *H. ergaster*, traceable to at least 1.8 Mya. Under this hypothesis, the most plausible explanation for these traits is that this species, or its precursor, possessed knowledge of cooking with fire. In line with this proposal, we suggest that this precursor may have existed around 2.3 Mya, coinciding with the emergence of Acheulean tools and, as a secondary effect, fire control. This estimate is significantly earlier than the 0.35 Mya date proposed by other authors and supports the Cooking Hypothesis as a basis for brain size increase. However, before fire control, brain size expansion beyond 400 cc was likely enabled by the earliest stone tool technologies (Lomekwian and Oldowan), which facilitated energy extraction by slicing meat or processing USOs and grains. These tools provided the energy necessary to sustain brain sizes such as those seen in *H. rudolfensis* (ECV 752 cc) and *H. georgicus* (ECV 780 cc), but not beyond. The emergence of Acheulean technology likely did not significantly enhance energy extraction from food, as its processing methods resembled those of Lomekwian and Oldowan tools, with the true advancement occurring only with fire control and cooking.

The primary counterargument to the Cooking Hypothesis—the lack of direct evidence for frequent fire use around 1.8 Mya—lacks both scientific and epistemological foundation. Moreover, direct evidence of fire use has been identified from 1.5 to 1.6 Mya, and the use of fire for cooking fish dates back to 780,000 years ago. Additionally, indirect analyses, independent of visible heat exposure, have detected evidence of fire control between 1.0 and 0.8 Mya. If these analytical techniques are applied to reassess other Lower Paleolithic sites that lack observable signs of pyrotechnology, as proposed, it is plausible that evidence of fire use could be traced even further back in time.

If brain size increase was an indirect consequence of cooking and fire control, the cognitive abilities required for these tasks must have already been present in small-brained hominins, such as australopithecines. Evidence indicates that enhanced cognition is not solely dependent on brain size; other factors, including neuron size and density, dendritic complexity, and noncoding regulatory DNA and RNA, also played critical roles. Many of these traits likely emerged before the development of larger brains, as seen, for instance, in great apes. The substantial brain size increase observed in *H. sapiens* further optimized the cognitive potential of brains that were already highly complex.

The phylogenetic tree in Figure 1 illustrates a general trend of increasing brain size since the emergence of Lomekwian technology, with two notable exceptions: *H. naledi* in Africa and *H. floresiensis* in Southeast Asia.

H. naledi achieved an ECV of only 610 cc, whereas its sister lineage, *H. ergaster*, reached cranial volumes exceeding 1000 cc. According to our analysis, their common ancestor had a minimum ECV of 582 cc. In other words, *H. naledi* exhibited minimal brain growth compared to *H. ergaster*, which underwent significant cranial expansion within a shorter timeframe and went extinct 0.6 Mya before *H. naledi*. As proposed in this and other studies, the emergence of genetic variants associated with brain growth in different populations, followed by hybridization, likely facilitated the expansion and fixation of these traits in contexts involving fire control and cooking. This process would have accelerated changes in brain size. The Dinaledi Chamber, where *H. naledi* fossils were discovered, appears to contain remains from a single population, with a level of variation comparable to or smaller than that observed within localized modern human groups. This suggests that *H. naledi* may have been isolated from other populations, preventing participation in hybridization processes that could have introduced new genetic factors related to brain size growth. Based on the estimated age of the last common ancestor between *H. naledi* and other hominins, this lineage maintained little variation in brain size for at least 1.5 Mya. Estimates average 1.9 Mya, with a range of 1.58 to 2.35 Mya [26], or possibly more than 2.5 Mya [183]. This suggests that reproductive isolation from other populations may have been complete from the outset, precluding the possibility of fertile hybrids.

The case of *H. floresiensis* from the island of Flores represents an evolutionary trajectory characterized by a reduction in brain size, contrary to the trend observed in other hominins. Part of this reduction can be attributed to the smaller body size of the species, but this factor accounts for no more than 50% of the decrease [190], indicating a genuine decline in encephalization (see Box 1). Fossil evidence suggests that the small body size of these insular hominins was an adaptive success in their environment, a trait that persisted until the arrival of modern humans and their subsequent extinction [188]. This process may have begun with the arrival of hominins on the island of Flores around 1 Mya [189]. During this time, *H. floresiensis* likely became reproductively isolated from *H. sapiens*, a factor that may have contributed to its extinction following the arrival of our species [188]. Although no DNA data for *H. floresiensis* are available, indirect analyses of human genomes suggest that interbreeding between this species and modern humans did not occur. However, this possibility cannot be entirely excluded, as such encounters may have failed to produce viable offspring or hybrids that persisted [210].

A possible explanation is that, in the cases of *H. naledi* and *H. floresiensis*, with their small and isolated populations, the fixation of significant chromosomal changes became more likely. This may have led to some form of chromosomal speciation that accounted for their reproductive isolation [179], even if they were genetically compatible with surrounding or newly arrived *Homo* populations.

We acknowledge that even if cooking knowledge was a necessary condition for the development of large brains, it was not sufficient to achieve the level of cognitive complexity observed in *H. sapiens*, such as symbolic behavior, syntactic language, and cumulative technological innovation. Beyond cooking, the social and ecological challenges present in Africa were also encountered in Asia by *H. erectus* for hundreds of thousands of years. Nevertheless, this species did not develop complex technologies. Even with brain sizes comparable to modern humans, neither *H. neanderthalensis* nor other hominins in Europe or Asia exhibited the full range of traits associated with that cognitive complexity, as defined above. The notably high genetic variability found exclusively in Africa may have played a pivotal role, especially in the final phase, in driving brain changes on this continent. These changes might have occurred in parallel, with mutants arising in different populations, eventually interbreeding, synergizing, and accelerating the pace of brain evolution. This perspective aligns with a mosaic model of brain evolution and the notion of a syngameonic semispecies structure. In this context, social and ecological drivers shaped the size and structure of human brains, but only within the energetic framework provided by cooking knowledge and the unique genetic variability present in Africa.

Finally, the recent reduction in brain size in *H. sapiens*, beginning as early as the Late Pleistocene and continuing through the Holocene, represents a notable deviation from the long-term trend of encephalization in hominin evolution. This decrease, estimated at up to 17% in cranial volume, is accompanied by evidence of structural reorganization rather than simple shrinkage, underscoring the brain's plasticity. These changes highlight the complexity of interpreting brain size in isolation and suggest that cognitive capacity may have been maintained despite, or perhaps because of, these morphological shifts.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.
TABLE S1: Endocranial volumes across species and geographical regions in hominid evolution.