

Our ancestors' cognitive and behavioral abilities and the underlying brain morphology and function are critical for understanding the evolution of modern humans. Multiple lines of evidence from paleoanthropology, archeology, and genetics are informative about the evolution of brain and behavior in the *Homo sapiens* lineage, but there is no consensus about the tempo and mode of these biological and behavioral changes. In the absence of fossilized brains, we can study internal casts of the bony braincase. These endocasts approximate outer brain morphology because the brain, meninges, and cranial bones interact in an integrated and highly coordinated way during early development. Present-day modern humans have globular brains and globular endocasts with steep frontal, bulging parietal, and enlarged, rounded cerebellar areas. Together with small and retracted faces, this globularity characterizes the modern human skull. In contrast, Neandertals and other archaic *Homo* individuals have anterior-posteriorly elongated endocasts.

Ontogenetic data show that the adult endocranial shape differences between *H. sapiens* and Neandertals develop prenatally or during a perinatal globularization phase found only in the former group. Developmental globularization therefore occurs in a period of high brain growth rates and is largely driven by the brain. A large body of literature including clinical evidence shows that the tempo and mode of brain growth during this period are related to neural wiring underlying brain function and behavioral capabilities. Developmental globularization leading to more globular brains in modern humans and differences in early brain growth rates leading to slightly larger adult brains in Neandertals are consequently interesting in the discussion of brain evolution and related behavioral changes. Endocranial shape changes during later ontogeny (that is, after the eruption of the deciduous dentition) are similar among present-day humans, Neandertals, and great apes with only some adjustments in the amount of shape changes. This shared segment of the ontogenetic pattern is thought to reflect interactions between the brain and the face, because the latter continues to grow after adult brain size has been achieved.

Hominin fossils from Jebel Irhoud (Morocco) that are associated with Middle Stone Age artifacts dated to around 300,000 years ago display key features of modern human craniodental morphology including facial, mandibular, and dental characters comparable to later *H. sapiens* fossils or even present-day humans as well as modern timing of dental development that suggests a human-like paced life history. Given these craniodental similarities, the Jebel Irhoud fossils are either interpreted as the currently earliest known members of the *H. sapiens* lineage or as part of an ancestral population related to the origin of *H. sapiens*. However, the braincases of the Jebel Irhoud fossils are not globular. This demonstrates some independence of facial and neurocranial evolution in spite of important integration between these cranial modules via the cranial base. Together with other African fossils such as Omo Kibish [dated to around 195,000 years ago, the Jebel Irhoud specimens force us to rethink the evolution of our species. Here, we therefore (i) investigate when and how the endocranial globularity typical of present-day modern humans emerged, (ii) analyze how this process is related to evolutionary brain size increase, and (iii) explore potential links between the evolution of the brain and genetic as well as behavioral changes.

Contrasting interpretations of the archeological record either see a rapid emergence of behavioral modernity at the transition to the Upper Paleolithic in Europe and the Later Stone Age in Africa possibly related to a mutation and consequently to neural changes ("human revolution" model), or a gradual emergence as documented by the African Middle Stone Age without a specific biological correlate triggered by factors such as environmental changes or demographic developments. Features used to mark behavioral modernity range from worked bone, ornaments, pigments, and complex multicomponent lithic technologies to material indicators of manipulations of symbols and

abstract thought such as unequivocal art. Some of those features are not exclusively known from modern human sites, and others are documented systematically only since the Upper Paleolithic.

Ancient DNA of archaic *Homo* representatives and *H. sapiens* fossils revealed derived genetic features that were fixed in *H. sapiens* after the population split from the clade including Neandertals and Denisovans more than 500,000 years ago. These genetic data suggest positive selection within our lineage on genes important for brain function and behavior and, especially, the development of the nervous system [for example, genes involved in axonal and dendritic growth or synaptic transmission including *NOVA1*, *SLITRK1*, *KATNA1*, *LUZP1*, *ARHGAP32*, *ADSL*, *HTR2B*, and *CNTNAP2* ]. Another example is *FOXP2*, a gene that is important for normal development of speech and language. Although amino acid substitutions specific to modern humans were also found in Neandertals, one substitution in an intron of this gene that affects a binding site for a transcription factor and likely alters the regulation of *FOXP2* expression and associated behaviors is absent or polymorphic in Neandertals . On the other hand, a recent analysis showed that Neandertal genetic material that introgressed in the modern human lineage affects cranial and brain morphology of present-day humans.

Here, we analyzed endocasts of *H. sapiens* fossils from different geologic time periods. Previous quantitative analyses used smaller samples and were based on the endocranial midsagittal plane only , external landmarks only on the posterior neurocranium , or a set of some endocranial landmarks . Here, we used geometric morphometrics based on three-dimensional coordinates of endocranial landmarks and hundreds of curve and surface semilandmarks measured on computed tomographic (CT) scans (fig. S1). We obtained landmark data for 20 *H. sapiens* fossils that can be divided into three groups according to geologic ages: (i) early *H. sapiens* from North and East Africa that lived about 300,000 to 200,000 years ago and therefore document the morphology of the currently earliest known representatives of our clade since the population split with Neandertals, (ii) Levantine and East African individuals that lived about 130,000 to 100,000 years ago, and (iii) Upper Paleolithic and geologically younger individuals that are about 35,000 to 10,000 years old. We compiled the same data for comparative samples of cranially diverse present-day humans from all over the world and archaic *Homo* representatives (Neandertals, Middle Pleistocene *H. heidelbergensis* sensu lato, and *H. erectus* sensu lato) and computed Procrustes shape variables (see Materials and Methods). Incomplete and distorted fossils were reconstructed using established methods of computer-assisted paleoanthropology [see Materials and Methods and previous studies.

### **Variation of endocranial shape**

To explore endocranial shape variation of the *H. sapiens* fossils, we computed a between-group principal components analysis (bgPCA) of Procrustes shape variables. This space spans from the ancestral *H. erectus* shape to the derived shapes of Neandertals on the one hand and present-day humans on the other (Fig. 2 and fig. S2), according to the differences in species average endocranial shapes (fig. S3). The fuzzy borders of group convex hulls illustrate the uncertainty introduced by the reconstructions of incomplete fossils (see Materials and Methods). This reconstruction uncertainty does not alter the conclusions of our study. A multivariate shape regression on geologic age within archaic *Homo* individuals reveals a temporal trend from African *H. erectus* (*H. ergaster*) via Asian *H. erectus* to Neandertals (explained shape variance: 29.2%;  $P < 0.01$ ). The Middle Pleistocene *H. heidelbergensis* sensu lato specimens Kabwe and Petralona plot along this temporal trend.

The earliest members of the *H. sapiens* clade (geologic age group 1) have endocranial shapes intermediate between *H. erectus* and Neandertals and seem to be part of the archaic temporal trend. Individuals of geologic age group 2 plot at the fringe of present-day humans, whereas the Upper Paleolithic and younger specimens (geologic age group 3) overlap with present-day human variation. Given the geologic age spans of age groups 2 and 3, the range of today's shape variation is therefore reached approximately between 100,000 and 35,000 years ago. *H. sapiens* fossils from different geologic time periods therefore capture evolutionary shape changes leading to the globular endocranial shape of present-day humans. A multivariate regression of endocranial shape on geologic age explains 21.9% of shape variance ( $P < 0.01$ ) and corresponds to a change from an elongated to a globular shape: From geologically older to younger *H. sapiens*, the frontal area becomes taller, the parietal areas bulge, the side walls become parallel, and the occipital area becomes rounder and less overhanging. Moreover, the cerebellum becomes relatively larger and more bulging, the cranial base more flexed, and the temporal poles narrower and oriented anterior-medially. Color-coding areas of size increase reveals that parietal bulging is not associated with an increase of the parietal surface but that cerebellar bulging is. Both processes contribute to increased globularity. In addition to the PCA and regression analysis, we also visualized evolutionary globularization in *H. sapiens* as changes between the mean shapes of geologic age groups. Endocranial shape changes from geologic age group 1 to geologic age group 2 are associated with size increase in cerebellar and lateral parietotemporal areas. In the second step (geologic age group 2 to 3), shape changes are associated with size increase primarily in cerebellar and occipital areas. The shape changes associated with both steps contribute to globularization in *H. sapiens*. The trajectory from *H. erectus* to Neandertals reveals a contrasting pattern: The cerebrum increases in size in relationship to the cranial base.

Notably, the overarching pattern of globularization in *H. sapiens* is not related to geographic variation but represents a general temporal trend: The North and East African specimens of geologic age group 1 have similar endocranial shapes, the East African specimen Laetoli Hominid (L.H.) 18 clusters with the contemporaneous Levantine individuals (geologic age group 2), the Hofmeyr endocranial from South Africa, and the Levantine individual Ohalo II H2 group with the European specimens of comparable ages (geologic age group 3).

### **Relationship of endocranial shape and size**

To explore whether globularization helped overcome constraints on encephalization, we computed a bgPCA in form space that allows interpreting allometric relationships. The first PC of form space is highly correlated to size variation ( $R = 0.98$ ) and, as expected, separates *H. erectus* from Neandertals and present-day humans. Although endocranial form of *H. sapiens* fossils demonstrates a temporal trend toward present-day human variation, their size variation overlaps among all geologic age groups of *H. sapiens* fossils, as well as with the size variation in present-day humans and Neandertals. This finding is mirrored by endocranial volume estimates of our fossil reconstruction. The endocranial volumes of early *H. sapiens* individuals (Jebel Irhoud 1,  $1375 \pm 6$  ml; Jebel Irhoud 2,  $1467 \pm 6$  ml; Omo 2,  $1491 \pm 4$  ml) fall within the range of our samples of present-day humans (mean, 1328 ml; SD, 164 ml) and Neandertals (mean, 1450 ml; SD, 189 ml) and are considerably larger than those of our *H. erectus* sample (mean, 919 ml; SD, 108 ml).

In archaic Homo individuals, endocranial size and geologic age are negatively correlated ( $R = -0.84$ ), and size explains a similar amount of variance as geologic age (multivariate shape regression on the logarithm of centroid size; explained shape variance: 24.4%;  $P < 0.01$ ). Visualizations of this allometric regression reveal shape changes that differ from the temporal trend within *H. sapiens* in an important way: Overall, archaic Homo individuals maintain an elongated endocranial shape along the allometric regression. With increases in endocranial size, the cerebrum gets enlarged on top of the brain stem and cerebellum.

In contrast to archaic Homo, geologic age and size are not correlated in *H. sapiens* fossils ( $R = -0.02$ ), and size does not account for endocranial shape variation (multivariate shape regression on the logarithm of centroid size; explained shape variance: 4.8%;  $P = 0.99$ ). This finding is also expressed by nearly orthogonal regression lines of the temporal and the allometric trend in the first two PCs of form space.

### **The brain of early *H. sapiens***

In line with genetic data that suggest a population split between modern humans on the one hand and Neandertals and Denisovans on the other more than 500,000 years ago, we view *H. sapiens* as an evolving lineage with deep African roots. Our results, in combination with evidence from craniofacial morphology and dental development, suggest that modern human brain shape was not established at the origin of our species together with other key features of craniodental morphology: Our analyses confirm that early *H. sapiens* [geologic age group 1, that is, not only Jebel Irhoud individuals but also the geologically younger, presumably 195,000-year-old specimen Omo 2] did not have globular brains. Instead, they had shapes intermediate between *H. erectus* and Neandertals. Yet, the size of their brain was already substantially larger than that in *H. erectus* (at the upper boundary of *H. heidelbergensis sensu lato*) and in the range of geologically younger *H. sapiens* fossils and present-day humans. We therefore suggest that early members of the *H. sapiens* lineage initially attained large brains via the archaic allometric pathway and only subsequently diverged from this pattern to evolve the globular brain characteristic of present-day humans. Some authors have challenged the interpretation of the Jebel Irhoud hominins as early *H. sapiens* and view them instead as ancestral to *H. sapiens*. However, we note that our interpretation is robust against the species label attached to the Jebel Irhoud fossils (and by extension also to Omo 2) and that later *H. sapiens* individuals from geologic age group 2 still do not exhibit present-day human-like brain globularity (see Discussion below). Two fossils also related to the origin of our species [Omo 1 and the approximately 260,000-year-old Florisbad specimen] are unfortunately too fragmentary to be included in the analysis.

### **Gradual globularization within *H. sapiens***

Indisputable *H. sapiens* individuals from about 130,000 to 100,000 years ago (geologic age group 2) have more globular brains than the earliest *H. sapiens* fossils and are more similar to, but still different from, present-day humans. *H. sapiens* individuals that are younger than about 35,000 years (geologic age group 3) overlap with the range of variation in present-day humans. Our analyses therefore demonstrate that the evolution of modern human brain shape is characterized by directional and gradual changes resulting in the typical globular modern human shape established at

some point after about 100,000 years ago and probably before 35,000 years ago. We expect that future analyses based on additional fossil specimens filling the temporal gaps between our geologic age groups will further elucidate the mode of evolutionary shape change and help to pinpoint the exact time when present-day human brain shape was established. Unfortunately, no CT data of the Herto skull (BOU-VP-16/1) dated to about 160,000 years old were available for this study. If this specimen exhibits an endocranial shape intermediate between the mean shapes of geologic age groups 1 and 2, then this will further strengthen our hypothesis of a gradual emergence of present-day human globularity.

Investigating brain shape changes as a two-step process between our three geologic age groups suggests some variation in the overarching gradual pattern of globularization. Although both steps include parietal and cerebellar bulging, it is interesting to note that the first step (from geologic age group 1 to geologic age group 2) includes only subtle shape changes of brain regions associated with the anterior and middle cranial fossae. Because this part of the cranial base acts as the interface between the brain and the face, this suggests that the initial globularization was driven by changes in brain organization and not by changes in facial size and shape. The second step of globularization (from geologic age group 2 to 3) also comprises shape changes in these regions, suggesting that integration of the endocranium with the face might have contributed to endocranial globularization but only in later phases of *H. sapiens* evolution.

### **Implications of evolutionary globularization**

Evolutionary brain globularization in *H. sapiens* corresponds to the shape changes during the developmental globularization phase found in present-day humans. In light of the documented differences between the ontogenetic patterns in present-day humans, Neandertals, and great apes, we suggest that this evolutionary globularization is linked to a gradual evolution of the developmental globularization phase and therefore caused by changes to perinatal brain development.

Two features of this process stand out: parietal and cerebellar bulging. Parietal areas are involved in orientation, attention, perception of stimuli, sensorimotor transformations underlying planning, visuospatial integration, imagery, self-awareness, working and long-term memory, numerical processing, and tool use. Because parietal bulging is not associated with an increase of outer parietal surface area [mirroring ontogeny], it is likely that a size increase of regions that are not visible on the external surface of the brain is responsible for parietal bulging. For example, the precuneus is hidden in the interhemispheric fissure and was shown to be larger in humans than in chimpanzees. Furthermore, parietal bulging in present-day humans has been linked to large shape variation in the precuneus. The precuneus is a central node of the default-mode network and an important hub of brain organization. Bruner *et al.* therefore concluded that precuneus expansion in *H. sapiens* is related to cognitive specializations.

The cerebellum is associated not only with motor-related functions like the coordination of movements and balance but also with spatial processing, working memory, language, social cognition, and affective processing. The developmental and evolutionary shape changes of the posterior cranial fossa are linked to the rapid cerebellar expansion during perinatal brain growth. Clinical neuroimaging data from modern humans show that in the first 3 months of life, the cerebellum grows at the highest rate of all brain parts.