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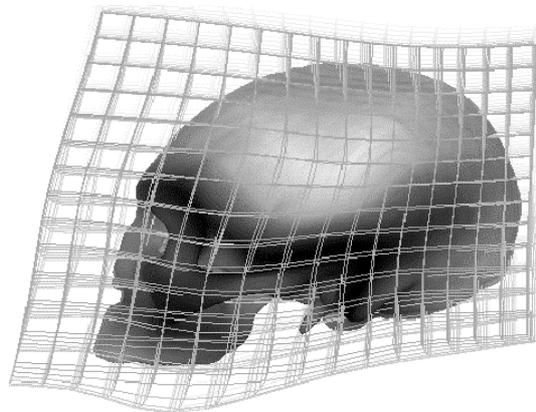
Three-Dimensional Imaging in Paleoanthropology and Prehistoric Archaeology

Edited by

Bertrand Mafart
Hervé Delingette

With the collaboration of

Gérard Subsol



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VIRTUAL PALEOANTHROPOLOGY: THE 4TH DIMENSION

Christoph P. E. ZOLLIKOFER & Marcia S. PONCE DE LEÓN

Résumé: La paléanthropologie utilise des outils informatiques pour l'acquisition tridimensionnelle de données numériques, la reconstitution virtuelle de fossiles fragmentaires et la morphométrie assistée par ordinateur. Néanmoins, il faut considérer qu'au cours de la formation de fossiles la dimension temporelle est aussi importante que les trois dimensions spatiales. Le facteur temps, la «quatrième dimension», intervient dans trois composantes différentes mais interdépendantes en paléanthropologie: l'ontogenèse (le développement individuel), la phylogenèse (la spéciation) et la diagenèse (la fossilisation). – Nous proposons des méthodes morphométriques assistées par ordinateur qui permettent d'analyser les effets du temps sur la morphologie des fossiles selon ces trois échelles.

Abstract: In paleoanthropology, computer-based technologies are used as tools for 3-dimensional data acquisition, virtual fossil reconstruction and virtual morphometry. Nevertheless, one must take account of the fact that during the formation of fossils the temporal dimension is equally important as the spatial dimensions. Time – the fourth dimension – has three distinct yet interconnected aspects in paleoanthropology, namely ontogeny, phylogeny and diagenesis. – We propose computer-based models of geometric morphometric analysis that deal with the effects of time on fossil morphology at these three levels.

INTRODUCTION

One of the major difficulties that arises during the analysis of fossil hominid morphologies is the scarcity and incompleteness of the fossil remains. Their reconstruction as well as their morphometric analysis are typically considered to represent essentially 3-dimensional tasks, in which «static» organismic structures are compared with each other and with extant samples. In this paper we investigate the role of time as the fourth dimension of virtual fossil reconstruction and morphometry. In evolutionary biology – especially in paleontology – we may discriminate between three different but interconnected aspects of temporal processes that affect the morphology of an organism: ontogeny, phylogeny and diagenesis. Accordingly, it is sensible to discriminate between ontogenetic, phylogenetic and diagenetic time scales, along which fossils must be analyzed. Morphogenesis accumulates form change over ontogenetic time, i.e. an individual's development and, in a wider sense, its entire lifetime. This process is constrained by the genome, which itself accumulates and integrates ontogenetic changes over phylogenetic time scales. While the morphology of an extant organism represents the result of processes on phylogenetic and ontogenetic time scales, diagenesis as a post-mortem process represents an additional phase of morphological modification. It is evident that the loss of information during this latter process is dramatic, both in terms of the number of available specimens and – within specimens – in terms of morphology and anatomy.

From this perspective, fossils can be characterized as organisms encountered at some (3-dimensional) point in diagenetic, phylogenetic and ontogenetic time. Accordingly, their reconstruction represents the task of resetting the diagenetic clock to zero, and their comparative morphometric analysis corresponds to the task of inferring their position along the ontogenetic and phylogenetic time scales. In

practice, this endeavor is complex, since the three time scales are intertwined along one single physical dimension of time and none of them can be observed directly in fossils. Here, we report on concepts and methods for the analysis of fossil morphologies in 4 dimensions and the disentanglement of the three time scales.

RESETTING THE DIAGENETIC CLOCK: COMPUTER-ASSISTED FOSSIL RECONSTRUCTION

Over the past few years, we developed a suite of computer-assisted methods, which permit the acquisition of volume data from fossil hominids, their electronic preparation on a computer screen, the recombination of isolated fragments in virtual reality, the morphometric analysis of virtual fossils and their computer-guided physical replication. Computer-assisted paleoanthropology (CAP) combines techniques of computer tomography (CT), computer graphics and rapid prototyping (stereolithography), which permit a completely non-invasive approach to the study of fossils (Zollikofer *et al.*, 1995; Seidler *et al.*, 1997; Spoor & Zonneveld, 1997; Conroy *et al.*, 1998; Zollikofer *et al.*, 1998).

How can the diagenetic clock be reset with these methods? The principal aim of this task is to recover the original state of the specimen's skeletal structure at the time of its death. To do so, specimens must first be freed from matrix, then restored through the re-fitting of scattered and isolated fragments and finally brought into their original shape through the correction of diagenetic deformation. The former two steps are essentially spatial tasks; they exploit topological relationships between various anatomical structures preserved in the isolated fossil fragments and rely on the general bilateral symmetry of the vertebrate skeleton (Zollikofer *et al.*, 1998;

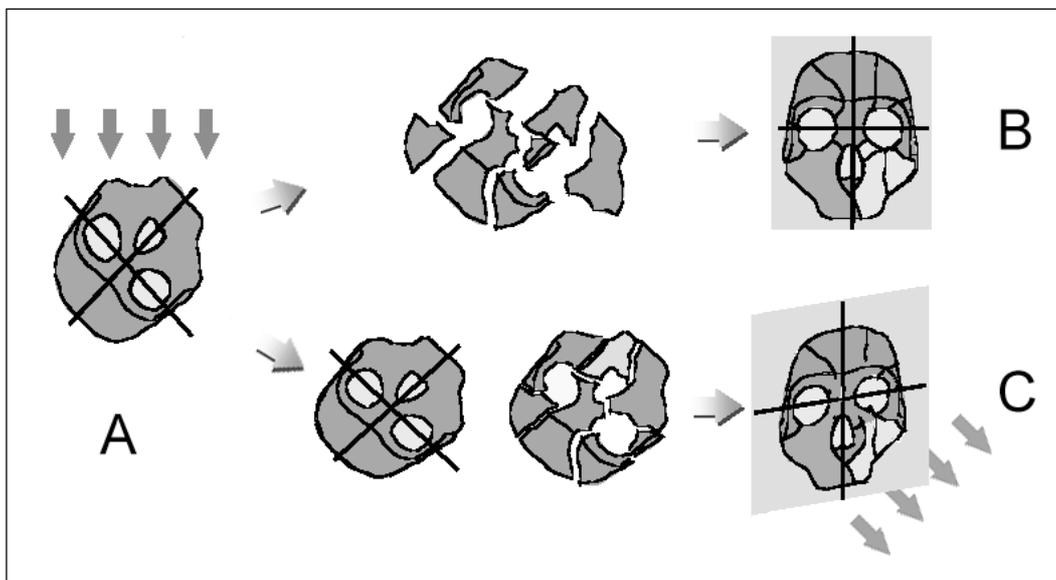


Figure 1 - Taphonomic deformation and its virtual correction. Loading exerted by overlaying strata (A, arrows) may result in fracturing (B) or plastic deformation (C) of fossilizing bone. In (B) the reassembly of the dislocated fragments results in only little residual deformation. In (C), residual deformation in the recomposed fossil manifests itself by systematic deviation from bilateral symmetry, which can be corrected by reversal of the deformation along the principal direction of compression (arrows).

Ponce de León & Zollikofer, 1999), such that missing parts on one side of the morphology can tentatively be completed with mirror-images of preserved counterparts. To correct taphonomic deformation, both ontogenetic and diagenetic time scales must be considered, as the deformation observed in a fossil may represent the combined effects of *in-vivo* and *post-mortem* processes. First and foremost, therefore, any potential deviation from standard anatomical conditions must be checked against normal anatomical variation and potential cultural modification, and assessed using paleopathological criteria. Once ontogenetic (*in-vivo*) effects have been identified, the residual deformation can tentatively be attributed to diagenetic (*post-mortem*) processes.

The original *in-situ* position and orientation of the fossil fragments relative to each other and relative to the embedding strata as well as the geometry of the deformed fossil convey important information about the spatial and temporal nature of these processes. From a biomechanical perspective, bone embedded in sediments can yield to loading by overlaying sediments in two different, but not mutually exclusive, ways (Fig. 1): (a) it may behave as a rigid material and fracture along lines of maximum strain, while the resulting fragments are dislocated relative to each other; (b) it may behave as a ductile material and undergo plastic deformation, with relatively little dislocation of neighboring anatomical structures. As was shown in a theoretical model (Ponce de León & Zollikofer, 1999), under scenario (a), the recovered morphology remains relatively undisturbed with respect to bilateral symmetry, while under scenario (b), the fossil exhibits substantial deviation from symmetry. Accordingly, the effects of fracturing deformation (a) are typically already corrected during fossil reconstruction, while plastic deformation (b) manifests itself most conspicuously by left/right discordance, which can be assessed and measured in virtual reality by

superposition of parts from one side with their mirror-imaged counterparts. Based on this information the temporal sequence of diagenetic events that led to the observed *post-mortem* modifications can be inferred, and deformation can be corrected as follows: As the outcome of plastic deformation depends on the direction of gravitational forces relative to the anatomy (Fig. 1), the virtual specimen must be positioned «*in situ*» on the computer screen. Subsequently, the taphonomic forces are simulated in reverse spatial and temporal order to recover the original morphology. It is evident that these procedures remain tentative, as the disentanglement of ontogenetic from diagenetic modifications may be incomplete, and as the complex succession of diagenetic events cannot be fully resolved in every instance.

VISUALIZING FORM CHANGE DURING ONTOGENY AND PHYLOGENY

In traditional paleoanthropology, the form of specimens is characterized by a suite of linear and angular measurements taken between anatomical points of reference, which are chosen to represent locations of biological homology. Accordingly, form change and/or difference is studied with multivariate analysis applied to arrays of such measurements. Linear and angular data are readily gathered «by hand» (once access to fossil specimens is granted), but a major disadvantage of their analysis arises from the fact that the original geometric interrelations between the *positions* of the landmarks in space are only partially represented. Over the past few years, geometric morphometric methods (GMM) have opened up new ways in which variation of organismic form can be measured and treated statistically (Rohlf & Marcus, 1993). These methods use configurations of

anatomical landmarks to characterize the form of specimens. Evaluating the 2- or 3-dimensional position of landmarks is technically more demanding than the measurement of interlandmark distances and typically involves digitizing devices or – in a CAP environment – interactive measuring tools permitting 3-dimensional data sampling from virtual fossil specimens.

Landmark configurations simultaneously represent locations of biological *and* geometric homology, such that the real-space geometric properties of the biological structures under investigation can be fully integrated into the subsequent multivariate analyses. The mathematical equivalent of the biological homology relation can be established in various ways. A first possibility consists in the exhaustive analysis of all between-landmark distances in a configuration (Euclidean Distance Matrix Analysis, EDMA; Lele, 1993; Richtsmeier & Lele, 1993). The second possibility is to superimpose the specimen's landmark configurations according to an optimum criterion (e.g. Procrustes superimposition by minimizing the sum of squared distances from an average configuration; Rohlf & Slice, 1990). This procedure eliminates differences in position, orientation and scaling (size) between the configurations and establishes a «linearized Procrustes shape space» (Rohlf & Slice, 1990), in which the shape of each specimen is given by its linear deviation (landmark coordinate by landmark coordinate) from the average configuration, the so-called consensus). These linearized «Procrustes residuals» can then be analyzed with classical methods of multivariate analysis, e.g. using principal components analysis (PCA) to reduce the dimensionality of the analysis and to capture major trends of shape change in the sample. The third possibility – which may be combined with the second – is especially appealing for the visualization of shape change and shape difference. It uses Thin Plate Spline interpolants (TPS), which act as spatially pervasive non-linear deformation functions between landmark configurations (Bookstein, 1991). PCA can be performed on the TPS coefficients characterizing each specimen's deviation from a consensus configuration, such that major trends of shape change in the sample can directly be expressed and visualized as deformation functions applied to the consensus (Bookstein, 1991). To visualize complex patterns of shape change and/or difference between specimens, D'Arcy W. Thompson introduced the ingenious concept of deformation grids, which provide an immediate visual grasp of the transformation of one into another morphology (Thompson, 1948). The TPS functions introduced by Bookstein (1991) provide an elegant mathematical formulation and extension of the graphical concepts of Thompson.

GMM are well-suited to study shape variation in fossil morphologies, notably of the cranium, since the skull is a rigid structure, whose surface displays a large number of landmarks representing locations of homology. Notably TPS analysis and visualization is being used extensively to study cranial shape change in various vertebrate species (Zelditch *et al.*, 1992; Loy *et al.*, 1993; Lynch *et al.*, 1996; Yarooh, 1996; O'Higgins & Jones, 1998; Rao & Suryawanshi, 1998; O'Higgins, 2000). Most studies, however, confine themselves to the analysis of 2-dimensional data sets – typically

projections of landmark coordinates onto the midsagittal plane or data from one side of the skull. In fact, during the visualization of patterns of shape variability in 3 dimensions, the utility of Thompson-style deformation grids is limited for several reasons. The first is a practical one. 3D cuboid grids or 2D square grids positioned in space (and projected onto paper) tend to be unintelligible, since our visual attention is directed towards undesired boundary effects at the edges of the grid (Dryden & Mardia, 1998; O'Higgins & Jones, 1998). The second reason is a biological one: Deformation grids introduce an external system of geometric reference which is not directly related to the original biological structure. This makes it difficult to interpret geometric «deformation» in terms of potential biological mechanisms of shape variation, both in time and space.

A possible solution to this problem consists in taking account of the fact that the original landmarks used for the geometric morphometric analyses are typically derived from surface structures (Zollikofer & Ponce de León, *in press*). During visualization, it is therefore sensible to make explicit reference to the surfaces of the specimens rather than to an arbitrary Cartesian coordinate grid. To do so, it is necessary to re-express the TPS transformation functions resulting from geometric morphometric analysis as deformations of a specimen's object surface. In engineering terms, a TPS function can be imagined as a displacement field: for every point in space, an individual vector of displacement defines the local amount and direction of shape change. Accordingly, for the visualization of the specimen's shape change, we only consider displacement vectors at object surfaces. With this procedure, the original problem of visualizing volume deformation is reduced to the visualization of 2-dimensional surface deformation in 3D space. However, 3D surface vectors of shape change depicted on paper (i.e. 2D) are still difficult to grasp visually. It is therefore sensible to decompose the displacement vectors into two components, one vertical and one parallel to the local surface orientation, respectively (Fig. 2). This permits the visualization of patterns of shape change in directions normal and tangential to the object surface. While the normal component of shape change can be visualized using color- or gray-scale coding, the tangential component can be rendered as a vector field spread out over the cranial surface (see Fig. 4).

The biological motivation of this procedure is as follows: Organs typically grow through cell divisions *at tissue surfaces*. Accordingly, skeletal structures grow through apposition/resorption of extracellular matrix perpendicular to the bone surface. During development of complex 3-dimensional structures such as the vertebrate skull, anatomical subregions grow by surface-bounded expansion or drift, and/or by passive displacement relative to neighboring structures (Moss & Young, 1960; Enlow, 1990). The independent visualization of the normal and tangential components of shape change thus provides a tentative visual grasp of how much and in which direction anatomical subregions expand, drift and/or are displaced relative to each other.

How does this method of visualization impinge on the geometric morphometric analysis of *temporal* changes in

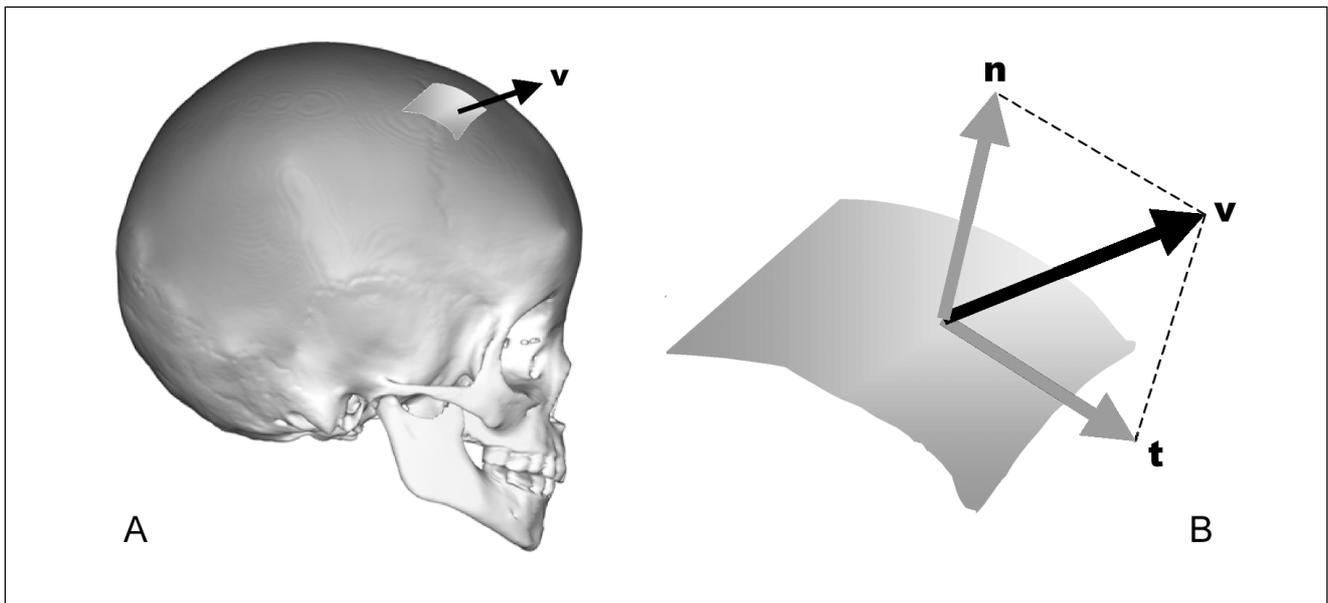


Figure 2 - Decomposition of a 3-dimensional displacement vector relative to the surface of a cranium. **A:** a small cranial surface patch and its associated displacement vector v . **B:** Decomposition of v into its normal (n) and tangential (t) components.

fossil morphologies? Any *patterns* of shape change (e.g. along an ontogenetic trajectory) or shape difference (e.g. between specimens belonging to different species) revealed with GMM ultimately reflect different stages or different types of ontogenetic *processes*. The proposed method of visualization greatly facilitates the interpretation of the observed patterns in terms of underlying processes. As one example, we consider here the comparative geometric morphometric analysis of growth and development in Neanderthals and modern humans (Ponce de León & Zollikofer, 2001). Using methods of CAP, an ontogenetic series of Neanderthal crania comprising specimens from dental age 2 through to adulthood was reconstructed, and a similar ontogenetic series of anatomically modern humans (both fossil and extant) was used for comparison. The form of each skull in the pooled Neanderthal/modern human sample was characterized by the 3D coordinates of 63 landmarks. Generalized least-squares superposition was used to evaluate the centroid size (Bookstein 1991) and linearized Procrustes shape (Rohlf & Slice, 1990) of each specimen. Relative Warp (RW) analysis (Rohlf, 1993) was used to capture major trends of shape variation in the sample. As a result, shape variation related to dental age, centroid size and taxon was concentrated in the first two relative warps (RW1 and RW2, Fig. 3), which account for 60.6% of the total shape variation in the sample. The Neanderthal and modern human subsamples are separated from each other along RW2 (10.1% of the total shape variation), while the specimens in each subsample are ordered along RW1 according to their age (50.5% of the total shape variation). One salient feature of this analysis is that within-species shape variation (i.e. along ontogenetic trajectories) is considerably larger than shape variation between species (i.e. across ontogenetic trajectories). Nevertheless, the characteristic difference in shape between Neanderthals and modern humans is already established around the age of 2

years and remains unchanged during further development, as evinced by the fully separated, parallel postnatal ontogenetic trajectories of the two species.

Overall, the utilization of GMM permits the characterization of Neanderthals and modern humans as separate dynamical «ontogenetic entities» rather than static «morphological structures». This difference in perspective is crucial, since it impinges on the question as to whether Neanderthals and modern humans must be considered separate species or subspecific variants of the same species. Adopting the static, structural perspective (e.g. by restricting the comparison to adults or peer groups of both taxa,) tends to overemphasize within-taxon relative to between-taxon variation, since the developmental background of variation is not considered. The dynamical approach, on the other hand, reveals that taxon-specific differences appear early and persist during later development, despite considerable within-taxon variation along the ontogenetic trajectory. The parallel trajectories further indicate that, once the taxon-specific differences are established (around age 2) the development of Neanderthals and modern humans is largely similar. One additional ontogenetic inference that can be made on the basis on these data is that the developmental processes that account for the principal differences between Neanderthals and modern humans must have occurred early during development. This early differentiation further hints at a strong genetic rather than environmental background of the morphological differences between these taxa.

The proposed graphical methods can now be used to visualize the morphological effects of (a) shape change corresponding to the advancement along the parallel ontogenetic trajectories (arrow along RW1 in Fig. 3) and (b) shape difference

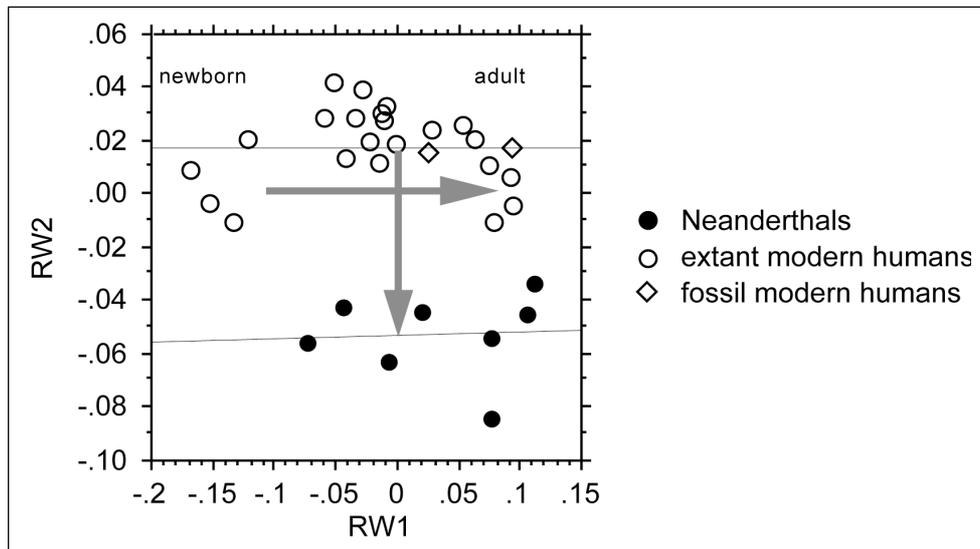


Figure 3 - Relative Warp analysis of an ontogenetic series of Neanderthal specimens (from left to right: Pech de l'Azé, Roc de Marsal, Devil's Tower, Teshik, Tash, Le Moustier, Tabun 1, Forbes' Quarry, La Ferrassie 1) and modern human craniomandibular specimens (fossil specimens: Qafzeh 9, Qafzeh 11). Taxa are clearly separated along relative warp 2 (RW2), while each of them follows an ontogenetic trajectory parallel to relative warp 1 (RW1).

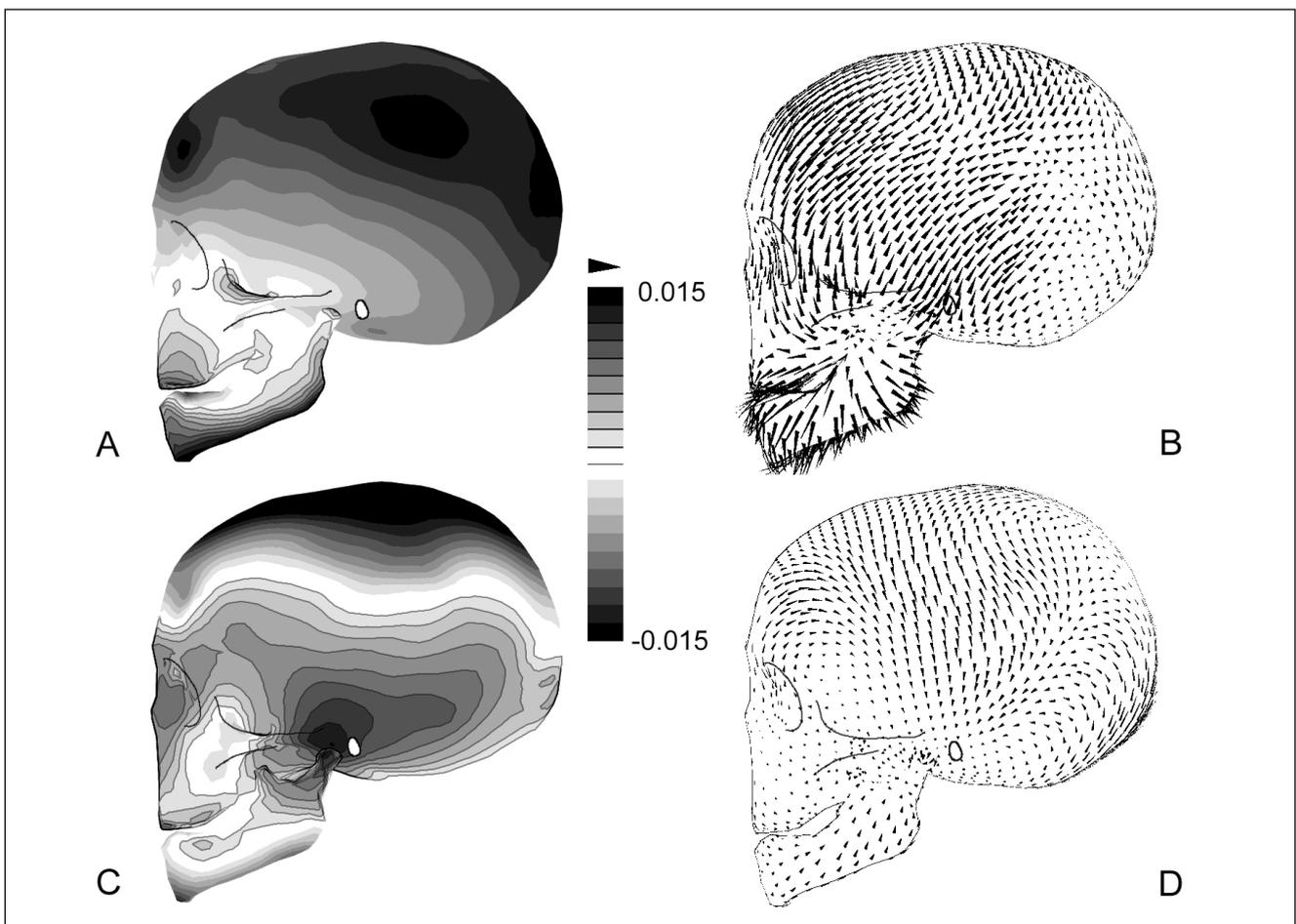


Figure 4 - Visualization of Neanderthal/modern human shared craniomandibular growth patterns (**A, B**, corresponding to advancement along horizontal arrow in Fig. 3) and patterns of shape differences between Neanderthals and modern humans (**C, D**, corresponding to vertical arrow in Fig. 3). **A,C/B,D**: normal/tangential vector maps accounting for shape difference perpendicular/parallel to the cranial surface (in **A,C**, shaded and outlined-shaded areas indicate inward and outward orientation of the normal vectors, respectively; scale is in units of centroid size). Growth patterns are characterized by expansion of the viscerocranial parts, as opposed to relative contraction of the neurocranium. Neanderthals, relative to modern humans, show broadening of the temporomandibular region, flattening of the cranial vault and projection of the face and occipital region.

corresponding to the distance between the trajectories (arrow along RW2 in Fig. 3). The resulting patterns of shape change/shape difference are visualized in Fig. 4. As indicated by the parallel trajectories along RW1, patterns of morphological change during postnatal development are similar in Neanderthals and modern humans and can therefore be visualized using a Neanderthal/modern human consensus cranium (Figs. 4 B). The most conspicuous feature arising from these graphs is the distinct pattern of development of the viscerocranium and the neurocranium: while the former expands in anterior and caudal direction, the latter exhibits relative «contraction», i.e. it assumes a steadily smaller proportion of the growing skull. This pattern most probably represents a general developmental feature of the hominid cranium.

The difference in craniomandibular shape between Neanderthals and modern humans (Figs. 4 C, D) is visualized as the pattern of shape difference resulting from transformation of a modern human into a Neanderthal, using the Neanderthal/modern human consensus cranium. Note that this pattern of shape transformation expresses the distance between the taxon-specific ontogenetic trajectories through shape space and is therefore independent of the age at which the comparison is performed (the consensus cranium represents an juvenile individual of approx. 8 years of age). Figs. 4 C, D therefore account for the principal morphological features of the cranium of Neanderthals relative to that of modern humans. The graphs show a suite of classical Neanderthal features such as a relatively flat cranial vault with a broad temporal region, projection of the midface face and occipital region, and a receding symphyseal region of the mandible (Stringer & Gamble, 1993). Since all these features are already established around the age of 2 years, it can readily be inferred that the taxon-specific Neanderthal and modern human morphologies were essentially brought about prior to that age, probably already during prenatal development (Lieberman, 1998; Lieberman, 2000; Ponce de León & Zollikofer, 2001). From this perspective, the «static» postnatal differences between taxa represent contrasts between taxon-specific early developmental programs.

Combining these observations, the following conclusions can be drawn: Neanderthals and modern humans share their postnatal patterns (most probably also their processes) of development, as evinced by their parallel trajectories through shape space. The phyletic difference in shape between these species, as quantified and visualized by the distance between their postnatal ontogenetic trajectories, reflects evolutionary modifications leading to divergent prenatal/early postnatal developmental programs. Fig. 3A therefore encapsulates shape change on both ontogenetic and phylogenetic time scales, corresponding to RW1 and RW2, respectively. The pattern of taxon-specific difference can be linked to (no longer observable) differences in early ontogenetic process. – This example demonstrates that virtual paleoanthropology is an indispensable tool for the analysis of spatiotemporal change – i.e. change in four dimensions – at the level of diagenesis, phylogeny and ontogeny.

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Authors' addresses:

Ch. P. E. ZOLLIKOFER (zolli@ifi.unizh.ch; <http://www.ifi.unizh.ch/staff/zolli>)

M. S. PONCE DE LEON (marcia@ifi.unizh.ch; <http://www.ifi.unizh.ch/staff/marcia>)

Anthropologisches Institut
und MultiMedia Laboratorium/Institut für Informatik
Universität Zürich-Irchel, CH-8057 Zürich/Schweiz

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