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Endocranial ontogeny and evolution in early *Homo sapiens*: The evidence from Herto, Ethiopia

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Fossils and artifacts from Herto, Ethiopia, include the most complete child and adult crania of early *Homo sapiens*. The endocranial cavities of the Herto individuals show that by 160,000 y ago, brain size, inferred from endocranial size, was similar to that seen in modern human populations. However, endocranial shape differed from ours. This gave rise to the hypothesis that the brain itself evolved substantially during the past ∼200,000 y, possibly in tandem with the transition from Middle to Upper Paleolithic techno-cultures. However, it remains unclear whether evolutionary changes in endocranial shape mostly reflect changes in brain morphology rather than changes related to interaction with maxillofacial morphology. To discriminate between these effects, we make use of the ontogenetic fact that brain growth nearly ceases by the time the first permanent molars fully erupt, but the face and cranial base continue to grow until adulthood. Here we use morphometric data derived from digitally restored immature and adult *H. sapiens* fossils from Herto, Qafzeh, and Skhul (HQS) to track endocranial development in early *H. sapiens*. Until the completion of brain growth, endocasts of HQS children were similar in shape to those of modern human children. The similarly shaped endocasts of fossil and modern children indicate that our brains did not evolve substantially over the past 200,000 y. Differences between the endocranial shapes of modern and fossil *H. sapiens* adults developed only with continuing facial and basicranial growth, possibly reflecting substantial differences in masticatory and/or respiratory function.

paleoanthropology | Ethiopia | endocast | Herto | digital restoration

Significance

Fossils of early *Homo sapiens* from Herto, Ethiopia, show that populations living in Africa 160,000 years ago had already evolved brains broadly equivalent in size to those of humans living today. However, these early human braincases were shaped differently than ours, raising the question of whether the actual brains they housed were also structurally different. We used high-resolution computed tomography to perform accurate digital restorations of the fossil remains. These data allowed direct comparisons between endocranial shape development from childhood to adulthood in both fossil and living humans. Our results suggest that the peculiar shape of early *Homo sapiens* adult braincases was likely due to dietary and lifestyle differences rather than different brain anatomy.

The brains of living humans are about three times larger than those of our closest living relatives, the great apes, and human brains exhibit marked structural differences, notably in areas involved in complex cognitive tasks such as language (1). When and how the characteristic features of the human brain evolved, however, is a matter of ongoing discussion because fossil endocasts—the shapes and sizes of natural or virtual fillings of braincases—can only partially inform about brain anatomy (2, 3). Brain size can be estimated from endocranial size, brain shape from endocranial shape, and external brain structures such as sulci and gyri from their imprints on the endocranial surfaces. Fossil evidence suggests that key features of the brains of living humans, such as expanded cerebral association areas of the inferior frontal and posterior parietal lobes, evolved relatively late (<1.7–1.5 million years ago [Ma]), rather than at the beginnings of our genus *Homo* at approximately 2.5 Ma (4). The brains of fossil *Homo* younger than 1.5 Ma therefore were likely structurally similar to those of present-day humans (4). However, our brains and their surrounding braincases are now more rounded in shape (5). Indeed, endocranial globularity in combination with facial retraction is characteristic of Late Pleistocene-to-recent *Homo sapiens*, but rarely present in earlier fossils (4).

Various hypotheses have been proposed to explain how the modern human endocranial morphology evolved and developed after the split from the last common ancestor with our close fossil relatives, the Neanderthals (5–8). Endocranial ontogeny is relatively well documented in Neanderthals, permitting inferences about brain ontogeny. Compared to present-day humans, Neanderthals had similar endocranial sizes at birth, indicating similar neonatal brain sizes. However, Neanderthals had higher postnatal endocranial (and brain) growth rates, resulting, on average, in larger adult brain sizes [but not in earlier completion of brain growth (9)]. Furthermore, tracking Neanderthal endocranial development (i.e., change in shape) from birth to adulthood suggests marked differences in brain development compared to present-day humans, either in utero (10), or during early postnatal life (11).

When and how the modern human mode of endocranial and brain ontogeny evolved, however, remains an open question. This is because, on the one hand, the adult endocranial shape of recent humans is markedly different from that of Pleistocene fossil *H. sapiens* (5, 8); and on the other, because only few immature fossil specimens

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have been available with which to document endocranial ontogeny in fossil *H. sapiens*. The difference between fossil and recent adult *H. sapiens* endocranial shapes has been interpreted as evidence for developmental and structural novelties of the brain that evolved gradually over the past 200 ka (thousand years ago) probably in concert with techno-cultural innovations during the Middle to Upper Paleolithic transition (8).

This hypothesis assumes that evolutionary changes in endocranial shape reflect changes in brain shape that were ultimately caused by structural changes in the brain. Endocranial shape does largely represent brain shape (12). However, this does not signify that the brain alone influences endocranial shape. Other external constraints also influence endocranial shape. Overall, evolutionary and developmental changes in endocranial shape are due not only to intrinsic changes in the brain but also to extrinsic factors such as the changing proportions of the neurocranium (the skull region enclosing the brain) relative to the viscerocranium (the face and cranial base) (7, 13). Facial size in members of the *H. sapiens* species lineage gradually reduced during the past 200–300 ka (14), a period during which techno-cultural changes and changes in subsistence strategy had impacts on facial size and shape as well as on masticatory function (15).

Consequently, it is necessary to assess the effects of both viscerocranial and cerebral factors on changes in endocranial size and shape during both ontogeny of fossil *H. sapiens* and also during the past 200 ka of our evolution. Fortunately, there is now a growing sample of immature and adult fossil *H. sapiens* with which to investigate these relations. Key among them are the crania of a child (age at death estimated to 6–7 y, based on dental maturation patterns) and an adult from Herto, Ethiopia (14), recovered in archaeological (16) and chronostratigraphic (~160 ka) contexts that have rendered them crucial referents in discussions about the biological evolution and behavior of early *H. sapiens* (17, 18). Although well-preserved, both the child (BOU-VP-16/5) and adult (BOU-VP-16/1) from Herto suffered slight but significant prerecovery taphonomic distortion that limited their initial metric characterization. To accurately compare and illuminate the evolutionary and developmental biology of fossil and recent *H. sapiens*, we employ newly rendered digital restorations of these two crania.

We apply an evolutionary developmental approach to compare endocranial and viscerocranial growth and development between fossil and recent *H. sapiens* and to examine how facial size reduction affected endocranial shape in evolving *H. sapiens*. The human brain nearly ceases its growth around the age of 5–6 y (19) whereas the face and cranial base continue to grow. This rate transition occurs around the time when the first permanent molars (M1s) fully erupt into functional occlusion. This allows us to test the hypothesis that adult endocranial shape is influenced by viscerocranial (i.e., facial and basicranial) development.

Here, we describe and illustrate our stepwise field and laboratory recovery and physical restorations of the two original Herto fossil crania (Fig. 1 and *SI Appendix*, Figs. S1–S14), as

Fig. 1. Discovery and restoration of the Herto adult (BOU-VP-16/1) and child (BOU-VP-16/5) crania. Adult cranium (*A*–*F*). (*A*) D. DeGusta examines scatter of surface cranial vault fragments of (yellow flags); (then) seasonally abandoned Herto Afar village in background. When occupied, hundreds of domestic ungulates (camels, cows, sheep, goats) cross this surface each day. View is to the west. (*B*) Tight concentration of cranial vault pieces indicated relatively limited scatter after recent erosional exposure. (*C*) Indurated sandstone cemented to the right side of the cranium obscures most bone. (*D*) Removal of sand and sandstone reveals the intact right side of the cranium. (*E*) The frontal sinus is large, with thin anterior and posterior walls. Even more fragile maxillary, ethmoidal and sphenoid bone is left encased in the hardened sandstone because it cannot be safely cleaned. (*F*) Right lateral view of the cranium after physical restoration. Child cranium (*G*–*K*). (*G*) B. Asfaw points to fragments of cranial vault. View is to the north, Central Awash Complex in background. (*H*) Larger cranial vault pieces indicated by yellow arrows. Other surface lag comprises indurated sandstone fragments and artifacts. Wet sieving recovered smaller pieces. (*I*) Recovered pieces. (*J*) Refitting. (*K*) Three-quarter view of the restored specimen. An extended set of photographs documenting the recovery and restoration procedures is provided in *SI Appendix*, Figs. S1–S14.

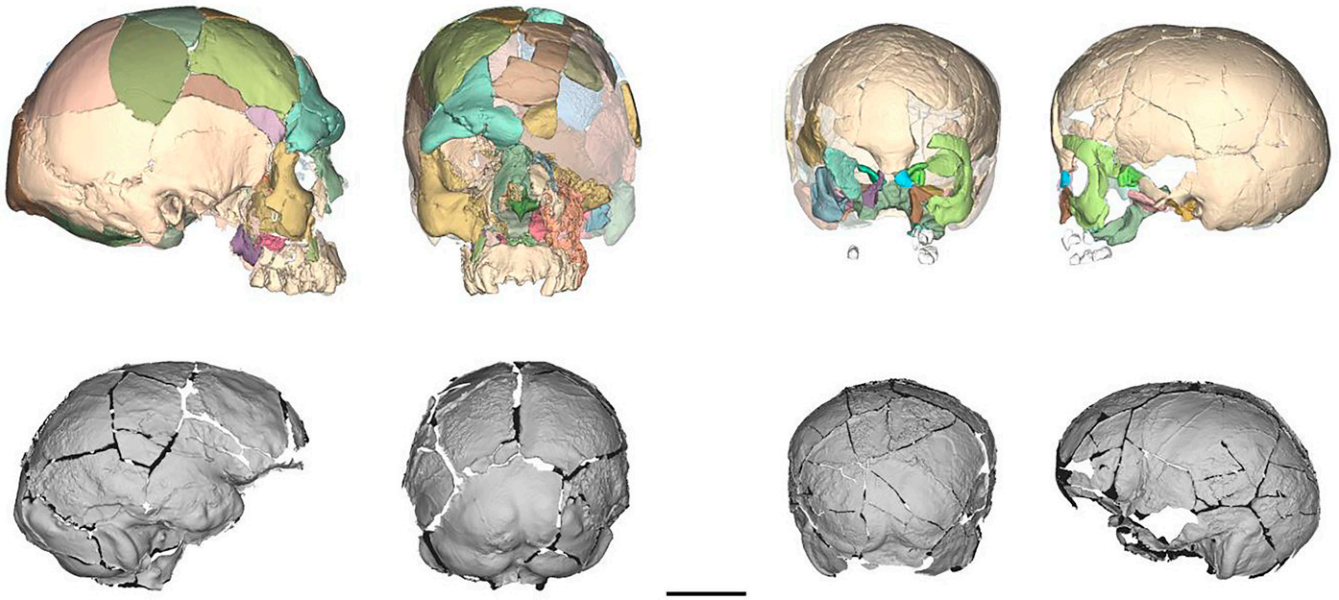

Fig. 2. Digital restoration of the Herto crania and their endocasts. *Left*: Herto adult BOU-VP-16/1. *Right*: Herto child BOU-VP-16/5. Crania are shown in anterior and lateral views; endocasts in posterior and lateral views. (Scale bar: 5 cm.) Details of the restoration procedure and full sets of the six standard views are provided in *SI Appendix*, Figs. S15–S22.

well as the methods used to digitally render and accurately restore them (Fig. 2 and *SI Appendix*, Figs. S15–S22). We then generate comprehensive metric datasets for comparative uses and apply geometric morphometric methods to quantify endocranial and viscerocranial size and shape of these key specimens. Finally, we compare them with similarly processed child and adult fossils from Skhul and Qafzeh (~120–100 ka) and a large comparative sample spanning the evolutionary time from early *Homo* to recent humans.

Results

Fig. 3 shows patterns of endocranial and viscerocranial growth in fossil and recent *H. sapiens*, *Homo neanderthalensis*, mid-Pleistocene *Homo* and *Homo erectus* (*sensu lato*). Fossil *H. sapiens* is at the upper end of variation of the endocranial and viscerocranial growth trajectories of living humans (Fig. 3*A* and *B*), indicating that fossil humans relative to living humans typically had larger endocranial and viscerocranial sizes at any ontogenetic stage. The proportion of neurocranial to viscerocranial size is expressed here as the "neuro-viscerocranial proportion" or NVP, defined as the cube root of endocranial volume (ECV) divided by viscerocranial centroid size. The NVP decreases along all ontogenetic trajectories as an effect of the higher rate and longer duration of viscerocranial relative to neurocranial growth (Fig. 3*C*). Most notably, fossil *H. sapiens* have comparatively lower NVP values than living humans at corresponding ontogenetic stages. This indicates that throughout ontogeny, early humans in general had larger viscerocrania relative to their endocranial volumes (Fig. 3*C*). Overall, after the near completion of brain growth, fossil humans achieved substantially larger viscerocrania than their living counterparts (Fig. 3*B*), whereas endocranial size was at the upper end of living human variation (Fig. 3*A*).

Fig. 4*A* and *B* show principal patterns of endocranial and viscerocranial shape variation in the sample. Each taxon occupies a distinct region in shape space, with *H. erectus* and living humans at opposite poles of the variation, reflecting an evolutionary trend toward paedomorphy. Fig. 4*A* shows evolutionary shape change from the relatively wide and low endocasts of *H. erectus* to the rounded, narrow, and high endocasts of living humans (*SI Appendix*, Fig. S23 shows a similar pattern based on linear endocranial dimensions). Fig. 4*B* shows the corresponding evolutionary shape change for the viscerocranium, from the projecting faces and wide cranial bases of *H. erectus* to the retracted faces and short cranial bases of living humans.

In all taxa, cranial ontogenetic development is largely characterized by widening and elongation of the endocast (Fig. 4*A*) and by elongation of the cranial base and antero-inferior projection of the face (Fig. 4*B*). The endocranial shapes of fossil human children prior to completion of brain growth lie at the boundary of variation for living human children (Fig. 4*A*) but do not differ significantly ($P = 0.36$; see *Materials and Methods* for statistical tests of shape differences between groups). The endocranial shapes of fossil human adults ≥100 ka are at the boundary (Skhul 5) or outside (Herto 1, Qafzeh 9) of the variation of living human adults (Fig. 4*A*, $P = 0.002$). In contrast, viscerocranial shape differences between fossil and living humans are less pronounced (Fig. 4*B*). Fossil human children are within the range of viscerocranial variation seen in living children ($P = 0.20$), whereas fossil adults are at the boundary of living adult variation (Fig. 4*B*, $P = 0.20$).

We further analyzed the possible effects of changes in neuro-viscerocranial size proportions on endocranial shape. A substantial proportion (46%) of the total endocranial shape variation in our sample can be accounted for by variation in NVP. The fossil human children (Herto 5, Qafzeh 11, and Skhul 1) fall within the pattern of NVP-endocranial shape covariation that characterizes living humans (Fig. 4*C*). However, these fossils are situated at the upper range of variation of modern human children and within the lower range of modern adults (Fig. 4*C*). Adult fossil humans are mostly situated at the upper end of modern human adult variation, except for the Herto and Qafzeh adults, which are outliers. Changes in neuro-viscerocranial proportions, both during evolution and ontogeny, thus have an impact on endocranial shape variation.

To further study endocranial shape variation independent of neuro-viscerocranial proportions, we partialled out the effects of NVP on endocranial shape. Fig. 4*D* shows the residual

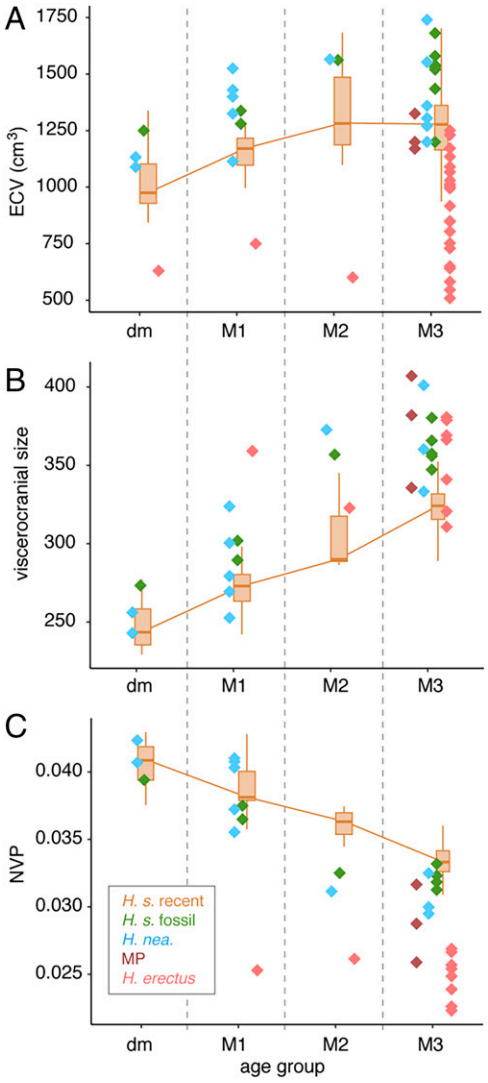

Fig. 3. Endocranial and viscerocranial growth in fossil *Homo* and modern humans as a function of dental age. (*A*) Endocranial volume (ECV). (*B*) Viscerocranial size (defined as centroid size of viscerocranial landmarks; see *Materials and Methods*). (*C*) Neuro-viscerocranial proportion (NVP), defined as the ratio between $ECV^{1/3}$ and viscerocranial size. The abscissa represents successive dental age groups (dm/M1/M2/M3: after full eruption of deciduous molars, permanent molars M1/M2/M3). Diamonds represent individual fossil data; boxplots represent living human data (median, first and third quartiles, minima and maxima; line connects median values).

endocranial shape variation in the sample. In this graph, the fossil human children fall well within the range of residual endocranial variation of living human children ($P = 0.5$), and fossil adults generally fall within modern adult variation. However, the adult fossils from Herto and Qafzeh fall outside the variation that characterizes adult living humans (Fig. 4*D*, $P = 0.01$). Compared to both fossil and modern *H. sapiens*, Neanderthals already exhibit clearly different endocranial and facial morphologies early in ontogeny (Fig. 4*B*), a finding in agreement with earlier studies revealing distinct modes of endocranial and facial development (9–11, 20, 21).

Fig. 5 shows how, in fossil and modern *H. sapiens*, endocranial and viscerocranial morphologies change after the completion of brain growth. In both groups, the endocranial base expands relative to the vault (as indicated by the yellow surface areas in Fig. 5*A*; also see *SI Appendix*, Fig. S23), reflecting the continuing growth of the viscerocranial region of the skull. In fossil humans, these changes are more pronounced, resulting in adult endocranial shapes that appear more elongate, comparatively low, and less rounded in lateral view.

Discussion

The endocranial evidence from the digitally restored Herto child and adult individuals, and from the immature and adult individuals from Skhul and Qafzeh, now permit a tentative reconstruction of endocranial ontogeny in fossil compared to recent *H. sapiens*, allowing inferences about our brain's evolutionary developmental history. The growth trajectory of the endocranial volume (ECV) of fossil *H. sapiens* is at the upper end of variation of the modern human trajectory (Fig. 3*A*), and a similar pattern can be seen in the Neanderthals (Fig. 3*A*), as reported earlier (9). These observations lead us to the hypothesis that in terms of brain growth dynamics, Pleistocene *H. sapiens* might have had more in common with the largely coeval *H. neanderthalensis* populations than with modern *H. sapiens* populations. Large infant brains imply high early postnatal brain growth rates, which presuppose enhanced maternal and allomaternal investments that, in turn, are typically associated with a slower pace of life history (22). This hypothesis implies a contrast between the life histories of Late Pleistocene and modern *Homo* populations rather than a contrast between slow human and fast Neanderthal life histories (23).

Our data further offer a perspective on the developmental mechanisms underlying the contrasting endocranial shapes of fossil and recent *H. sapiens*. The endocranial shapes of the fossil children from Herto, Skhul, and Qafzeh are at the fringe of endocranial variation in modern human children of comparable age, but well within modern adult endocranial variation (Fig. 4*A*). The difference between fossil and modern immature endocranial shapes could be due to various factors, such as actual differences in brain morphology, differences in viscerocranial morphology, or a combination of both. Fig. 4*C* and *D* indicate that the endocranial shape difference can largely be accounted for by the different neuro-viscerocranial size proportions of fossil and modern children, with fossil children having markedly larger viscerocrania, both in absolute terms and relative to endocranial volume (Fig. 3*B* and *C*). Differences in brain structure may also have contributed to endocranial shape differences, but there is currently no positive evidence to support that hypothesis. Taking into account the effects of neuro-viscerocranial integration on endocranial shape, it is most parsimonious to infer that the brains of fossil *H. sapiens* were structurally similar to those of modern *H. sapiens*, and had evolved at least as early as ~160 ka, as evidenced by the Herto child, and earlier than previously inferred by some workers (8, 24).

The evolutionary and developmental causes and mechanisms that led to the remarkably distinct adult neurocranial and endocranial morphologies of the early members of *H. sapiens* such as Herto (14) and Qafzeh (Fig. 4*A*) remain to be elucidated along similar lines of evidence. MRI-based studies have revealed structural changes in the brain after the completion of brain growth, especially in the frontal cortex during adolescence (13, 19, 25). However, these changes have only little effect on the shape of the endocast and cannot account for endocranial shape change from immature to adult fossil *H. sapiens* (Fig. 4*A*). Changes in endocranial shape after the near completion of brain growth are thus unlikely to reflect changes in brain structure, but rather "alteration of external brain shape under the influence of nonbrain parts of the head.

Assuming a broad perspective on neuro-viscerocranial interaction, it appears that brain shape in mammals is indeed highly

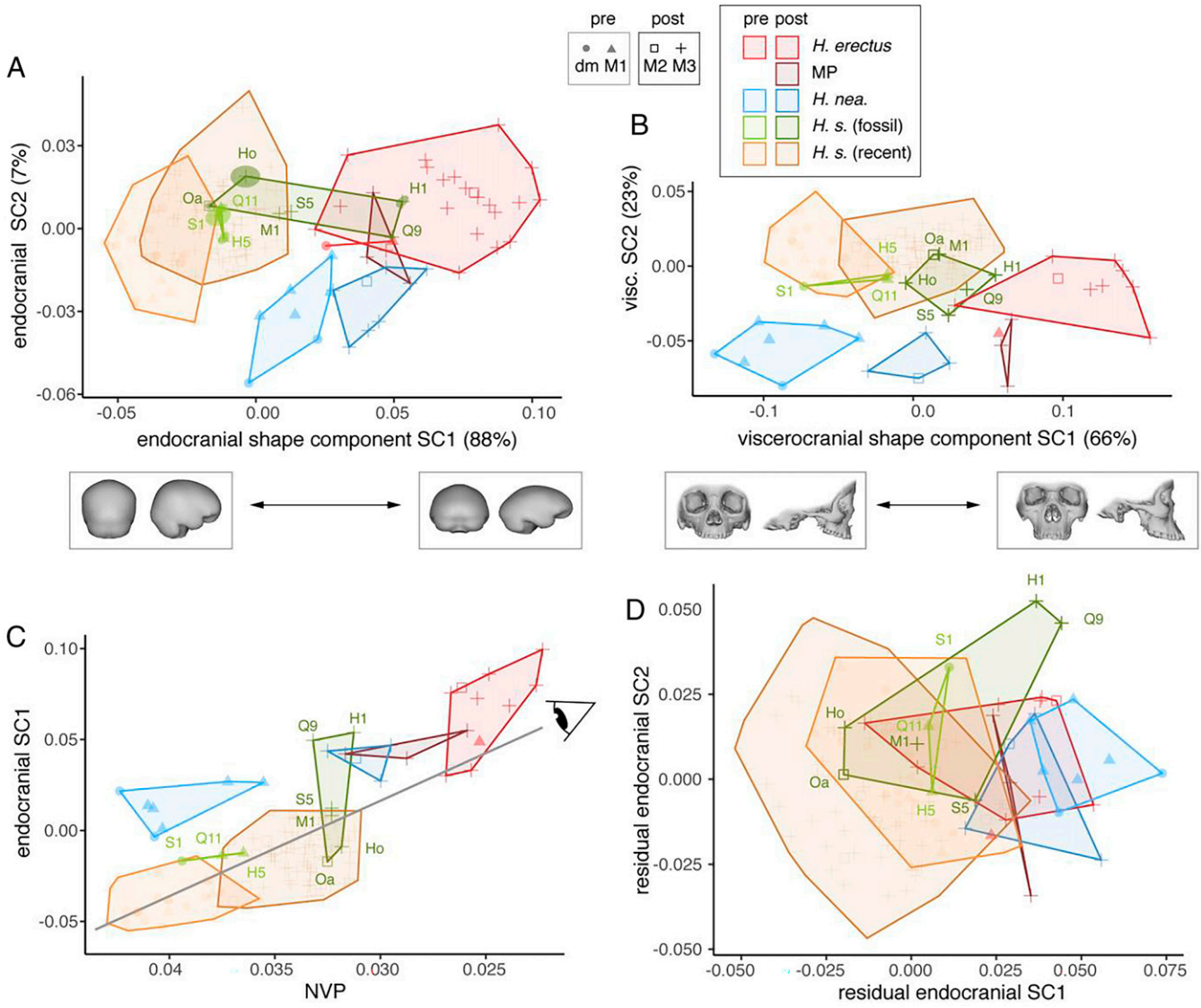

Fig. 4. Endocranial and viscerocranial shape variation in fossil *Homo* and modern humans. (*A*) Endocranial shape components 1 and 2 resulting from between-group principal components analysis (bgPCA). The 95% density ellipses around fossil *H. sapiens* specimens indicate reconstructive variants (see *Materials and Methods* and *SI Appendix*, section 1.3.5). *Inset* graphs visualize endocranial shape (posterior and lateral views) at the lower and upper range of PC1, respectively. (*B*) Viscerocranial shape components 1 and 2 resulting from bgPCA. Inset graphs visualize endocranial shape (anterior and lateral views) at the lower and upper range of PC1, respectively. (*C*) A substantial proportion (46%) of total endocranial shape variation in the sample can be attributed to variation in neuro-viscerocranial proportion (NVP). Shown here is the covariation of the endocranial shape component 1 with NVP (note: to achieve graphical correspondence with (*A*) and (*B*), the scale of NVP is reverted). (*D*) Residual endocranial shape variation after partialling out the effects of NVP (i.e., looking at endocranial shape variation along the axis indicated by the eye symbol in *C*). Symbols indicate dental age; colors indicate major *Homo* taxa; convex polygons are drawn around taxon-specific subsamples representing dental ages ≤M1 and ≥M2, respectively, corresponding to ontogenetic stages before (pre) and after (post) completion of brain growth. Fossil *H. sapiens* specimens (and approximate geological ages): H1, H5: Herto BOU-VP-16/1 and 16/5 (160ka); Ho: Hofmeyr (36ka); M1: Mladec 1 (31ka); Oa: Oase 2 (40ka); S1 and S5: Skhul 1 and 5 (100ka); Q9, Q11: Qafzeh 9 and 11 (100ka). [Note on fossil specimens affiliated by others with *H. sapiens* but not included in analyses: Omo1: too fragmentary; Omo2 and LH18: geological dates not well constrained; Jebel Irhoud 1 and 2: data not available; see (18)].

malleable and tends to follow external adaptive and developmental constraints imposed on neurocranial shape (26). In adult *H. sapiens*, we observe that the viscerocranium underwent remarkable size reduction over the past ∼160 ka, but only moderate change in shape (Figs. 3*B* and 4*B*) (24, 27). During the same time period, the endocranium underwent moderate reduction in size, but substantial change in shape (Figs. 3*A* and 4*A*) (24, 27). Given the current dearth of fossil evidence from >100 ka, various hypotheses about the functional significance of this complex pattern remain to be tested.

One possible explanation is that pronounced neurocranial sexual dimorphism in fossil *H. sapiens* is no longer present in living human populations. However, Herto 1 and Qafzeh 9 are typically seen as male and female individuals, respectively, but both are endocranially most distant from living humans. The endocranial morphology of the Skhul 5 fossil, likely male, is at the border of endocranial variation of living humans. An alternative hypothesis is that maxillofacial reduction and the concomitant endocranial shape change reflect major changes in techno-culture, subsistence strategy and food processing, resulting from a trend toward softer diets and less extensive mastication. Studies on model animals have revealed both short-term as well as long-term effects of softer diets on craniofacial size and shape (28–30), and field studies on primate species (31) suggest an important, although complex, influence of dietary differentiation on craniofacial morphological differentiation among

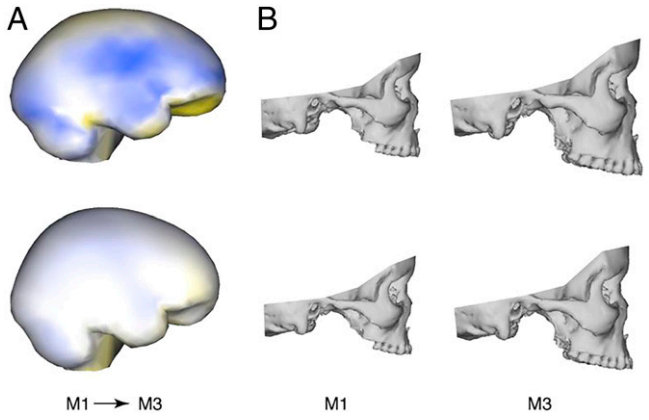

Fig. 5. Changes of endocranial and viscerocranial morphologies after completion of brain growth (from dental stage M1 to M3) in fossil (*Upper* row) and recent (*Lower* row) *H. sapiens*. (*A*) Endocranial shapes are shown for adults, endocranial shape change is visualized by positive (yellow) versus negative (blue) allometric expansion of local surface area. Note more intense shape change in fossil compared to recent *H. sapiens*. (*B*) Changes in viscerocranial shape and size are illustrated with mean shapes at dental stages M1 (left) and M3 (right, adult), respectively, while viscerocranial size is scaled relative to the smallest group-mean size, that of M1 recent *H. sapiens* (lower left graph). Note larger viscerocranium at stage M1, and more intense viscerocranial growth in fossil compared to recent *H. sapiens*.

taxa. The general pattern is that softer diets are associated with relatively shorter but wider faces and more rounded neurocrania. Craniodental data from recent human populations during the transition from Upper Paleolithic hunter-gatherer to Neolithic agricultural lifestyles also indicate that subsistence on softer diets is correlated with increased neurocranial globularity and decreased facial size (15, 32–35). A further hypothesis is that viscerocranial size reduction and concomitant endocranial shape change reflect reduced metabolic demands, given that oxygen uptake is constrained by the dimensions of the nasal passageways (36, 37).

Overall, the Upper Paleolithic to Neolithic pattern of neurovisceral size and shape change is similar to the one described here for the Middle to Upper Paleolithic transition (Figs. 3 and 4), although less significant in magnitude. Diet-related adaptation, changes in metabolic demands, and developmental plasticity might have contributed to the marked changes in viscerocranial size and in endocranial/brain shape at the transition from Middle to Upper Paleolithic lifestyles. More fossil evidence is required to address these questions. Meanwhile, the restored Herto fossils confirm that endocranial shape in *H. sapiens* has long been related to nonbrain factors, such that shape alone should not be used as an indicator of the brain's functional evolution in the human lineage during the past 200,000 y.

Materials and Methods

The fossilized Herto BOU-VP-16/1 and BOU-VP-16/5 crania were digitally restored following the methods described in (38) and according to the protocols described in the *SI Appendix*. Equivalent procedures were used to digitally restore the fossil specimens from Skhul and Qafzeh. The comparative sample documents cranial ontogeny from the eruption of the deciduous maxillary molars (dm) to adulthood. The sample comprises 125 recent human crania, and 50 fossil *Homo* crania representing *H. erectus*, mid-Pleistocene *Homo*, *H. neanderthalensis*, and *H. sapiens*. Details of the sample structure, computed tomography-based data acquisition, and geometric-morphometric analyses are provided in the *SI Appendix*. Endocranial morphology was quantified with 921 three-dimensional (3D) landmarks, and viscerocranial morphology with 36 3D landmarks. Geometric morphometric analyses were performed with the R packages Geomorph (39) and Morpho (40). Landmarks in missing regions of fossil endocasts were estimated with thin plate spline interpolation from complete specimens, resulting in the 95% ellipses around specimen means in Fig. 4*A*. Shape variation in the sample was visualized with between-group principal components analysis (bgPCA) to explore commonalities and differences between groups. Given the limitations inherent to bgPCA (41), this method was used for data visualization and exploration only, while between-group differences were analyzed in Procrustes shape space. To this end, Procrustes shape distances D between group means and significance levels p of shape difference were evaluated with residual randomization in 9999 permutations of the original Procrustes shape data, using R procedure RRPP (42).

Data Availability. All study data are included in the article and/or *SI Appendix*.

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