Computerized Paleoanthropology and Neanderthals: The Case of Le Moustier 1

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Using the Le Moustier 1 specimen as a test case, this study establishes a framework for computer-assisted "fossil differential diagnosis." It demonstrates how computer tools can be applied to differentiate between various causes that contributed to the present state of a fossil, with the ultimate goal of inferring its morphology at the time of death and of assessing skeletal modifications that occurred during life and after death.

At the time of its discovery almost one century ago, the Le Moustier 1 specimen was one of the best-preserved Neanderthal skeletons.[1] In the course of its complicated history, the fossil suffered considerable damage. Most of the postcranial remains perished in flames, while the cranial remains temporarily disappeared.[2–4] In its current state, the fossil constitutes a peculiar admixture of various reconstructions aimed at the correction of taphonomic distortion and completion of missing parts. In spite of the general loss, degradation, and alteration of the original material, Le Moustier 1 still occupies a key position in the interpretation of Neanderthal ontogeny, since it is the only fairly complete adolescent individual of this taxon. It is therefore a primary challenge to recover as much information as possible from the preserved fragments, notably to infer the specimen's original morphology as well as its taphonomic history.

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Today, computer-assisted paleoanthropology (CAP) offers the opportunity to perform these tasks in a noninvasive and comprehensive manner.[5] Using the Le Moustier 1 specimen as a test case, this study establishes a framework for computer-assisted "fossil differential diagnosis." It demonstrates how computer tools can be applied to differentiate between various causes that contributed to the present state of a fossil, with the ultimate goal of inferring its morphology at the time of death and of assessing skeletal modifications that occurred during life and after death.

The basic principle of fossil differential diagnosis resides in inverting the temporal order in which modifications of fossil morphology have occurred. This procedure cannot be expected to yield an unequivocal result. It merely provides a means to establish a sequence of consecutive causes and effects that explains the observed patterns of modification in the most parsimonious manner. The procedure starts with the identification of *post-recovery* modifications of the original material. These modifications can be corrected through a new reconstruction of the fossil material. In the subsequent step, potential *postmortem* modifications are analyzed, notably deformation of the specimen due to diagenetic events. Geometric models are devised to explain the observed distortions and to correct them by the application of reverse deformation. At this stage, the morphology of the specimen at the time of death can be tentatively characterized. Skeletal modifications that persist after exclusion of *postmortem* causes most likely reflect the effects of *in vivo* causes. These may be of unspecific, pathological, or traumatic nature, and their discrimination requires extensive comparative studies, using modern skeletal material as well as clinical evidence.

VIRTUAL RECONSTRUCTION

In the course of at least four consecutive previous reconstructions of the Le Moustier specimen, various filling materials were used to complete missing regions.[6] Following the acquisition of CT data, semiautomated image segmentation algorithms as well as an electronic chisel were used to isolate the approximately 100 craniomandibular fragments from the CT data volume (Fig. 1). These fragments provided the basis for the subsequent virtual reconstruction of the craniomandibular anatomy. During the process of reassembly, the anatomical information contained in the original fragments was used exclusively, and reference to supposed "typical" Neanderthal morphologies was avoided.

The reconstruction started with the reestablishment of dental occlusion.

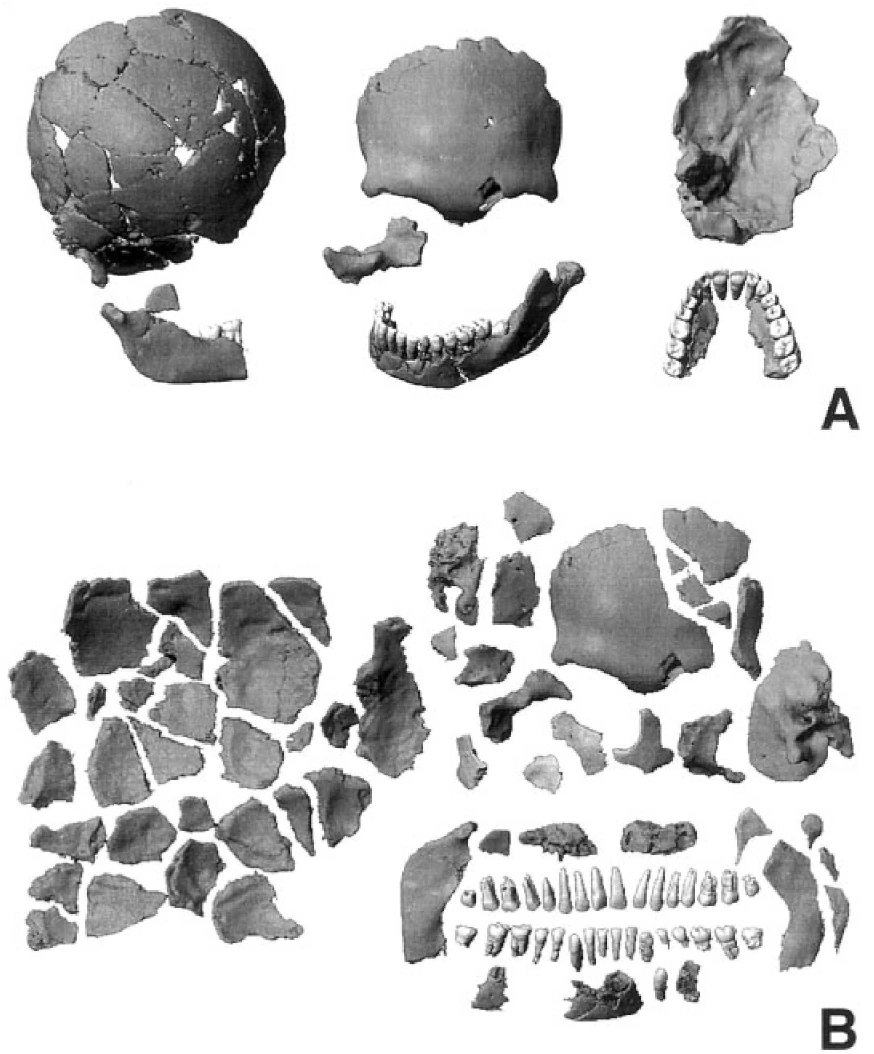

Figure 1. Virtual disassembly of Le Moustier 1 specimen. **A:** In its current state, specimen consists of seven isolated pieces, each of which is composed of smaller fragments. **B:** Virtual decomposition yields approximately 100 fragments. These form the basis for subsequent reconstruction.

Using three-dimensional (3D) object representations derived from high-resolution CT data, it was possible to identify patterns of dental wear and to match the upper and lower dentition accordingly. In the following step, the bony fragments of the maxilla and the mandible were accommodated. These procedures yielded a virtually symmetric morphology of the jaws, and demonstrated that the asymmetry present in the current physical reconstruction is an artifact.

Subsequently, distortions in the cranial base were corrected. Due to the fragmentary preservation of external anatomical points of reference on the temporal pyramids, internal clues were used to orient these bones in anatomical space. The cavities of the inner ear were isolated and used as an anatomical compass according to the following criteria: in a generalized hominid skull, the posterior and superior semicircular canals assume an angle of 45° relative to the midsagittal plane, whereas the lateral semicircular canal is approximately at a right angle relative to this plane.[7] Following the orientation of the temporal bones, it was possible to accommodate the isolated basioccipital fragment into the space between the temporal pyramids (Fig. 2). This fragment was positioned by reestablishing the correspondence between the floor of the jugular fossa (preserved on its rear part) and the roof of this structure (preserved on the temporal bone). As a result, the basioccipital fragment had to be shifted anteriorly, leading to a more anterior position of the foramen magnum.

The currently reconstructed braincase of the Le Moustier 1 specimen exhibits considerable asymmetry, most probably as a consequence of a "reconstructive error propagation" originating from the distorted cranial base. During the virtual reconstruction of the vault bones, these effects could be corrected by reestablishing anatomical contacts between isolated fragments and exploiting symmetry relations between fragments preserved on both sides of the skull.

ASSESSMENT AND CORRECTION OF TAPHONOMIC DEFORMATION

Although a large part of the distortion present in the current physical reconstruction of the specimen could be corrected with computer-assisted procedures, the virtual reconstruction of the specimen exhibited residual deformation that required further consideration. A comparison of the positions of bilaterally symmetric anatomical landmarks showed that most landmarks on the left side were in an anterior-superior position relative to their counterparts on the right side. The most parsimonious scenario that accounts for global skewing of the cranial geometry is postmortem taphonomic deformation resulting from a compression of the strata in which the fossil was embedded (Fig. 3). Interestingly, the skull and the mandible reacted in different ways to compressive forces. The mandible was fractured and the fragments were dislocated but not distorted, so that it was possible to restore symmetry during its virtual reconstruction. The skull, on the other hand, initially underwent plastic deformation, while fractures occurred during a later stage of fossilization. To correct the effects of plastic deformation of the skull, various taphonomic scenarios were simulated

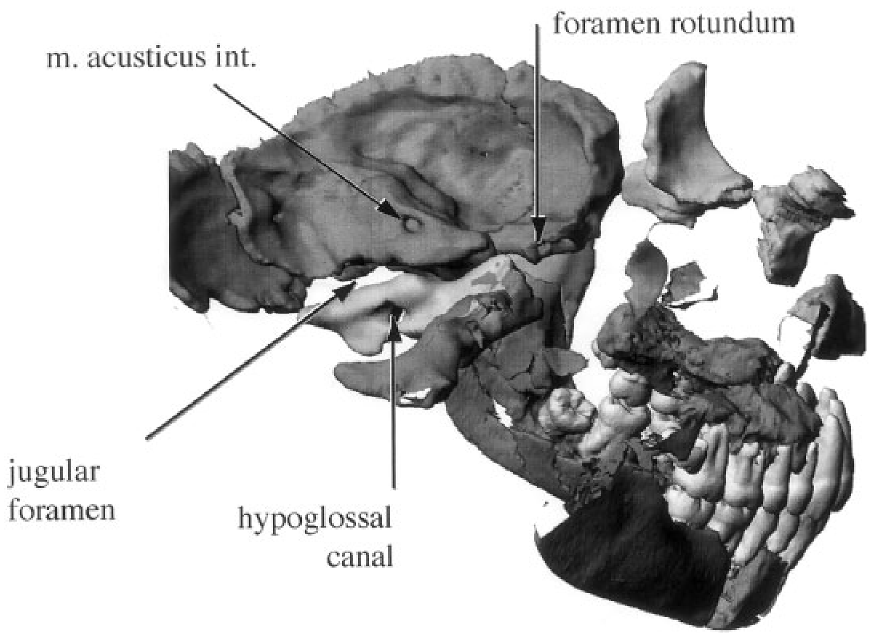

Figure 2. Virtual reconstruction of cranial base. Mirror image (light grey) of right basioccipital fragment was adjusted to preserved left temporal pyramid. This permitted reestablishment of anatomy of jugular fossa and of correct topological relationships between foramina of cranial base.

on the computer screen. These models showed that the result of compression critically depends on the in situ position of the fossil. Consequently, distortion can only be corrected properly if this position can be inferred with fair precision. In the case of Le Moustier, historical photographs taken at the site show that the skull was found with its left occipital pole in highest and its right frontal in lowest position.[8] The virtual reconstruction was oriented on the computer screen according to this condition (Fig. 3), and the distortion was corrected by extending the skull in vertical direction until the slanted geometry was rendered symmetric with respect to its midsagittal plane. This virtual correction showed that the skull suffered a compression of approximately 2.5%.

ANALYSIS OF IN VIVO DEFORMATIONS

Following the correction of taphonomic distortion, some residual deformation could still be observed at the left occipital pole. This region is less rounded than its counterpart on the right side. Applying the differential diagnostic scheme established above, two causes have to be considered: localized taphonomic compression or in vivo modification of the cranial vault. Close inspection of the internal and external morphology of this region hints at a mild form of in vivo plagiocephaly. As shown in Figure 4, there exists a marked disparity in the positions of the external midsagittal landmark lambda and the internal position of the sagittal sinus. The latter is displaced towards the right side, corresponding to the situation observed in plagiocephalic modern skulls, in which the brain and the associated venous sinuses are displaced from the less voluminous toward the more voluminous occipital pole. This condition is common in modern human skulls and cannot be considered to represent a pathology.[9]

Asymmetry between the left and right mandibular rami and glenoid processes has received attention since the first description of the Le Moustier specimen, and was interpreted as resulting from a mandibular ramus fracture.[1,10] While the discordant heights of the left and right rami as well as the asymmetry of the mandibular corpus could be equalized during virtual reconstruction, the left glenoid process turned out to be deformed and smaller than its right counterpart. Its degraded state of preservation makes it difficult to assess potential in vivo modification due to a degenerative process, but a comparison of the left condylar neck with its mirror-imaged counterpart shows bone remodelling in this area that is indicative of a healing process following a fracture. According to clinical data from modern humans, fracture of the condylar neck is relatively common as a consequence of blunt trauma or a fall.[11] In spite of its severity, this type of injury does not entail malocclusion, since dislocation of the fractured glenoid process is impeded by the strong liga-

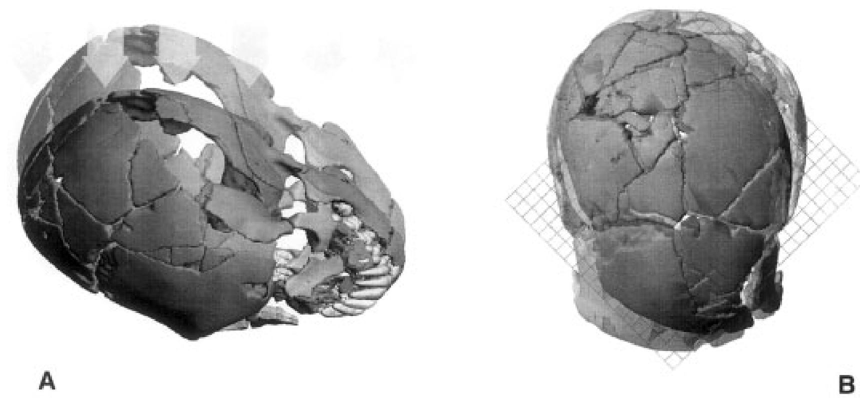

Figure 3. Modelling taphonomic deformation on computer screen. **A:** Specimen is shown in inferred in situ position, before and after application of compressive deformation. To clarify effects of distortion, actual amount of compression (−2.5%) was enhanced by a factor of 10. **B:** Resulting skewed geometry of specimen is most conspicuous in vertical view (grid indicates plane of view of A).

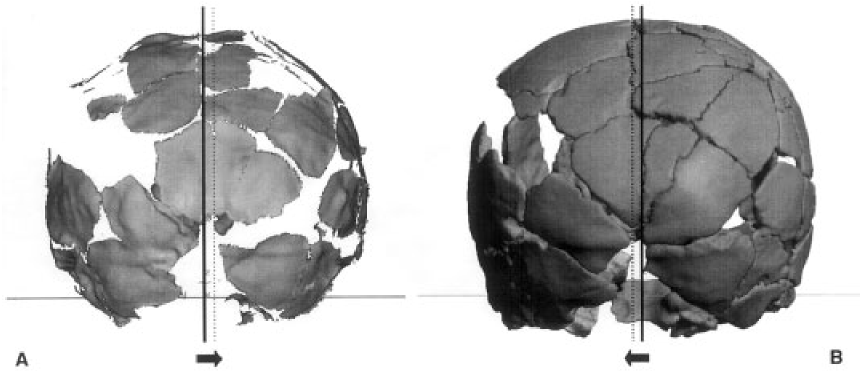

Figure 4. Assessing plagiocephaly in occipital region. Comparison of endocranial and exocranial midsagittal regions shows that impression of sagittal sinus is shifted to right (**A**), while external anatomical landmark lambda is shifted to left (**B**) of anatomical midplane (bold line). This indicates displacement of endocranial tissue to right side, as an effect of reduced skeletal volume on left side.

Figure 5. Virtual reconstruction of Le Moustier 1 cranium (left lateral view). Right cranial side had been removed to show articulated dentition, fragmentary cranial endocast, cavities of right inner ear, and developing frontal sinus.

ments of the articular capsule. However, fracture of the condylar neck is often accompanied by contusion of the anterior wall of the external acoustic meatus, a condition that entails extensive bone remodelling in the glenoid region as a whole. In the Le Moustier specimen, the conspicuous asymmetry between the left and right external acoustic meati suggests an involvement of this area in the traumatic event.

The left deciduous canine of the mandible was retained in position, while the fully developed permanent canine did not erupt. Although the root of the milk canine was partially resorbed, this tooth was still functional. Milk tooth retention is fairly common in modern populations. Typically, the small size of the retained milk tooth does not cause asymmetries in the dental arcade, because occlusional locking between upper and lower premolars and molars prevents positional shifts.

The finalized reconstruction of the Le Moustier 1 cranium (Fig. 5) represents an attempt to infer the original morphology of this fossil specimen by carrying out a set of reproducible actions in virtual reality and following predefined criteria. The proposed framework for a fossil differential diagnosis permits the assessment and consecutive elimination of postmortem distortions and the reestablishment of the in vivo morphology, using a maximum of intrinsic and a minimum of extrinsic information. The virtual reconstruction of this adolescent Neanderthal cranium and the interpretation of its in vivo state represent just a first step toward a more profound understanding of Neanderthal developmental morphology.

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