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Virtual Reconstruction of the Neanderthal Amud 1 Cranium

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Abstract

Here we describe a new computer reconstruction to obtain complete anatomical information of the ecto- and endocranium from the deteriorated skull of the Neanderthal Amud 1. Data were obtained from computed tomography scans of the fossil cranium. Adhesive and plaster were then virtually removed from the original specimen, and the fragments comprising the fossil cranium were separated. These fragments were then mathematically reassembled based on the smoothness of the joints. Both sides of the cranium were reassembled separately, and then aligned based on bilateral symmetry and the distance between the mandibular fossae obtained from the associated mandible. The position of the isolated maxilla was determined based on the position of the mandible that was anatomically articulated to the mandibular fossae. To restore missing basicranial and damaged endocranial regions, the cranium of Gibraltar 1 was warped onto that of La Chapelle-aux-Saints 1, and the resulting composite Neanderthal cranium was then warped onto the reconstructed Amud 1 by an iterative thin-plate spline deformation. Comparison of the computer reconstruction with the original indicated that the newly reconstructed Amud 1 cranium was slightly shorter and wider in the anteroposterior and mediolateral directions, respectively, suggesting that it was relatively more brachycephalic. The endocranial volume was estimated to be 1736 $cm^3$, which was quite similar to the original estimated value of 1740 $cm^3$. This new computer reconstruction enables not only measurement of new cranial metrics, but also inclusion of the Amud 1 specimen in three-dimensional geometric morphometric analyses that were previously difficult due to its incompleteness.

## Introduction

In 1961, the skull of Neanderthal Amud 1, dated 50,000–70,000 years old (Valladas et al., 1999; Rink et al., 2001), was excavated from the Amud Cave site on the northwestern coast of Lake Tiberias in Israel by the University of Tokyo Scientific Expedition to Western Asia (Suzuki and Takai, 1970). This find is currently considered important fossil evidence for clarifying the evolution and diversification of Neanderthals and archaic modern humans in Western Asia. The Amud 1 cranium is also regarded as one of the most famous specimens of the Neanderthal skull due to its cranial capacity (Holloway et al., 2004), which is estimated at 1740 $cm^3$ based on water displacement of the endocranial cast (Ogawa et al., 1970), making it the largest ever recorded among hominids.

The skull had initially been compressed bilaterally during fossilization, and the right side of the cranium was considerably damaged. After immersing the skull in acetic acid solution for cleaning, the cranium broke into small fragments due to fracturing that had been covered by a thick calcareous incrustation and were thus effectively unobservable. In contrast, the mandible was better preserved with less fragmentation. Hisashi Suzuki, the team leader who had discovered the fossil, then manually reassembled and reconstructed the cranium using a bonding adhesive and plaster filler. Due to its apparent morphological similarity to Amud 1, Shanidar 1 was used as a reference (Suzuki, 1970).

With ongoing advances in computer-assisted morphological techniques, computer reconstruction is more frequently being used for reconstruction of cranial fossils (e.g., Zollikofer and Ponce de Leon, 2005; Gunz et al., 2009; Weber and Bookstein, 2011; Ogihara et al., 2015). Virtual reconstruction is particularly useful for correcting possible anatomical inconsistencies in cases in which physical reconstruction has already been accomplished manually using adhesive and plaster, such as Amud 1. The validity of virtual reconstruction is widely recognized, and has recently been performed for the crania of the Le Moustier 1 Neanderthals (Ponce de Leon and Zollikofer, 1999), the OH 5 *Paranthropus* (Benazzi et al, 2011), and the KNM-ER 1813 *Homo habilis* (Benazzi et al., 2014). Virtual reconstruction usually involves a series of assumptions, including bilateral symmetry and smooth assembly, as well as anatomical constraints such as occlusion and articulation. It often employs the thin-plate spline (TPS) function to reconstruct missing regions and correct possible distortions (see Gunz et al., 2009 for review).

In this study, we attempted to reconstruct the Amud 1 Neanderthal cranium using computer techniques. First, we virtually removed the adhesive and plaster from the original specimen and separated the fragments of the fossil cranium. We then mathematically reassembled the fragments based on joint smoothness. The crania of Gibraltar 1 and La Chapelle-aux-Saints 1 were then warped onto the new reconstruction using an iterative TPS deformation to restore the complete ecto- and endocranial morphology of the Amud 1 cranium.

## Methods

### Virtual reassembly

Data for the virtual reconstruction were obtained from computed tomography (CT) scans of the manually reconstructed Amud 1 cranium. The scan data were acquired with a helical CT scanner at the Elscint CT factory in Haifa, Isreal. Tube voltage, tube current, and slice thickness were set to 120 kV, 200 mA, and 1 mm, respectively. Cross-sectional images were reconstructed at 1 mm intervals, with a pixel size of 0.375 mm. The serial images were then transferred to commercial software for further data processing. After virtually removing the adhesive and plaster from the skull, we isolated and disassembled the original fragments. We then applied manual segmentation procedures based on thresholding and region growing techniques using Avizo 6.1 software (FEI Visualization Sciences Group, Burlington, MA, USA). Next, we used Analyze 9.0 software (Biomedical Imaging Resource, Mayo Clinic, Rochester, MN, USA) to generate three-dimensional (3D) surface models of the isolated fragments as triangular mesh models based on the marching cube method. 3D digital models of Amud 1 as originally reconstructed by Suzuki both with and without plaster are shown in Figures 1A and 1B, respectively. As can be clearly seen in Figure 1B, the cranium was composed of fragmentary pieces, and substantial portions of the facial and basicranial regions were missing.

To reassemble the isolated fragments, we applied a newly proposed computerized assembly method based on surface extrapolation (Kikuchi and Ogihara, 2013). Briefly, we used a parametric Bézier surface to extrapolate the surface of each neurocranial fragment and mathematically predict the shapes of neighboring fragments. The positions and orientations of the fragments were then calculated individually by minimizing the fitting errors and employing a smoothness penalty function so that the fragments could be reassembled smoothly and continuously (Figure 2A). This calculation method is described in detail by Kikuchi and Ogihara (2013). Fractured objects are typically assembled based on the geometric similarities of the fracture surfaces (e.g., Papaioannou et al., 2002; Huang et al, 2006). However, in the present study, many of the fracture surfaces of the Amud 1 cranial fragments were thin and eroded; therefore, we decided that surface extrapolation would be the best method for assembly.

For reconstruction, the entire cranium was divided into eight portions (Figure 2B), and fragments within each portion were reassembled in numerical sequence. Then, the six portions of the left hemicranium were reintegrated mathematically in the same manner based on surface extrapolation. The two right portions of the hemicranium were aligned by referring to the left, as their mirror-image models were confirmed to be generally congruent to those on the left, suggesting that post-mortem plastic deformation of the cranium was negligible.

The left and right hemicrania were aligned based on bilateral symmetry, the distance between the mandibular fossae, and the smoothness of the juncture. Specifically, about 20 bilateral pairs of corresponding points were obtained by superimposing the left and right hemicrania. To ensure bilateral symmetry, each vector connecting the hemicrania should be perpendicular to the midsagittal plane of the cranium (Ogihara et al., 2006). Moreover, according to the associated mandible, the distance between the mandibular fossae was calculated to be 146 mm (measured on a research-quality cast, as CT scan data of the mandible was not available). Therefore, to minimize the smoothness of the junction between the two hemicrania, we calculated both the position and orientation of the right with respect to the left hemicranium (Kikuchi and Ogihara, 2013) while satisfying the above two geometrical constraints (Figure 2C). Further details on this calculation are provided in the Appendix.

We determined the position of the maxilla with respect to the neurocranium based on the mandible articulated with the reassembled neurocranium (Figure 2D). First, we placed the maxilla on the mandible in a natural occlusal position. The mandibular condyles were then articulated with the cranium at the mandibular fossae. The orientation of the mandible in the sagittal plane was determined based on the observation that the sagittal angle between the Frankfurt plane and the plane defined by the maxillary alveolar process was approximately 10° in the well-preserved maxillofacial regions of the Gibraltar 1 and La Chapelle-aux-Saints 1 crania. The reassembled Amud 1 cranium, noticeably lacking most of the face, cranial base, and endocranial surface, is shown in Figure 3.

Interpolation

To estimate the complete ecto- and endocranial morphology of the Amud 1 cranium, two Neanderthal crania were warped onto the newly reconstructed cranium using TPS deformation. Specifically, we obtained CT scan data and generated 3D surface models of Gibraltar 1 and La Chapelle-aux-Saints 1 crania as described previously (Figure 4). The Gibraltar 1 endocast preserved the basal region including the frontal lobe, but except for the occipital bone, most of the left side was missing. In contrast, although some portions of the basal region including the frontal lobe were missing, the La Chapelle-aux-Saints 1 endocast was almost complete.

To define a TPS deformation function from one Neanderthal cranium to the other, a set of landmark coordinates that can be homologously digitized on both crania must be acquired. Therefore, we defined 62 anatomical landmarks on the external surface of human cranium (Table 1). In addition, we approximated the superior nuchal curve between the inion (#3) and the intersection of the superior nuchal line and occipitomastoid suture (#11), the temporal curve between the frontomalare temporale (#8) and stephanion (#9), and the supraorbital curve between the glabella (#2) and frontomalare temporale (#8) using a seventh-order Bézier curve (Morita et al, 2013). We then defined 14 additional equally-spaced points along the curves, resulting in a total of 76 landmarks.

Next, we introduced sliding semi-landmarks (Bookstein, 1997; Gunz et al., 2005, 2009; Perez et al., 2006) onto the ovoid ectocranial surface. We defined semi-landmarks based on the shortest paths between pairs of anatomical landmarks (Morita et al, 2013) on one modern human specimen (Japanese male, KUMA-2591, housed at Kyoto University) chosen as a template. Specifically, we used the above non-sliding landmarks, as well as the 14 equally-spaced points along the midsagittal curve between the nasion (#1) and inion (#3), to calculate the shortest paths. We obtained a total of 71 equally-spaced points along the paths that we subsequently designated as sliding semi-landmarks (Figure 5). Therefore, including the 14 equally-spaced midsagittal points, we introduced a total of 85 ectocranial sliding semi-landmarks.

Similarly, we defined 30 anatomical landmarks (Table 2) on the endocranial surface and 22 equally spaced points along four curves on each side as follows: (1) the curve along the anteroinferior border of the anterior cranial fossa between the foramen caecum (#1) and the most lateral point of the posterior border of the lesser wing of the sphenoid (#6); (2) the curve along the lower border of the sulcus sinus transversi between the internal occipital proturberance (#2) and the intersection of the lower border of the sulcus sinus sigmoidei and transversi (#9); (3) the curve along the posterior border of the lesser wing of the sphenoid between the tip of the processus clinoideus anterior (#5) and the most lateral point of the posterior border of the lesser wing of the sphenoid (#6); and (4) the curve along the crista pyramidis between the petrosal apex (#7) and the intersection of the crista pyramidis and the upper edge of the sulcus sinus transversi (#8) (Figure 5; Table 2). These 52 non-sliding landmarks, in combination with the 14 equally-spaced points along the midsagittal curve between the foramen caecum (#1) and the internal occipital protuberance (#2), were used to define sliding semi-landmarks based on the calculation of shortest paths, resulting in a total of 119 equally-spaced points that were subsequently defined as sliding semi-landmarks. Accompanied by the 14 midsagittal points that we also designated as sliding semi-landmarks, the total number of endocranial sliding semi-landmarks was 133.

The sliding landmarks from the template configuration were transferred to a target cranium using the TPS function, and then projected and slid along the cranial surface of the target specimen to minimize the bending energy. Templand in the EVAN Toolbox (www.evan-society.org) was used to calculate the positions of all the sliding landmarks in this study.

The Gibraltar 1 cranium was warped onto the La Chapelle-aux-Saints 1 cranium using the TPS function to interpolate the missing portions. To compensate for any deficiencies, this composite Neanderthal cranium was then warped onto the reassembled Amud 1 cranium. The numbers of non-sliding and sliding semi-landmarks acquired on the ecto- and endocranial surfaces of the Neanderthal crania are provided in Table 3. In the present study, a total of 161 and 185 landmarks were defined on the intact human ecto- and endocranial surfaces, respectively, for interpolation. Due to the deficiencies, many of the above-mentioned landmarks were unable to be defined on the three Neanderthal crania; however, we were able to define two successive TPS deformations by using common existing landmarks on the ecto- and endocranial surfaces. While increasing the number of arbitrarily defined landmarks on the surfaces, this warping process was iterated several times to merge the craniums. Due to the ill-preserved state of the Amud 1 cranium, no landmarks were defined on the endocranial surface (Table 3). Therefore, the composite Neanderthal cranium was warped onto the Amud 1 based solely on the ectocranial landmarks, while the endocranial landmarks of the composite Neanderthal were mapped onto the endocranial surface.

Finally, to obtain a smooth, continuous reconstruction of the complete ectocranial surface of the Amud 1, two modern Japanese crania (KUMA-554 and KUMA-720, housed at Kyoto University) were warped onto the Amud 1 using the TPS deformation, and the reconstruction of the Amud 1 cranium was complete.

## Results

The 3D reconstruction of the external surface of the Amud 1 cranium is shown in Figure 6. In general, it was found to be quite similar to the original manually reconstructed cranium, with the most noticeable difference being the position of the maxilla. In the 3D reconstruction, the maxilla was more superiorly positioned, the occipital region was less protruded, and the parietal region was more laterally expansive, indicating that it was slightly shorter, wider, and lower than the original reconstruction in the anteroposterior, mediolateral, and superoinferior directions, respectively.

A comparison between the maximum cranial length (MCL), maximum cranial breadth (MCB), and auriculo-bregmatic height (ABH) of the newly reconstructed cranium and those of the original reconstruction and other Neanderthal crania, the anthropometric measurements of which were taken from the literature, is shown in Table 4. Corresponding cranial indices were also presented for comparison (Index 1 = MCB / MCL (cranial index); Index 2 = ABH / MCL; Index 3 = ABH / MCB). The comparisons are also presented in Figure 7 as plots of the MCL vs. MCB and ABH. The newly reconstructed Amud 1 cranium was 11 mm shorter and 4 mm wider in the anteroposterior and mediolateral directions, respectively, indicating that it was relatively more brachycephalic than the original (Index 1). No difference in height was apparent between the reconstructions; therefore, Index 2 and Index 3 were larger and smaller, respectively, in the new reconstruction. Due to the extraordinarily long MCL, the plots of the original reconstruction did not closely follow those of other Neanderthals, but the plots of the new reconstruction were quite similar (Figure 7).

Figure 8 displays the reconstructed endocast of the Amud 1 cranium. As shown in Figure 8, the complete Amud 1 endocast was generated mainly based on interpolation of the missing basicranial region by warping the composite Neanderthal cranium. The endocranial capacity of the newly reconstructed cranium was estimated as 1736 $cm^3$, which was very close to the original estimated value of 1740 $cm^3$.

## Discussion

The present study reported a new 3D reconstruction of the Amud 1 cranium using virtual anthropology-based computer techniques. The complete geometry of the restored ecto- and endocranium was also presented. Although the newly reconstructed Amud 1 cranium was slightly shorter and wider than the original, they were both quite similar. The maximum length of the new reconstruction was shorter than the original, which, at 215 mm in length, was longer than large Neanderthal crania such as La Ferrassie 1 and La Chapelle-aux-Saints 1. In addition, in the new reconstruction, the maxilla was positioned more superiorly. The estimated endocranial volume was 1736 cm$^3$, which was surprisingly similar to that of the original.

The original Amud 1 cranium was manually reconstructed largely based on the knowledge and experience of a skilled anthropologist and state-of-the-art reconstruction techniques (Suzuki, 1970). However, using adhesive to assemble cranial fragments like a jigsaw puzzle in a gravitational environment is difficult and requires substantial amounts of time and patience. The severe degradation of the Amud 1 cranial fragments added to the difficulty of this manual assembly, which could only be completed by referring to the cranium of Shanidar 1 (Suzuki, 1970). Furthermore, even if only minimal errors are made in the placement of each fragment, these errors accumulate during sequential assembly, leading to a significant variation at both endpoints. Therefore, reproducible results are unlikely in manual reconstructions, and could be susceptible to subjective considerations. Therefore, to realize a more objective and reproducible reconstruction of the cranium, we employed computerized assembly of cranial fragments based on tangent continuity (smoothness). The predictive accuracy of this computerized assembly method is reportedly $0.3 \pm 0.3$ mm for the human cranium, which is a level of accuracy similar to that of manual assembly in a virtual environment (Kikuchi and Ogihara, 2013). In addition, it should be noted that computerized assembly is not prone to subjectivity. It is also possible to document the assembly of each cranial fragment in order to evaluate and ensure the reproducibility of the reconstruction results.

The Amud 1 cranium was noticeably lacking most of the face, cranial base, and endocranial surface; therefore, we tried to compensate for these missing portions by using geometric interpolation using the TPS function (Gunz et al, 2009). However, it is difficult to assess the accuracy of TPS interpolation because it depends on not only the size and location of the missing region, but also the specimen used for interpolation and the number and distribution of landmarks used to define the warping function. Furthermore, TPS interpolation is generally known to result in comparatively large errors in estimating the shapes of missing portions over large areas (Neeser et al. 2009). To evaluate the accuracy of the present interpolation based on the same landmark configurations, we also created virtual human crania with missing portions estimated using TPS interpolation (Amano et al, 2014). We found that the accuracy was within about 1 and 3 mm for the small and large missing regions, respectively, in the neurocranium (Amano et al, 2014). However, it must be noted that the prediction errors in the basicranium ($\approx$ 4 mm) were reportedly worse, possibly due to the fact that its shape correlates less closely with the other parts of the cranium (Bruner and Ripani, 2008), but this region was largely missing in the Amud 1 cranium. Consequently, the reliability of the restored basicranial region may be comparatively low. Although our restoration represents the best estimation of the missing basicranial region currently possible, a more powerful statistical method should be investigated in future studies to ensure or improve upon its accuracy.

Our virtual reconstruction of the complete geometry of the ecto- and endocranium of the Amud 1 enabled the measurement of new cranial metrics, which was not previously possible due to the poorly preserved state of the specimen. For example, this specimen can now be included in principal component analysis of Neanderthal endocranial metric variables (Bruner et al., 2003) to investigate allometric changes in endocranial shape. Furthermore, this important specimen can also be included in 3D geometric morphometric analyses (Adams et al., 2004; Mitteroecker and Gunz, 2009) for a more detailed investigation of ecto- and endocranial morphology. The new reconstruction also provides a more detailed estimation of endocranial volume. Although it may require further verification, the present computer reconstruction of the Amud 1 cranium is expected to contribute to morphological analyses of ecto- and endocranial shape, thereby allowing a better understanding of the evolution and diversification of Neanderthals and early modern humans (e.g., Bruner et al, 2003, 2014; Gunz et al., 2010, 2012; Ogihara et al., 2015).

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Appendix

${}^{L}\mathbf{p}_i$ and ${}^{R}\mathbf{p}_i$ are the 3D coordinates of the left and right bilateral pair of $i$th landmarks, respectively, and superscripts $L$ and $R$ refer to the left and right hemicranium coordinate frames, respectively. In order for the left and right hemicrania to be bilaterally symmetrical and the distance between the mandibular fossae to be equal to the given distance between the mandibular condyles, the following geometrical conditions must be satisfied:

$$\sum_{i=2}^{N} ({}^{L}\mathbf{v}_1 \cdot {}^{L}\mathbf{v}_i)^2 = 0 \qquad (1)$$

$$\left| {}^{L}\mathbf{v}_{MF} \right| - d = 0 \qquad (2)$$

where ${}^{L}\mathbf{v}_i$ is the vector connecting the $i$th bilateral pair of landmarks represented in left hemicranial coordinate frame, $\left| {}^{L}\mathbf{v}_{MF} \right|$ is the distance of the vector connecting the mandibular fossae, and $d$ is the distance between the mandibular condyles obtained from the associated mandible. ${}^{L}\mathbf{v}_i$ which can be calculated as follows:

$${}^{L}\mathbf{v}_i = {}^{L}\mathbf{p}_i - \{\mathbf{R}(\theta_x, \theta_y, \theta_z) \cdot {}^{R}\overline{\mathbf{p}}_i + {}^{L}\mathbf{t}\} \qquad (3)$$

where $\mathbf{R}(\theta_x, \theta_y, \theta_z)$ is a rotation matrix representing the orientation of $L$ with respect to the $R$ coordinate system, and ${}^{L}\mathbf{t}$ is a translation vector connecting the origins of the $L$ and $R$ coordinate systems. Equation (1) represents the condition that the vectors connecting the paired landmarks are parallel, which is necessary for the paired landmarks to be bilaterally symmetrical. Equation (2) represents the condition that the distance between the mandibular fossae should be equal to the corresponding distance measured on the associated mandible (Fig. 2C). The mandible is seemingly undeformed, but the right mandibular condyle is partially missing. Therefore, the left condyle was mirrored and superimposed to the right for the correct distance measurement.

The six degrees of freedom of the right hemicranium were determined with respect to the left ($\theta_x$, $\theta_y$, $\theta_z$, ${}^{L}\mathbf{t}$) in order to minimize the smoothness of the junction between the left and right hemicrania, $E$, in Kikuchi and Ogihara (2013), while satisfying the above constraint equations (1, 2). For this, the following optimization problem was solved using a quasi-Newton method.

$$E + \gamma \sum_{i=2}^{N} ({}^{L}\mathbf{v}_1 \bullet {}^{L}\mathbf{v}_i)^2 + \delta(\left| {}^{L}\mathbf{v}_{MF} \right| - d)^2 \rightarrow \min \qquad (4)$$

where $\gamma$, $\delta$ are the weighting coefficients.

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Figure captions

Figure 1. Digital models of Amud 1 as originally reconstructed by Suzuki (1970) with (A) and without (B) plaster. The cranium is composed of numerous fragmentary pieces, and substantial portions of the facial and basicranial regions are missing.

Figure 2. Reassembly procedure. (A) The cranial fragments were assembled based on surface extrapolation. The surface of each neurocranial fragment was approximated using a bicubic Bézier surface to extrapolate the surface and mathematically predict the shape of adjacent fragments. The positions and orientations of adjacent fragments were calculated by minimizing the fitting errors. (B) The entire cranium was then divided into eight portions (a-h), and fragments within each portion were reassembled in a numerical sequence. All eight portions were reassembled in the same manner to obtain the left and right hemicrania. (C) The left and right hemicrania were aligned based on bilateral symmetry, the distance between the mandibular fossae, and the smoothness of the juncture. (D) The position of the maxilla with respect to the neurocranium was determined based on the mandible articulated with the neurocranium.

Figure 3. Reassembled Amud 1 cranium. (A) Ectocranial surface. (B) Endocranial surface. Note that the facial and basicranial regions of the cranium are largely missing.

Figure 4. Interpolation procedure. The cranium of Gibraltar 1 was warped onto that of La Chapelle-aux-Saints 1, and the composite Neanderthal cranium was then warped onto Amud 1 by iterative thin-plate spline deformation.

Figure 5. Landmarks used in the present study. (A) Ectocranial surface. (B) Endocranial surface.

Figure 6. Reconstructed ectocranial surface of the Amud 1 cranium. (A) Original reconstruction. (B) Reassembled cranium. (C) Interpolated cranium based on a modern Japanese cranium (KUMA-554).

Figure 7. Scatter plots of cranial measurements in Neanderthals. Blue circle = original Amud 1. Red square = newly reconstructed Amud 1. Triangles = other Neanderthals listed in Table 3.

Figure 8. Reconstructed endocranial surface of the Amud 1 cranium. (A) Endocast of the original reconstruction. (B) Endocast of the new reconstruction. (C) Interpolated endocranial surface based on the composite Neanderthal.

Table 1. Ectocranial landmarks used in the present study

| Number | Landmark | Type |
|---|---|---|
| 1 | nasion | m |
| 2 | glabella | m |
| 3 | inion | m |
| 4 | opisthion | m |
| 5 | maxillonasofrontale | b |
| 6 | uppermost point on the orbital margin | b |
| 7 | frontomalare-orbitale | b |
| 8 | frontomalare-temporale | b |
| 9 | stephanion | b |
| 10 | asterion | b |
| 11 | intersection of nuchal line and occipitomastoid suture | b |
| 12 | mastoidale | b |
| 13 | posterior end of the margin of temporal fossa | b |
| 14 | porion | b |
| 15 | rhinion | m |
| 16 | akathion | m |
| 17 | prosthion | m |
| 18 | alveolon | m |
| 19 | sphenobasion | m |
| 20 | basion | m |
| 21 | alare | b |
| 22 | zygoorbitale | b |
| 23 | orbitale | b |
| 24 | zygomaxillare | b |
| 25 | ektomolare | b |
| 26 | jugale | b |
| 27 | most inferior point of the temporozygomatic suture | b |
| 28 | most anterior point of the posteior margin of the palate | b |
| 29 | most lateral point of the margin of the foramen magnum | b |
| 30 | infratemporale | b |
| 31 | stenion | b |
| 32 | midpoint of the labial margin of the canine alveolar foramen | b |
| 33 | midpoint of the labial margin of the 2nd premolar alveolar foramen | b |
| 34 | most medial point of the margin of the lacerated foramen | b |
| 35 | most medial point of the margin of the carotid canal | b |
| 36 | posterior root of the styloid process | b |
| 37-39 | equally spaced points along the nuchal line | b |
| 40-41 | equally spaced points along the temporal line | b |
| 42-43 | equally spaced points along the supraorbiral line | b |

Note: m = midsagittal landmark; b = bilateral landmark

Table 2. Endocranial landmarks used in the present study

| Number | Landmark | Type |
|---|---|---|
| 1 | foramen caecum | m |
| 2 | internal occipital protuberance | m |
| 3 | opisthion | m |
| 4 | basion | m |
| 5 | end of processus clinoideus anterior | b |
| 6 | most lateral point of posterior border of lesser wing of sphenoid | b |
| 7 | petrosal apex | b |
| 8 | intersection of crista pyramidis and the upper edge of sulcus sinus transv | b |
| 9 | intersection of lower border of sulcus sinus sigmoidei and transversi | b |
| 10 | most lateral point of the margin of the foramen magnum | b |
| 11 | posterior end of crista galli | m |
| 12 | posterior sphenoid | m |
| 13 | pitutary | m |
| 14 | dorsum sellae | m |
| 15 | antero-lateral border of cribriform plate | b |
| 16 | most posterior point of cribriform plate | b |
| 17 | most anterior point of foramen ovale | b |
| 18 | most anterior point of foramen spinosum | b |
| 19 | most medial point of the margin of canalis condylaris | b |
| 20-23 | equally spaced points along the anteroinferior border of anterior cranial f | b |
| 24-26 | equally spaced points along the lower border of sulcus sinus transversi | b |
| 27-28 | equally spaced points along the posterior border of lesser wing of spheno | b |
| 29-30 | equally spaced points along the crista pyramidis | b |

Note: m = midsagittal landmark; b = bilateral landmark

Table 3. Number of landmarks acquired on the ecto- and endocranial surfaces of the Neanderthal crania

| | Ectocranial surface | | Endocranial surface | |
|---|---|---|---|---|
| | Non-sliding landmark | Sliding semi- | Non-sliding landmark | Sliding semi- |
| Intact cranium | 76 | 85 | 52 | 133 |
| Amud1 | 33 | 51 | 0 | 0 |
| La Chapelle-aux-Saints1 | 64 | 58 | 20 | 95 |
| Gibraltar1 | 54 | 32 | 27 | 46 |

Table 4. Comparison of linear measurements and indices of Neanderthal crania

| Fossil name | Linear measurement | | | Index | | | Reference |
|---|---|---|---|---|---|---|---|
| | Max. Length | Max. breadth | Height | Index 1 | Index 2 | Index 3 | |
| Amud 1 (new) | 204 | 158 | 120 | 0.77 | 0.59 | 0.76 | |
| Amud 1 (original) | 215 | 154 | 121 | 0.72 | 0.56 | 0.79 | Suzuki 1970 |
| Gibraltar 1 | 193 | 149 | 107 | 0.77 | 0.55 | 0.72 | Weidenreich, 1943 |
| Saccopastore 1 | 181 | 142 | 101 | 0.78 | 0.56 | 0.71 | Condemi, 1992 |
| Circeo 1 | 204 | 155 | 111 | 0.76 | 0.54 | 0.72 | Sergi, 1974 |
| La Chappelle-aux-Saints 1 | 208 | 156 | 111 | 0.75 | 0.53 | 0.71 | Boule, 1913 |
| La Ferrassie 1 | 208 | 158 | 114 | 0.76 | 0.55 | 0.72 | Heim, 1976 |
| Le Moustier | 196 | 150 | 111 | 0.77 | 0.57 | 0.74 | Weinert, 1925 |
| Shanidar 1 | 207 | 154 | | 0.74 | | | Trinkaus, 1983 |
| Tabun 1 | 183 | 141 | 98 | 0.77 | 0.54 | 0.70 | McCown & Keith, 1939 |
| Spy 1 | 200 | 144 | 111 | 0.72 | 0.55 | 0.77 | Vandermeersch, 1981 |
| Spy 2 | 200 | 153 | 114 | 0.77 | 0.57 | 0.74 | Vandermeersch, 1981 |
| Neanderthal 1 | 199 | 147 | | 0.74 | | | Vandermeersch, 1981 |