Supplementary Information for:

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

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SI Dataset S2: SI_endocast_data.xlsx
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1. METHODS

1.1 Field Recovery

1.1.1 Field recovery of the BOU-VP-16/5 child’s cranium

Middle Awash field operations are guided by logistical and scientific project priorities and protocols (see main text and references therein). Vertebrate fossils were collected from a variety of locations during the 1997 field season, including Bouri Vertebrate Paleontology Locality 16 in the area encompassing the modern Afar village known as Herto Bouri. This locality was first intensively collected in this field season because unseasonal heavy rains in the Middle Awash study area had resulted in the nomadic pastoralists occupying areas farther from the permanent water of the nearby Awash River (1). As a result, the sediments that form the bedrock of the modern Herto Village were unusually dust- and dung-free, and many fossils were exposed partially in situ, eroding from variably indurated sandstone of the Upper Herto Member.

The child’s cranium BOU-VP-16/5 was a surface find made by Dr. Berhane Asfaw on December 3rd, 1997. The fossil had eroded from Upper Herto Member sandstones of the Bouri Formation. The cranium had shattered into many small fragments that were scattered across several meters of flat erosional surface through the action of post-exposure trampling (humans and livestock occupying the adjacent Herto Village), frequent whirlwind activity, and water movement during heavy rains; Fig. S1). Surface crawl recovered the exposed fragments, and a dry sieve operation recovered additional pieces. Wet sieving the dry sieve concentrate was done to recover even smaller pieces (Fig. S2).

1.1.2 Field recovery of the BOU-VP-1/16 adult’s cranium

The more complete of two adult crania found near Herto Village was found eroding from the same sandstone unit, but in contrast to the child’s cranium found ~150m to the SSE, more than half of the adult BOU-VP-16 cranium remained in situ after the specimen’s discovery by then-Berkeley graduate student David DeGusta on November 27th. The first fragment recovered was a small vault fragment that had detached and scattered on the surface (Fig. S3). A cluster of pin flags marking adjacent cranial fragments showed that the distribution of pieces had been limited (Fig. S4). With such concentration, it was likely that some of the cranium remained in situ, embedded in the variably indurated sandstone. Brushing revealed this to be the case (Fig. S4) and the application of cryoacrylate to the fragile unconsolidated pedestal was required, particularly because the dense bunch grass root mass in the sands had penetrated the fossil. Further consolidation and plaster jacketing allowed safe removal of the fossil, followed by a surface sweep to recover more scattered pieces (Figs. S5 and S6).

1.2 Laboratory Cleaning and Physical Restoration

1.2.1 Laboratory cleaning and physical restoration of the BOU-VP-1/5 child’s cranium

The child’s cranium had been the nucleus for carbonate cementation of manganese-stained fine sand that was firmly attached to the fossil. This black, highly indurated matrix was removed from each of the many pieces (Fig. S2) by an air scribe
and is still present adhering within sutural spaces. Further removal from these or other spaces flanked by thin bone would jeopardize the fossil’s integrity and/or external surfaces. This matrix infill should not be mistaken for premature sutural fusion. The bone strongly adhering to this matrix is also stained very dark in color, but in places in which the sandstone had naturally exfoliated prior to collection the bone is lighter in color. After thorough cleaning of the individual fragments, the cranium was reassembled to the extent possible. Joins were generally across fresh breaks, and combined with the dense scatter of pieces, it was obvious that the cranium had been relatively recently exposed by erosion of the sandstone’s upper surface. There was little to no EMD (expanding matrix distortion) involved, and this allowed the numerous joins required to restore the vault contours accurately. Loss of the fragile bones connecting the face to the vault required careful digital restoration described below.

1.2.2 Laboratory cleaning and physical restoration of the BOU-VP-1/16 adult’s cranium

Fossilization of the adult cranium was strong and it had been embedded in largely medium grained sandstone with some gravels. Platy, carbonate-cemented sandstone that was retained on the underside of the jacketed cranium was not so strongly cemented to the bone. As a consequence removal of this matrix was far easier than was the case for the child’s cranium. However, the less well fossilized bone of the adult had been affected by EMD and subsequent penetration by rootcasts. This required careful application of a reversible consolidant in each step of the cleaning and de-jacketing process. This process is illustrated in detail in Figs. S7 through S11.

After restoration of the cranium to the extent safely possible, teff seed was used to fill the right half of the vault in order to estimate cranial capacity. Other metrics reported for both the child and adult crania were afforded plus-minus values in order to reflect uncertainty regarding the extent of postmortem distortion suffered by the cranium. The digital restoration has now made it possible to adjust some of the earlier published measurements, and to add new measurements. These are reported in here.

1.3 Digital Restoration

1.3.1 Computed Tomography of the BOU-VP-16/1 and BOU-VP-16/5 crania

The BOU-VP-16/1 and BOU-VP-16/5 fossils are heavily mineralized, as evidenced by the high X-ray density of the fossilized bone. The cranial vault fragments of both specimens have been completely freed from adhering matrix except for minor amounts of indurated sandstone left in sutures and voids during manual preparation to preserve strength and avoid damage. In BOU-VP-16/1, the maxillofacial region was left partly embedded in preservative-hardened sandstone during mechanical preparation. This matrix tends to exhibit lower density than the bone. This physical complexity posed several challenges during CT scanning. On the one hand, the strong density contrast between the fossil and the surrounding air, and the variable bone thickness (<1mm in the nasofacial region to ~10 mm in the cranial vault region), resulted in beam hardening (differential attenuation of lower-energy X-ray radiation) and various digital reconstruction artifacts. On the other hand, thin bone structures embedded in low-density matrix tend to be blurred due to partial-volume effects. Increasing the X-ray energy (pre-hardening) to minimize the former effect
typically results in less contrast resolution, which hampers imaging of fine structural detail in the face. Furthermore, increasing the X-ray flux to improve the signal-to-noise ratio in the raw (projection) data would result in inordinately long scanning times, and/or less spatial resolution. Scanning these structurally heterogeneous fossils thus required careful optimization of the signal-to-noise ratio, contrast resolution, and spatial resolution.

Digital volumetric data of the cranial were acquired with micro-computed tomography (microCT) on the TX225-Actis device of the University Museum, the University of Tokyo. Data acquisition and image reconstruction parameters were as follows. Specimen BOU-VP-16/1: 190kVp, 0.3mA, 4.0mm Cu prefilter, 1800 projections, 512x512 matrix; isometric voxel size of reconstructed image volume: 0.38mm³. Specimen BOU-VP-16/5: 200kVp, 0.3mA, 2.0mm Cu prefilter, 1800 projections, 512x512 matrix; isometric image voxel size 0.33mm³, voxel depth 16 bit.

Beam hardening artifacts could not be completely corrected for and are mostly located in the cranial vault region. This region also exhibits photon starvation artifacts (low signal-to-noise ratio of the raw data due to low X-ray photon count), especially around the internal cranial vault. To reduce image noise in these areas, a 3x3 median filter was applied to each cross-sectional image of the total volume data set. The prefiltered CT data volume was further processed to obtain surface representations of the fossil specimens, using the marching-cube algorithm. An automated thresholding procedure was applied to classify voxels with densities above/below a pre-defined threshold value as “bone” versus “non-bone.” Since the density of the sediment surrounding the facial skeleton of BOU-VP-16/1 is substantially lower than the density of the bony elements, digital sediment removal could be performed to some extent via automated thresholding. Finally, the surface structure representing the entire fossil cranium was further subdivided along the most conspicuous cracks into isolated fossil fragments. These fragments constituted the basic building blocks for the virtual restoration of the crania.

1.3.2 Virtual reconstruction: methods and aims

Virtual restorations of the fossils were performed with the principal aim to complement the existing physical restorations in several ways: 1) to examine and visualize the external and internal morphology of the fossils non-invasively (data visualization); 2) to apply non-invasive preparation methods for the isolation of fossil fragments (data segmentation); 3) to restore internal surface structures such as the endocranial cavity; 4) to correct taphonomic distortions with retro-deformation algorithms; 5) to reposition and re-assemble fossil parts according to pre-defined criteria in virtual anatomical space; 6) to complement missing parts of the original fossils with mirror-images of preserved counterparts; and 7) to derive morphometric data from the finalized reconstructions (2).

Understanding the taphonomic and diagenetic history of a fossil is an important prerequisite to identify postmortem alterations that bias the fossil’s morphology. Postmortem distortion has been shown to result from three main taphonomic mechanisms: fragmentation, plastic deformation, and expanding matrix deformation (3, 4). The relative contributions and the temporal sequence of these processes can be tentatively inferred from the micro- and macrostructural patterns of anatomical distortion of a given fossil specimen. Once a taphonomic sequence has been inferred it can be reversed to some extent by applying virtual retro-deformation methods.
A key aspect of virtual restoration is the methods of anatomical inference used to reconstruct a fossil’s 3D morphology. To minimize bias toward “preconceived” morphologies, primitive (generalized) rather than derived (unique) anatomical topographical constraints should guide the assembly of isolated fossil parts. These controls include features such as bilateral symmetry, dental occlusion, and articulation of elements along sutures and/or joints. Typically, these constraints are sufficient to substantially reduce the degrees of freedom of movement of each fossil fragment relative to each other, and to reliably establish the anatomical position and orientation of each fragment in three-dimensional anatomical space. Bilateral symmetry is an anatomical constraint with special significance. If left and right counterparts of a fossil are preserved, global deviations from bilateral symmetry can be used to infer the direction and magnitude of taphonomic deformations. Furthermore, if anatomical regions are preserved on only one anatomical side of the fossil, the missing regions can be completed with mirror-imaged counterparts.

Re-assembling fragments according to anatomical constraints is an iterative process, which requires several rounds of readjustments until a stable solution compatible with frequent consultations with the original fossil specimen has been identified. This is because even a slight reorientation of a single fragment in virtual space tends to influence the entire 3D-structure of the reconstructed fossil. Virtual restoration thus also serves as a tool with which to evaluate alternative reconstructions of the final morphology.

Since most fossils are incomplete, the outcome of a particular virtual restoration depends to some extent on the choice of restorative strategies and procedures, and on methods of inference of missing parts. These factors also determine the scope of comparative analyses to which virtual fossils can be submitted. For example, completion of missing regions with mirror-imaging procedures creates mathematical symmetry of left and right sides, thus precluding the analysis of natural patterns of fluctuating or directional asymmetry in reconstructed fossils. Furthermore, one needs to keep in mind that numerical methods used to infer missing regions (5) require comparative samples of living taxa, and thus tend to bias the virtually reconstructed parts toward the comparative sample employed. We refrain from using such methods during the virtual restoration of the fossils, leaving missing regions open. Nevertheless, during the geometric morphometric analysis of the endocranial morphology, missing anatomical landmarks are estimated with methods of thin plate spline (TPS) interpolation, as described in the Methods section of the main text.

Each of the Herto fossils posed its own challenges for virtual reconstruction. The BOU-VP-16/1 adult cranium is relatively complete but exhibits post-mortem fragmentation and some distortion. The virtual restoration of this specimen thus started with a detailed assessment of the patterns of deformation. After physical refitting of the dozens of cranial pieces was accomplished, the child’s cranium BOU-VP-16/5 was undistorted, but the face and cranial base were only partially preserved and remained detached. The virtual reconstruction of this specimen thus started with the restoration of the facial morphology from the limited but highly informative dentognathic evidence.

1.3.3 Digital restoration of the BOU-VP-16/5 child’s cranium

Figure S15 shows standard views of the BOU-VP-16/5 cranium in its refitted state. The cranium consists of a vault including the temporal bones, isolated fragments of the anterior cranial base and midface, and isolated tooth crowns representing both the deciduous and permanent dentition. The cranial vault, which
had been physically restored by refitting >100 separate fragments (6), exhibits only minor deviation from bilateral symmetry, and only in the temporal region. Since anatomical contact regions between the temporal fragments and the cranial vault are comparatively small, we surmise that deviations from symmetry in this region result from cumulative effects of physical reconstruction rather than taphonomic deformation. These fragments were therefore electronically detached from the vault and repositioned accordingly. Despite the residual strongly cemented, manganese-stained adhering sandstone, microCT-based analysis reveals fully patent coronal, midsagittal and lambdoidal sutures, which is characteristic for recent human children with similar dental age (permanent M1 in functional occlusion).

Restoration of the anterior cranial base started with placing the largest fragment in anatomical space. The fragment comprises the body and greater wings of the sphenoid plus the posterior parts of the alveolar process of the left maxilla. It preserves bilaterally symmetrical structures such as the bases of the pterygoids, the foramina rotunda, and the anterior margins of the oval foramina. These anatomical reference structures permitted secure placement of the fragment in the midsagittal plane of the cranium. Its anteroposterior position is constrained by anatomical continuity with the left temporal squama. Its inclination relative to the Frankfurt plane was adjusted later, as it is constrained by the reconstruction of the face.

The largest facial fragment comprises the left zygomatic bone, parts of the frontal bone representing the superior margin of the orbital rim (external angular process), and the orbital surface of the left greater wing of the sphenoid. The latter fragment exhibits anatomical continuity with the left frontal squama. Its position and orientation were constrained by establishing anatomical continuity along two maxillary fragments representing the medial orbital rim and frontal process of the left maxilla. The latter fragment articulates with the internal angular process of the frontal bone. The resulting reconstruction of the left orbital rim and lateral parts of the orbital cavity permitted appropriate placement of orbital fragments on the right side via mirror-matching the better-preserved counterparts on the left side. Finally, the large sphenoid fragment positioned during the first step of the reconstruction was rotated on its transverse axis so as to establish anatomical continuity along the inferior (pterygoid) and lateral (orbital) parts of the greater wing.

As mentioned, this basicranial fragment preserves the posteriormost part of the left maxillary alveolar process. A small fragment that was broken off anteriorly was re-attached to the alveolar process. This fragment is significant as it preserves the lingual side of the alveolar crypt of the left P4. The unerupted P4 tooth bud is well preserved and could be repositioned in its crypt. This bud served as a reference to position the unerupted crowns of P3 and C. The distalmost part of the alveolar process contains the broken root tips of the fully erupted M1. The crown of this tooth was recomposed from two fragments, and its mesiodistal position was determined according to the location of its roots. The crowns of the first and second deciduous left molars (m1 and m2) could then be positioned accordingly. The superoinferior position of the functional tooth row was inferred by estimating root lengths of M1 and m2. Finally, the only preserved tooth fragment from the right side, that of M1, was positioned via mirror-matching the left M1.

The final reconstruction of the BOU-VP-16/5 child’s cranium is visualized in Figure S16. The extracted endocranial surface is visualized in Figure S17. The endocranial volume of the reconstructed specimen is estimated to 1337 ccm. The virtual reconstruction differs only little from the overall appearance of the physical restoration of the specimen. Virtual reconstruction complements the known
1.3.4 Digital restoration of the BOU-VP-16/1 adult cranium

Figure S18 shows standard views of the BOU-VP-16/1 cranium in its original state at the conclusion of physical cleaning and refitting. The right side of the neurocranium is generally well preserved. On the left side, portions of the parietal and frontal vault area are missing, and the left temporal bone exhibits some damage. All preserved larger portions of the cranial vault exhibit postmortem fragmentation, and adjacent fragments are slightly displaced relative to each other. Most of the right side of the face is preserved. The left orbital region is missing. The left maxilla is strongly fragmented, and fragments are partially embedded in sediment hardened and left in place to strengthen the specimen. CT imaging confirmed and further revealed various matrix-filled cracks in the basicranium and face. These are probably the result of a combination of expanding matrix distortion and simple sediment fillings of existing gaps between dislocated fragments while the cranium was still in situ in the embedding sandstone. The sediment filling has two clearly distinct densities, reflecting at least two different processes.

To assess the overall distortion of the cranium, a set of $N=18$ bilateral anatomical landmarks was identified, and lines were drawn that connect corresponding left and right landmarks. Figure S19 shows that the left side of the cranium appears to be skewed in postero-inferior direction relative to the well-preserved right side. Deviations from this global pattern indicate localized taphonomic deformation of the maxilla and the cranial base. The midplane of the cranium also exhibits local distortion.

This pattern of global skewing indicates that the cranium was compressed within the sandstone in which it was embedded. The specimen was found in situ, exposed by erosion of the overlying sediment. To more precisely determine how the deformations that altered its shape occurred, we digitally calculated a transverse vector, which indicates the average direction of all lines connecting bilateral landmark pairs. Similarly, we used the midpoints of these lines to evaluate the average orientation of the midsagittal plane. The angle between the normal vector of the midsagittal plane and the mean vector connecting bilateral landmark pairs is $\alpha=5.9^\circ$ (compared to $0^\circ$ in undistorted crania exhibiting no directional asymmetry). A line at a $45^\circ$ angle relative to the bisector of the midplane normal vector and the transverse vector is a parsimonious estimate of the direction of taphonomic compression (3).

Reorienting the cranium accordingly gives a digital impression of how it was embedded in the sediment, confirmed by photographs taken at the time of its removal from the sandstone deposit in which it was found. It lay obliquely on the right side, the face higher than the occipital region. Compression then led to the observed pattern of overall skewing. The more extensive fragmentation and bone loss on the left side is attributed to the fact that this was the part of the cranium that was first exposed by erosion, and damaged while partially exposed on the surface by herds of domestic ungulates moving across the outcrop twice daily between the adjacent Herto village corrals and the water and pasture of the Awash River to the east.

Two different taphonomic scenarios are conceivable to explain the combination of overall distortion and fragmentation in the cranium. According to
scenario 1, compression primarily led to plastic deformation, whereas fragmentation and dislocation of rigid fragments occurred. According to scenario 2, taphonomic compression led to fragmentation of the cranium, followed by dislocation of the fragments, without significant plastic deformation. Virtual reconstruction methods can reliably discriminate between these scenarios. Under scenario 1, fragment re-composition cannot fully correct the overall distortion, and the effects of plastic deformation need to be undone by appropriate "decompression" of the fossil along the inferred direction of compression. Under scenario 2, reassembly of the isolated fragments should result in minimal overall deformation because the major agent of distortion was the displacement of fragments relative to each other. The latter was indeed the case in BOU-VP-16/1, as predicted in its brief original 2003 presentation ("…vault distortion is limited to a slight movement of rigid plates." See ref. 6; p. 742).

The first step of the virtual restoration consisted in virtual disassembly of the major fragments constituting the cranium. Fragments were separated from each other along major fracture lines. In the maxillofacial region, the sediment was removed electronically with semi-automated thresholding procedures. The many small and isolated fragments recovered from this region cannot reliably be repositioned relative to each other, such that they were left at their original positions.

Inspection of the middle and anterior cranial base revealed an array of diagenetic alterations compatible with the taphonomic scenario proposed above (Fig. S20). In general, the left side of the cranial base was displaced toward the right side. The resulting damage is most obvious in the collapsed sphenoid bone and crushed cribroid region. The right lesser wing of the sphenoid was detached from the frontal bone along the frontosphenoidal suture and displaced laterally. The left lesser wing was displaced medially and became superimposed on the sella. A similar pattern of mediolateral compression can be observed in the temporal and occipital portions of the cranial base. The left pyramid was detached from the temporal squama and shifted medially. Likewise, the left margin of the foramen magnum underwent medial displacement.

Taphonomic distortion of the face is also mainly a result of mediolateral compression. The right maxilla is almost completely preserved, but its delicate anterior surface is broken into several small fragments, such that the frontal, zygomatic and alveolar processes are displaced from each other. Most notably, the left frontal process together with the two nasal bones is displaced laterally. Furthermore, the right maxillary zygomatic process together with the zygomatic bone and the supraorbital process of the frontal bone are displaced superiorly such that, overall, the right orbit assumes a compressed shape. The palatal region is well preserved overall, but partly collapsed, such that fragments from the left and right sides interlock.

The virtual restoration began with establishing bilateral symmetry of the well-preserved elements of the cranial base. The pyramid of the left temporal bone, which was broken off and displaced during fossilization, was repositioned and reattached to the remainder of the temporal bone. The occipital condyles and the adhering margins of the foramen magnum were rearranged relative to the basal occipital and temporal elements. The relative position of these elements is constrained by the topographical relationships between the hypoglossal canal, the jugular fossa, and the carotid canal.

Reconstruction of the face started with re-adjustment of the displaced right zygomatic bone at the zygomatico-frontal suture, and re-adjustment of the maxillary frontal process along the anatomical midplane. In the following step, anatomical
continuity along the lower orbital rim and along the zygomatico-maxillary suture could be established. The dental arcade exhibits substantial displacement of parts relative to each other along fractures, as well as distortion. A part comprising the left M2 and M3, plus parts of the palate could be realigned to the anterior dental arcade. Similarly, re-establishing continuity along and across the palate permitted correction of displacement of the maxillary fragments in a superoinferior direction. The remaining apparent anomaly mostly concerns the posterior dentition, which exhibits an unusual inward (lingual) tilt. Since the left and right sides were similarly affected, we surmise that most of this occlusal anomaly resulted from in-vivo processes of wear-related dentognathic remodeling. As already observed in ref. (6), the premolars and molars on both sides exhibit an unusual pattern of wear on the buccal side, which led to in-vivo exposure of the root dentine, and which might have resulted in lingual (inward) tilting of the posterior teeth.

The reconstructed face and cranial base build a convenient framework for the reconstruction of the cranial vault, which is constrained by the width and length of the base, and by the width and height of the face. The right side of the vault, which is generally well preserved, was re-assembled by eliminating matrix-filled cracks between adjacent fragments, and by adjusting anatomical connections between the base and face. The preserved fragments on the left side of the vault were superimposed on mirror images of corresponding areas on the right side. Mirror-matching between left and right sides showed a pattern of slight mismatch between corresponding parts, indicative of slight plastic taphonomic distortion within each of the fragments on the left side, and/or fluctuating asymmetry between left and right sides. The fragments of the left side were thus first placed according to the mirror-imaged reconstruction of the right vault, then adjusted relative to each other along their anatomical contacts, which resulted in mild asymmetry of the frontal vault region. It is important to note that the conspicuous “slanting” of the left cranial vault of the original fossil (best visible in occipital view of the original cranium; see Fig. S18) could be eliminated through reorientation of the digitally isolated fragments along fracture lines, and appropriate placement in anatomical space, without the need to apply “decompression” procedures to correct for plastic deformation.

The final restoration of the BOU-VP-16/1 cranium is visualized in Figure S21. It confirms several anatomical features that were reported on the original specimen (6). The most obvious feature is the shape of the cranial vault. Digital separation of vault fragments, cleaning of matrix-filled cracks and subsequent refitting of fragments resulted in a highly arched vault, with vertical parietal walls and a steeply sloping frontal squama. Realignment of facial fragments resulted in a wide and tall face with squarish orbits, a double-arched supraorbital torus, and a prominent supranasal region. Despite its large size, however, the face exhibits only weak prognathism such that a line connecting prosthion with glabella is almost vertical relative to the standard (Frankfurt) plane. The restored endocast is visualized in Figure S22. The endocranial volume of the reconstructed specimen is 1681 ccm, which is substantially larger than the volume estimate that was derived from teff seed filling of the mediolaterally compressed original specimen [1450 ccm; ref. (6)].

1.3.5 Comparative fossil and recent sample

The extant sample comprises crania of N=125 recent humans (Homo sapiens). Specimens were grouped according to their maxillary dental eruption stage (dm: deciduous molars dm1 and dm2 fully erupted; M1/M2/M3: permanent molars M1/M2/M3 fully erupted; see Table S1). Specimens are from the Collections of the
Department of Anthropology and Anthropological Museum of the University of Zurich, the Peabody Museum of Archaeology and Ethnology at Harvard University, the Natural History Museum London, and the Duckworth Collection at Cambridge University. The fossil sample consists of the specimens listed in Table S2.

Computed Tomography (CT) of all specimens was performed with medical CT devices, using beam collimations between 0.5 and 1.0 mm, and performing cross-sectional image reconstructions with voxel sizes between 0.2³ and 0.5³ mm³. For each cranium, the endocranial surface was digitally extracted from the CT data volume using the software packages Avizo and Geomagic Studio. Endocranial volumes (ECV) were evaluated from the surface data using the software Avizo.

Endocranial shape was quantified with K=921 three-dimensional anatomical landmarks (LMs), which are distributed equally over the entire surface of the endocast, and represent fixed point LMs (K_p=27), curve semilandmarks (SLMs) (K_c=110), and surface SLMs (K_s=784) (see Table S3). SLMs were allowed to slide along tangents to the curves, and the surface SLMs along tangents to the surface. Missing endocranial landmarks in the fossil specimens were estimated with the following procedure: for a given fossil, the subset of preserved landmarks was used to define a thin-plate spline (TPS) mapping functions from a given complete specimen to that fossil specimen. The missing landmarks of the fossil were then estimated by applying the TPS function to the full set of landmarks of the complete specimen. This procedure was performed for all N_c complete specimens, resulting in N_c estimates of the fossil's missing landmarks. The reconstructive variants resulting from this procedure are represented as density ellipses in Figure 2 of the main text.

As mentioned in section 1.3.2, using mirror symmetry as an aid for digital reconstruction precludes the analysis of natural patterns of fluctuating or directional asymmetry in reconstructed fossils. All specimens in the sample (fossils as well as recent humans) were thus symmetrized via relabeled reflection of landmarks.

Viscerocranial shape was quantified with 36 fixed landmarks (see Table S4).

For each landmark data set, Generalized Procrustes Analysis (GPA) was applied to minimize differences in scale, position and orientation between the specimens' landmark configurations. Between-group Principal Components Analysis (PCA) of shape was then applied to the Procrustes-aligned specimens to explore major patterns of shape variation in the sample (see main Figure 4). All procedures were performed with the R packages Geomorph (7) and Morpho (8).
2. RESULTS
The finalized digital restorations of the Herto child and adult crania and endocasts are visualized in Figures S16 and S17, and S21 and S22, respectively. Craniometric measurements of the Herto crania [following ref. (9)] are presented in Excel file “SI_cranioometrics.xlsx”. 3D coordinates of endocranial and viscerocranial landmark configurations of all fossil and recent specimens are provided in Excel files “SI_endocast_data.xlsx” and “SI_viscerocranium_data.xlsx” available from the following site: osf.io/w3gc7
Figure S1. Discovery of child’s cranium BOU-VP-16/5.

A. Asfaw points to fragments of cranial vault. View is to the north, Central Awash Complex in background.
B. Larger cranial vault pieces indicated by yellow arrows. Other surface lag comprises indurated sandstone fragments and artifacts. Wet sieving recovered smaller pieces.
C. Closeup of (A.).
Figure S2. Physical restoration of child’s cranium BOU-VP-16/5.
A. Recovered pieces.
B. Refitting.
C. Refitting.
D. Frontal view.
E. Three-quarter view.
Figure S3. Discovery of adult cranium BOU-VP-16/1.
A. D. DeGusta examines scatter of surface cranial vault fragments (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. S. Simpson brushes largest vault piece to reveal the right half of the cranium *in situ* in the unconsolidated sandstone.
D. Brushing reveals thin glabellar surface (blue arrow), lower frontal (squama orange arrow), and left mastoid process (yellow arrow) still *in situ*, with left parietal fragments detached and lying horizontally. Note the invasion of modern bunch grass roots into the sandstone.
Figure S4. Exposure and consolidation of adult cranium BOU-VP-16/1.

A. The profile of the in situ fossil is revealed by brushing.
B. The in situ cranium is pedestaled but the unconsolidated sandstone and invasive modern grass roots threaten to collapse the specimen.
C. From left to right S. Simpson, B. Latimer, C. Pehlevan and discoverer D. DeGusta slowly apply cryoacrylate preservative to the sides of the sandstone pedestal.
D. A syringe is used to drip the preservative Vinac onto the specimen. Note the grass roots that have invaded the fossil.
Figure S5. Plaster jacketing the Herto adult cranium BOU-VP-16/1.

A. Application of Vinac hardener.
B. The *in situ* cranium and cryoacrylate-hardened pedestal are jacketed with medical plaster bandages by S. Simpson and B. Latimer.
C. Application of water to the jacket to harden it prior to lifting.
Figure S6. Removal of jacket and surface sweep of recovery site of the Herto adult cranium BOU-VP-16/1.

A. Local Afar villager observes the hardening jacket. View is to the northeast, with the Awash River marked by the line of green trees at his shoulder level. The white resistant horizon at his left elbow level is a bentonitic volcanic ash underlying the Upper Herto member sediments that yielded the *H. sapiens* cranium.

B. Slowly lifting the plaster jacket with the in situ cranium intact, cemented by the artificially cryoacrylate re-indurated sandstone backed by the jacket.

C. Sweeping loose surface sediment to be dry sieved and carefully pan-picked in the background. The crater at right mid frame is where the cranium was removed. Additional archaeological excavation of this horizon did not yield additional human remains.
Figure S7. Initial laboratory excavation of the Herto adult cranium BOU-VP-16/1 from the base of the jacket in Fig. S6.
A. Indurated sandstone cemented to the right side of the cranium obscures most bone.
B. Application of Vinac hardening agent via injection by needle syringe near the sutural junction of the right occipital, temporal, and parietal. Yellow arrow points to the matrix-filled external auditory meatus of the right temporal in this posterolateral view.
C. Removal of sand and sandstone reveals the intact right side of the cranium.
D. Closer view of the right cranium. Note the invasive modern grass roots that have infiltrated cracks on the cranium.
Figure S8. Continued laboratory exposure of the Herto adult cranium BOU-VP-16/1.

A. Admassu holds the partially exposed cranium. This was underside of the cranium when it was recovered in situ. The jacket walls were gradually lowered to allow access for cleaning under the binocular microscope.

B. Application of hardener was required because of the fragility of the fossil bone. Millimeter-by-millimeter exposure followed by hardening was required to keep the fossil intact.

C. Foramen magnum and right dentition exposed. Note modern grass roots that had infiltrated the cranium below the erosional surface and required careful removal.

D. Application of hardener to the right dentition.
Figure S9. Completion of cleaning the right side of the Herto adult cranium BOU-VP-16/1.
A. The underside of the plaster jacket is revealed when the right side of the cranium has been exposed. The displaced left vault pieces in Fig. S4A are embedded in the original jacket.
B. Removal of the remaining walls of the original field jacket is accomplished by cutting the plaster, which remains in place to secure the cranial edges exposed by the erosional surface.
C. All that remains is fine cleaning on the right side (underside when *in situ*) of the cranium.
D. Jacketing the right side of the fossil to secure the pieces in their *in situ* positions.
E. Removal of the remainder of the original field jacket.
Figure S10. Cleaning the left side of the Herto adult cranium BOU-VP-16/1.

A. With the freshly exposed right half of the fossil secured in a new laster jacket, the cleaning of unconsolidated sand within the endocranial vault surface proceeds.

B. Modern grass roots have penetrated into the vault itself through cracks and foramina, and are seen here behind the right temporal petrous and the lesser wing of the right sphenoid.

C. 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.

D. The endocranial surface is cleaned and reveals minor displacements across a series of matrix-filled cracks.
Figure S11. Matrix and endocranial exposure on the left side of the Herto adult cranium BOU-VP-16/1.
A. Closeup of the fractured left face of the fossil. Cemented sandstone adhering to the surfaces was left in place to prevent further damage.
B. The frontal sinus walls are exposed by cleaning. These were fractured as this side of the cranium surfaced first. The displaced vault bone fragments have been removed to facilitate endocranial cleaning.
C. Anatomical displacements if the endocranial surface are visible in this view. The aluminum foil is in the foramen magnum, protecting the cleaned ectocranial surface from the secondary reinforcing jacket that now supports the entire cranium during endocranial cleaning.
D. A posterosuperior view of the endocranial surface shows anterior endocranial ramp of the basioccipital, the anterior terminations of the petrous pyramids, the sella, and the lesser wings of the sphenoid.
Figure S12. Initial estimates of the cranial capacity of the Herto child and adult crania.
A. The reinforced cranial vault of the child’s cranium is filled with teff seed to estimate its cranial capacity.
B. The adult cranium placed on its more intact right side while being filled to the midline with teff seed to estimate its cranial capacity.
C. The estimated cranial capacity estimate was 1450 cubic centimeters. Digital corrections the residual deformation after the physical restoration allowed more accurate endocranial estimates.
Figure S13. Residual distortion of the original Herto adult face.
A. Matrix partially removed during the cleaning process described above.
B. The fossil after cleaning. Note the fracture of the maxilla into fragments separated by matrix-filled cracks. This expanding matrix distortion slightly alters the surface of the specimen, and a larger crack with more distortion is visible at the zygofrontal suture on the left orbit’s superolateral corner.
Figure S14. Standard views of the Herto adult BOU-VP-16/1 cranium after physical restoration.
Figure S15. Herto child cranium BOU-VP-16/5. CT-based visualization of the physical restoration. Standard views, orthonormal projections. Scale bar is 5 cm.
Figure S16. Digital restoration of the Herto child cranium BOU-VP16/5. Standard views, orthonormal projections. Scale bar is 5 cm.
Figure S17. Digital restoration of the endocast of the Herto child cranium BOU-VP16/5. Standard views, orthonormal projections. Scale bar is 5 cm.
Figure S18. Herto adult cranium BOU-VP-16/1. CT-based visualization of the physical restoration. Standard views, orthonormal projections. Scale bar is 5 cm.
Figure S19. Overall pattern of taphonomic distortion of the BOU-VP-16/1 cranium. Transverse lines connect corresponding left and right anatomical landmarks. The dashed lines connect the midpoints of the transverse lines to illustrate midplane distortion. Scale bar is 5 cm.
Figure S20. Taphonomic distortion of the BOU-VP16/1 cranium (left), and undistorted comparative morphology of a modern human cranium (right). CT-based visualizations. Arrows indicate displacement of fragments (red: lesser wing of right sphenoid; green: lesser wing of left sphenoid; blue: left temporal pyramid; yellow: part of anterior cranial base). Scale bar is 5 cm.
Figure S21. Digital restoration of the adult Herto cranium BOU-VP16/1. Standard views, orthonormal projections. Scale bar is 5 cm.
Figure S22. Digital restoration of the endocast of the adult Herto cranium BOU-VP16/1. Standard views, orthonormal projections. Scale bar is 5 cm.
Figure S23. Linear endocranial dimensions. Endocranial length \( L \) (distance between left frontal and occipital poles; in fossil specimens on the better-preserved side); endocranial width \( W \) (greatest bilateral distance at the level of the temporal lobes); endocranial height \( H \) (greatest distance from basion to apex). A-C: bivariate plots of relative dimensions: 
\[ L_{\text{rel}} = L / (L + W + H) \]; 
\[ W_{\text{rel}} = W / (L + W + H) \]; 
\[ H_{\text{rel}} = H / (L + W + H) \]. D: bivariate plot of principal components bgPC1 and bgPC2 of a between-group principal components analysis (bgPCA) of \( L_{\text{rel}} \), \( W_{\text{rel}} \), \( H_{\text{rel}} \). Colors and symbols as in Fig. 4 (main text).
| group               | dental age class | dm | M1 | M2 | M3 | N total |
|--------------------|------------------|----|----|----|----|---------|
| *H. erectus*       |                  | 1  | 1  | 1  | 21 | 24      |
| mid-Pleistocene    |                  | 0  | 0  | 0  | 3  | 3       |
| *H. neanderthalensis* |                | 2  | 5  | 1  | 6  | 14      |
| fossil *H. sapiens* |                  | 1  | 2  | 1  | 5  | 9       |
| recent *H. sapiens*|                  | 18 | 8  | 9  | 90 | 125     |
| group                      | specimen             | dental age class |
|----------------------------|----------------------|------------------|
| *H. erectus*               |                      |                  |
| Mojokerto                 | dm                   |                  |
| KNM-WT15000               | M1                   |                  |
| D2700                     |                     |                  |
| Bukuran                   |                     |                  |
| D2280                     | M3                   |                  |
| D2282                     | M3                   |                  |
| D3444                     | M3                   |                  |
| D4500                     | M3                   |                  |
| Daka                      |                     |                  |
| ER1470                    | M3                   |                  |
| ER1805                    | M3                   |                  |
| ER1813                    | M3                   |                  |
| ER3733                    | M3                   |                  |
| ER3883                    | M3                   |                  |
| OH9                       | M3                   |                  |
| Sambungmacan 3            | M3                   |                  |
| Sangiran 17               | M3                   |                  |
| Solo 1                    | M3                   |                  |
| Solo 5                    | M3                   |                  |
| Solo 6                    | M3                   |                  |
| Solo 9                    | M3                   |                  |
| Solo 10                   | M3                   |                  |
| Solo 11                   | M3                   |                  |
| ZKD 12                    | M3                   |                  |
| Mid-Pleistocene           |                      |                  |
| Kabwe                     | M3                   |                  |
| Petralona                 | M3                   |                  |
| Steinheim                 | M3                   |                  |
| *H. neanderthalensis*     |                      |                  |
| Dederiyeh 2               | dm                   |                  |
| Pech de l’Azé             | dm                   |                  |
| Engis 2                   | M1                   |                  |
| Gibraltar 2               | M1                   |                  |
| Roc de Marsal             | M1                   |                  |
| Subalyuk 2                | M1                   |                  |
| Teshik Tash               | M1                   |                  |
| Le Moustier 1             | M2                   |                  |
| Amud 1                    | M3                   |                  |
| Gibraltar 1               | M3                   |                  |
| Guattari 1                | M3                   |                  |
| Spy 1                     | M3                   |                  |
| Spy 2                     | M3                   |                  |
| Tabun 1                   | M3                   |                  |
| fossil *H. sapiens*       |                      |                  |
| Skhul 1                   | dm                   |                  |
| Herto BOU-VP-16/5         | M1                   |                  |
| Qafzeh 11                 | M1                   |                  |
| Oase 2                    | M2                   |                  |
| Herto BOU-VP-16/1         | M3                   |                  |
| Hofmeyr                   | M3                   |                  |
| Mladec 1                  | M3                   |                  |
| Qafzeh 9                  | M3                   |                  |
| Skhul 5                   | M3                   |                  |
Table S3. Endocranial landmarks

| landmark description                                                                 | landmark type | nr. per set   |
|-------------------------------------------------------------------------------------|---------------|---------------|
| Ethmoidal spine (LM 1)                                                               | fixed LM      | 1             |
| Foramen caecum (LM 2)                                                                | fixed LM      | 1             |
| Junction of both transverse sinuses (LM 3)                                          | fixed LM      | 1             |
| Opisthion (LM 4)                                                                    | fixed LM      | 1             |
| Basion (LM 5)                                                                       | fixed LM      | 1             |
| Sella turcica (LM 6)                                                                 | fixed LM      | 1             |
| Midsagittal posterior point of jugum sphenoidale (LM 7)                             | fixed LM      | 1             |
| Anterior clinoid process (LM 8-9)                                                    | fixed LM      | 2 x 1         |
| Postero-lateral point of the anterior cranial fossa (LM 10-11)                     | fixed LM      | 2 x 1         |
| Canalis opticus (LM 12-13)                                                          | fixed LM      | 2 x 1         |
| Foramen rotundum (LM 14-15)                                                         | fixed LM      | 2 x 1         |
| Foramen ovale (LM 16-17)                                                            | fixed LM      | 2 x 1         |
| Petrous apex (LM 18-19)                                                              | fixed LM      | 2 x 1         |
| Meatus acusticus internus (LM 20-21)                                                | fixed LM      | 2 x 1         |
| Junction of transverse sinus and petrous pyramid (LM 22-23)                         | fixed LM      | 2 x 1         |
| Canalis nervi hypoglossi (LM 24-25)                                                 | fixed LM      | 2 x 1         |
| Foramen jugulare (LM 26-27)                                                         | fixed LM      | 2 x 1         |
| Midsagittal cerebrum (between LM 2 and LM 3)                                        | curve SLM     | 31            |
| Midsagittal cerebellum (between LM 3 and LM 4)                                      | curve SLM     | 7             |
| Midsagittal brainstem (between LM 5 and LM 6)                                       | curve SLM     | 7             |
| Jugum sphenoidale (between LM 7 and LM 1)                                           | curve SLM     | 3             |
| Foramen magnum (between LM 4 and LM 5)                                              | curve SLM     | 2 x 7         |
| Posterior border of anterior cranial fossa (between LM 8-9 and LM 10-11)            | curve SLM     | 2 x 3         |
| Petrous pyramid (between LM 18-19 and LM 22-23)                                     | curve SLM     | 2 x 7         |
| Superior border of transverse sinus (between LM 3 and LM 22-23)                     | curve SLM     | 2 x 7         |
| Antero-lateral border of the frontal lobe (between LM 2 and LM 10-11)               | curve SLM     | 2 x 7         |
| Endocranial vault surface                                                            | surface SLM   | 2 x 392       |
| nr. | landmark            |
|-----|--------------------|
| 1   | nasion             |
| 2   | glabella           |
| 3   | opisthion          |
| 4   | basion             |
| 5   | sphenobasion       |
| 6   | staphylion         |
| 7   | prosthion          |
| 8   | nasospinale        |
| 9, 10 | maxillofrontale (R,L) |
| 11, 12 | foramen supraorbitale |
| 13, 14 | orbitale          |
| 15, 16 | frontomalare orbitale |
| 17, 18 | zygomaaxillare    |
| 19, 20 | jugale            |
| 21, 22 | foramen maxillare |
| 23, 24 | midpoint of dm2 or PM2 crown |
| 25, 26 | foramen stylomastoideum |
| 27, 28 | foramen caroticum |
| 29, 30 | foramen ovale     |
| 31, 32 | porion            |
| 33, 34 | midpoint of C crown |
| 35, 36 | pterygo-maxillare |
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