Middle Pleistocene human facial morphology in an evolutionary and developmental context

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Abstract

Neanderthals and modern humans exhibit distinct facial architectures. The patterning of facial morphology of their predecessors, the Middle Pleistocene humans, is more mosaic showing a mix of archaic and modern morphologies. Significant changes in facial size and robusticity occurred throughout Pleistocene human evolution, resulting in temporal trends in both facial reduction and enlargement. However, the allometric patterning in facial morphology in archaic humans is not well understood. This study explores temporal trends in facial morphology in order to gain a clearer understanding of the polarity of features, and describes the allometric patterning of facial shape.

The modern human sample comprises cross-sectional growth series of four morphologically distinct human populations. The fossil sample covers specimens from the Middle Pleistocene to the Upper Paleolithic. We digitized landmarks and semilandmarks on surface and computed tomography scans and analyzed the Procrustes shape coordinates. Principal component analyses were performed, and Procrustes distances were used to identify phenetic similarities between fossil hominins. In order to explore the influence of size on facial features, allometric trajectories were calculated for fossil and modern human groups, and developmental simulations were performed.

We show that facial features can be used to separate Pleistocene humans into temporal clusters. The distinctly modern human pattern of facial morphology is already present around 170 ka. Species- and population-specific facial features develop before two years of age, and several of the large-scale facial differences between Neanderthals and Middle Pleistocene humans are due to scaling along a shared allometric trajectory. These features include aspects of the frontal bone, browridge morphology, nasal aperture size and facial prognathism. Infraorbital surface topography and orientation of the midface in the European Middle Pleistocene hominins is intermediate between the African Middle Pleistocene and Neanderthal condition. This could suggest that the European Middle Pleistocene hominins display incipient Neanderthal features.

Introduction

The Eurasian and African Middle Pleistocene hominins (MPH) are characterized by a combination of craniofacial morphological features, variously aligning them with Homo erectus sensu lato, H. neanderthalensis and H. sapiens. The most complete faces include Bodo and Kabwe (i.e., Broken Hill) from Africa, and Arago 21, Petralona, and Sima de los Huesos 5 from Europe. MPH specimens are characterized by massive facial bones, broad upper faces, projecting browridges, especially in the lateral region, large interorbital breadth, and details of the nasal margin and palate (Stringer, 1974; Arsuaga et al., 1997; Rightmire, 1998, 2008; Trinkaus, 2003, 2006; Athreya, 2009). They also share several facial features with Neanderthals, such as facial prognathism, broad nasal apertures, and a lack of concavity in the infraorbital region (Rak, 1986; Trinkaus, 1987, 2003, 2006; Arsuaga et al., 1997; Harvati et al., 2010).

Striking differences between MPHs, Neanderthals and recent modern humans occur in their facial size and robusticity. In particular, Bodo, Petralona and Kabwe are characterized by their
massive facial bones compared with Neanderthals and recent modern humans (Rightmire, 1998), and both the MPVs and Neanderthals have longer and more prognathic faces than recent modern humans (Trinkaus, 2003). To what extent the facial differences among recent modern humans, MPVs, and Neanderthals are related to facial size is uncertain.

Allometry, as defined by Gould (1966), is the study of size and its consequences. Conventionally, it is used to investigate the relationship between the total body size of the organism and its shape, anatomy, and physiology among other characteristics (Gould, 1966). Julian Huxley (1932) introduced the concept of allometry into studies of growth, evolution and function, and later S.J. Gould’s seminal work in both allometry (e.g., Gould, 1966, 1975) and heterochrony (e.g., Gould, 1968, 1977), the dissociation of size, shape and age (Gould, 1977; Alberch et al., 1979), set the framework for comparative allometric ontogenetic investigations among living and extinct organisms. Since Gould, a substantial body of work investigating heterochrony and growth allometry in human and non-human primates has accumulated (e.g., Shea, 1981, 1983; Leigh and Cheverud, 1991; Ravosa, 1991, 1998; Collard and O’Higgins, 2001; Penin et al., 2002; Leigh et al., 2003; Berge and Penin, 2004; Strand Viðarsdóttir and Cobb, 2004; Mitteroecker et al., 2005; Leigh, 2006; Lieberman et al., 2007; Bruner and Ripani, 2008; Gonzalez et al., 2011), however studies on fossil hominins are less common.

Rosas (1997, 2000) and Rosas and Bastir (2004) identified several features on the Middle Pleistocene Sima de los Huesos (SH) mandibles associated with an increase in size, including the presence of a retromolar space, the curvature and orientation of the symphysis, and the position of the mental foramen with respect to the dentition. Similarly, in their geometric morphometric study on modern human and Neanderthal mandibular shape, Nicholson and Harvati (2006) found that the retromolar gap was related to an increase in mandibular size. Size-correlated shape changes in later hominins and recent modern humans have also been observed in the relative breadth of the nasal aperture (Rosas and Bastir, 2002; Holton and Franciscus, 2008), nasoglabellar profile (Rosas and Bastir, 2002), alveolar prognathism (Rosas and Bastir, 2002), and infraorbital surface topography (Maddux and Franciscus, 2009). In the latter study, Maddux and Franciscus (2009) identified an allometric relationship between infraorbital size and surface topography within Middle to Late Pleistocene Homo and modern humans. They found that individuals with large infraorbital regions tend to exhibit flat, or inflated, surface topographies (characteristic of Neanderthals), while individuals with small infraorbital areas possess depressed surface topographies (like modern humans). They argued that depressed versus inflated infraorbital shapes are not dichotomous configurations, but fall along a continuous size gradient. Together, these studies demonstrate that some Neanderthal apomorphies (e.g., retromolar space and infraorbital inflation) are size-correlated.

However, a major limitation to several of the studies mentioned above is the lack of ontogenetic data. Without a developmental growth series, these studies can only demonstrate that there are allometric shape changes among adults (i.e., static allometry). An understanding of the developmental basis of morphological features is crucial to interpreting the taxonomic importance of characters because features that develop earlier in ontogeny are thought to be less susceptible to epigenetic factors, or less likely to respond to exposure to environmental effects (Lieberman et al., 1996, 2002; Wood and Lieberman, 2001; but see; Roseman et al., 2010).

Due to a growing body of ontogenetic studies, it is becoming increasingly clear that taxon-specific craniofacial morphology among hominin species developed prenatally or very early postnatally (e.g., Ponce de León and Zollikofer, 2001; Ackermann and Krovitz, 2002; Lieberman et al., 2002; Strand Viðarsdóttir et al., 2002; Williams et al., 2002; Krovitz, 2003; Bastir and Rosas, 2004; Mitteroecker et al., 2004; McNulty et al., 2006; Gunz et al., 2010, 2012; Gunz, 2012). These morphometric studies largely support descriptive research identifying unique Neanderthal morphology at an early age (e.g., Tillier, 1989, 2011; Rak et al., 1994; Akazawa et al., 1995). For example, at birth the ear labyrinth of Neanderthals are different in size and shape when compared with modern humans (Hublin et al., 1996; Ponce de León and Zollikofer, 1999), and by at least two years of age Neanderthal features on the occipital, such as the suprainiac fossa and a bilaterally protruding occipital torus, have already developed (Hublin, 1980). Additionally, studies have shown that at the time of birth, the face of a Neanderthal is already larger than that of a modern human (Ponce de León and Zollikofer, 2001; Ponce de León et al., 2008; Zollikofer and Ponce de León, 2010; Gunz et al., 2010, 2011, 2012). On the other hand, several Neanderthal facial features, such as midfacial projection, maxillary inflation, and double-arched browridges, are not fully developed until later in childhood (Tillier, 1996).

Ponce de León and Zollikofer (2001) showed that Neanderthals and modern humans share a common pattern of cranial and mandibular shape change from an early age and onward. The general pattern of shape change comprised a projection and downward elongation of the face and mandible combined with a contraction of the cranial vault. They concluded that the craniofacial and mandibular differences between these two groups probably results from differential activity of growth fields early in ontogeny (Ponce de León and Zollikofer, 2001). Similarly, in their geometric morphometric study on facial development in great apes and Australopithecus africanus, Ackermann and Krovitz (2002) found that facial features arose very early in development followed by parallel postnatal developmental patterns (with the possible exception of the gorillas). Additionally, they found that aspects of facial growth were more similar between A. africanus and modern humans, relative to the great apes. Therefore, their study suggests that our early human ancestors were already demonstrating some human-like aspects of facial growth. The implications of these findings are that one can interchange hominid postnatal growth trajectories without producing significant differences in the end results. This has been further demonstrated by the study of McNulty et al.’s. (2006) on the taxonomic affinities of the subadult Taung fossil specimen. To evaluate the adult morphology of the Taung child, McNulty et al. (2006) performed a series of developmental simulations. They grew Taung along various hominine developmental trajectories and compared its adult morphology with adults of both Australopithecus and Paranthropus. While McNulty et al. (2006) found the developmental patterns of extant hominine species to be statistically different, the results from their developmental simulations indicate that the postnatal developmental differences between hominines have little impact on the estimation of the adult morphology. McNulty et al. (2006) demonstrated that the adult morphology of Taung can be reliably estimated even through the application of an incorrect developmental trajectory.

However, several geometric morphometric analyses on humans and primates have found that both early postnatal cranial morphology and later postnatal growth contribute to further differentiate populations and species (Richmsmeier et al., 1993; O’Higgins and Jones, 1998; O’Higgins et al., 2001; Strand Viðarsdóttir et al., 2002; Bastir and Rosas, 2004; Cobb and O’Higgins, 2004; Strand Viðarsdóttir and Cobb, 2004; Bastir et al., 2007). For example, Bastir et al. (2007) argued that both pre- and postnatal ontogenetic growth are important in establishing morphological differences in mandibular shape between
Neanderthals and modern humans. Their results showed divergent ontogenetic shape changes between Neanderthals and modern humans and significantly different allometric scaling patterns.

The aim of this study is to place the MPHs in both a geographically and chronologically broad evolutionary and developmental context to gain a clearer understanding of how archaic (i.e., MPHs and Neanderthals) and modern human facial features are affected by facial size and how they change through time. More specifically, the goals of this study are to: 1) explore temporal trends in facial morphology in order to gain a clearer understanding of the polarity of facial features, 2) describe the shape changes associated with allometric scaling in archaic and modern human faces, and 3) test whether differences in facial shape between archaic and modern humans are attributable to the differential extension or truncation of common growth allometries (i.e., ontogenetic scaling), or whether shape variation is due to divergent growth patterns.

Temporal trends in facial morphology are explored through the means of a principal component analysis (PCA) of Procrustes shape variables and Procrustes distance comparisons. The second and third objectives are addressed by comparing the angle and orientation of Neanderthal and modern human ontogenetic allometric trajectories in both shape and Procrustes form space, and by applying developmental simulations (McNulty et al., 2006; Neubauer et al., 2010; Gunz et al., 2010, 2012; Gunz, 2012) to grow modern human and Neanderthal faces to the size of selected Middle Pleistocene fossils. The predicted facial shapes are then visualized and compared between archaic and modern human groups.

In this study, we recognize three categories of allometry: ontogenetic, static and evolutionary (Cock, 1966; Cheverud, 1982; Klingenberg, 1998). We use cross-sectional data on recent modern and Pleistocene humans to explore patterns in ontogenetic allometry, defined as the covariation of traits with size across different age groups (i.e., ontogenetic stages) of a given species (Klingenberg, 1998). Static allometry reflects trait covariation with size within the same ontogenetic stage of a single species (Klingenberg, 1998). This type of allometry is observed among the adults in our sample. Lastly, evolutionary allometry arises from covariation of traits with size and their phylogenetic changes and can be analyzed either within one ontogenetic stage or across stages (Klingenberg, 1998).

In his influential paper evaluating the relationship between these three types of allometry, Cheverud (1982), following work by Cock (1966), Gould (1966) and Shea (1981), demonstrated that patterns of static adult allometry cannot be assumed to reflect ontogenetic processes (although see Klingenberg and Zimmermann, 1992; Klingenberg, 1998). This is mainly because adult data usually represent a very restricted (in both size and time) subset of the ontogenetic range (Inouye and Shea, 1997).

Following Gould (1975), an allometric regression line can act as an ontogenetic criterion of subtraction such that the points along the line can be explained in terms of size-required changes. Deviations from the line are non-allometric shape changes and the morphological differences may indicate specific functional adaptations (Gould, 1975). In this study, we used ontogenetic scaling as a criterion of subtraction because it is a powerful means for identifying shared effects of size change between groups or species, as well as derived dissociations of ancestral allometries (Gould, 1975; Shea, 1981, 1983; Inouye and Shea, 1997). Here we use a multivariate approach to allometric scaling that differs in certain methodological aspects from the classical allometric studies. Departing from the conventional definition and applications of allometry, e.g., we substitute facial size for body size because we are specifically interested in how differences in facial size influence the expression of facial features and overall facial shape. Surface semilandmark geometric morphometric techniques are used to quantify facial features that are otherwise difficult to capture, such as the infraorbital surface topography, and developmental simulations are applied to visualize the effects of allometry on the face.

**Evolutionary models of Middle Pleistocene hominins**

The two main competing phylogenetic interpretations of the Middle Pleistocene human fossil record are: 1) most of the MPHs comprise a single, cross-continental taxon, spanning Africa, Europe and possibly Asia, or 2) the European and African MPHs, at least those from Marine Isotope Stage 11 and onward, belong to separate clades. In the first model, the MPHs are assigned to the taxon *H. heidelbergensis* and are considered to be the last common ancestor to both Neanderthals and modern humans. This view is supported by the strong morphological and metric similarities between the European and African specimens (e.g., Stringer, 1974, 1983; Arsuaga et al., 1997; Rightmire, 1998, 2007, 2008; Mounier et al., 2009; Harvati, 2009a).

In the second model, the European MPHs are seen as ancestral to Neanderthals and are classified as either *H. neanderthalensis* (Hublin, 1998, 2009) or as the exclusive members of *H. heidelbergensis*, a chronospecies of the Neanderthal lineage (e.g., Arsuaga et al., 1997; Manzi, 2004; but see Wolpoff et al., 1994; Rosas et al., 2006; Tattersall and Schwartz, 2006; Hublin, 2009b for alternative interpretations of the fossil record). In this scenario, the African MPHs are interpreted as being ancestral to *H. sapiens* and often classified as *H. rhodesiensis* (Hublin, 2009). As evidence for the ‘Neandertalization’ process, proponents of this model refer to a series of features on the skeleton that foreshadow the Neanderthal condition and that occur uniquely in the European MPHs (Dean et al., 1998; Hublin, 1998, 2009). These features are found on the face, occiput, temporal bone and dentition. They include, but are not limited to, a convex and receding horizontal infraorbital profile, anteriorly advanced and sagittally oriented face, wide occipital torus, incipient suprainiac fossa, bilaterally protruding occipital torus, strong juxtamastoid eminence (Dean et al., 1998; Hublin, 1998), and derived conditions expressed in different non-metrical traits of the dentition (Martínón-Torres et al., 2012). However, quantitative support for this model is limited. This may in part be due to the difficulty in quantifying these complex features especially on the face (Harvati et al., 2010).

**Materials and methods**

**Sample**

This study includes a comprehensive sample of subadult and adult Middle to Late Pleistocene fossil hominins (Table 1) and recent modern humans (Table 2). The fossil sample was designed to include all available Middle to Late Pleistocene fossils that preserve relatively complete faces (see section on Missing data reconstruction below). Table 1 lists the 26 fossils, their broad geographical location, chronology and repository.

The modern human sample (Table 2) comprises a cross-sectional growth series from four geographically diverse human populations spanning three continents: Africa, North America and Europe. The individuals within each growth series range in age from two years to adulthood. The African sample consists of an archaeological Khoisan population from South Africa. The North American sample is divided into two groups: a combined Native American archaeological sample from Canyon del Muerto, Arizona, and Grand Gulch, Utah, and an archaeological population from Point Hope, Alaska. Lastly, the European sample consists of a temporally more recent combined sample from Strasbourg (France) and Greifenberg (Austria). The modern human cranial data were obtained from specimens housed in the American Museum of Natural History (AMNH, New York), Iziko South African Museum
Recent modern human adult and subadult specimens used in the analysis.

<table>
<thead>
<tr>
<th>Population/Geographic region</th>
<th>AG 1</th>
<th>AG 2</th>
<th>AG 3</th>
<th>AG 4 (adult)</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Khoisan, South Africa&lt;sup&gt;3,6&lt;/sup&gt;</td>
<td>8</td>
<td>8</td>
<td>4</td>
<td>38 (M&lt;sup&gt;+&lt;/sup&gt;: 14; F: 24)</td>
<td>58</td>
</tr>
<tr>
<td>Arizona, (Canyon del Muerto), Utah, (Grand Gulch), USA&lt;sup&gt;2&lt;/sup&gt;</td>
<td>7</td>
<td>6</td>
<td>4</td>
<td>52 (M: 25; F: 27)</td>
<td>69</td>
</tr>
<tr>
<td>Alaska, (Point Hope), USA&lt;sup&gt;1&lt;/sup&gt;</td>
<td>6</td>
<td>10</td>
<td>4</td>
<td>48 (M: 26; F: 22)</td>
<td>68</td>
</tr>
<tr>
<td>Strasbourg, France&lt;sup&gt;1&lt;/sup&gt; and Greifenberg, Austria&lt;sup&gt;1&lt;/sup&gt;</td>
<td>7</td>
<td>4</td>
<td>4</td>
<td>49 (M: 27; F: 22)</td>
<td>64</td>
</tr>
</tbody>
</table>

<sup>a</sup> The abbreviation AG represents Age Group. See text (Material and Methods — Sample) for definition of each age group.
<sup>b</sup> The specimen sex is denoted as M for males and F for females.
<sup>c</sup> Iziko South African Museum
<sup>d</sup> University of Cape Town
<sup>e</sup> American Museum of Natural History
<sup>f</sup> Medicine Faculty of Strasbourg
and after adolescence (e.g., Strand Viðarsdóttir et al., 2002; Bulygina et al., 2006). Adult individuals were sexed according to Howells (1973) criteria, and when possible an equal number of males and females were included.

**Measurement protocol**

Computed tomography (CT) and surface scans. CT or surface scans of the fossil and modern human crania were acquired. The CT scans were made with either an industrial (BIR ACTIS 225/300) or medical (Toshiha Aquilion) CT scanner, and the remaining specimens were surface scanned with either a Minolta Vivid 910 or a Concorde OptoTOP-HE. The pixel size of the CT scans ranged from 0.24 to 0.49 mm and the slice thickness was between 0.25 and 1.00 mm. The resolution of the surface scanners ranged from ~30 microns to ~6 microns in the z plane. The differences in resolution among these scanners are much smaller than the digitizing error and differences among the specimens. For example, although the adults and juveniles in the European sample were scanned using two different methods (adults: Minolta surface scanner; juveniles: medical CT scanner), they cluster together in a principal component analysis (PCA).

Three-dimensional surface models were extracted from either the surface or CT scans and saved as .ply polygon model file format. Surface scans were processed using either Geomagic Studio or OptoCat (Breuckmann) software, depending on the scanner model used. For the CT data, three-dimensional surfaces were extracted using Avizo (Visualization Sciences Group Inc.). The landmarks and semilandmarks were digitized on the surface models using Landmark Editor (Wiley et al., 2005). If CT or surface scan data of the original fossil material were not available, surface scans of high quality casts (see Table 1) from the Division of Anthropology of the AMNH (New York) or the Max Planck Institute for Evolutionary Anthropology (Leipzig) were made.

**Landmark data and semilandmarks.** Defining curves and surfaces, were digitized by one observer (S.F.). 3D coordinates of landmarks (Table 4) and semilandmarks along curves were digitized on all specimens and a mesh of surface semilandmarks was digitized on one ‘template’ individual (see Fig. 1) using Landmark Editor software (Wiley et al., 2005). This template mesh of surface semilandmarks was warped into the vicinity of the surface of every specimen using a thin-plate spline (TPS) interpolation according to the landmark and curve data. The warped points were then projected onto the surfaces by picking the closest vertices from the specimen’s .ply file following other studies (e.g., Gunz, 2005; Gunz and Harvati, 2007; Neubauer et al., 2009, 2010; Gunz et al., 2009a, b; Harvati et al., 2010; Stansfield and Gunz, 2011; Freidline et al., 2012). This protocol guarantees that every specimen has the same number of curve semilandmarks and surface semilandmarks in approximately corresponding locations. A detailed description can be found in Gunz et al. (2005, 2009b) and Mitteroecker and Gunz (2009).

The initially equidistant semilandmarks were slid along tangents to the curves and tangent planes to the surfaces so as to minimize the bending energy of the TPS interpolation between each specimen and the Procrustes consensus configuration. After sliding, landmarks and semilandmarks were treated the same in subsequent statistical analyses. To convert the landmark and semilandmark coordinates to shape variables, a generalized Procrustes analysis (GPA) was performed. GPA removes the effects of translation and rotation in the raw coordinate data and standardizes each specimen to unit centroid size, the square root of the sum of squared distances from each landmark to the specimen’s centroid (Dryden and Mardia, 1998). All data processing and statistical analyses were performed in Mathematica (Wolfram Research) and R (R Development Core Team, 2010).

Missing data reconstruction. As geometric morphometric methods require all specimens to have the same number of homologous points, some minor data reconstruction was necessary for some fossil specimens. First, bilateral symmetry was exploited by mirroring the right side of the skull to the left and vice versa.

**Table 3**

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Ontogenetic age (ca. yr.)</th>
<th>Age group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pech-de-l’Azé 1</td>
<td>2 (Tillier, 1996)</td>
<td>1</td>
</tr>
<tr>
<td>Teshik-Tash</td>
<td>9–11 (Tillier, 1989; Williams et al., 2002)</td>
<td>2</td>
</tr>
<tr>
<td>Grotte des Enfants 6</td>
<td>13–15 (Henry-Gambier, 2001)</td>
<td>4</td>
</tr>
</tbody>
</table>

* See text (Material and Methods — Sample) for definition of age group classifications.

**Table 4**

<table>
<thead>
<tr>
<th>Landmark landmarks used in the analysis.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Landmark</td>
</tr>
<tr>
<td>---</td>
</tr>
<tr>
<td>Alveolare</td>
</tr>
<tr>
<td>Anterior nasal spine</td>
</tr>
<tr>
<td>Auriculareb</td>
</tr>
<tr>
<td>Frontomalarialorbitala</td>
</tr>
<tr>
<td>Frontomalarialtemporaleb</td>
</tr>
<tr>
<td>Glabella</td>
</tr>
<tr>
<td>Jugaleb</td>
</tr>
<tr>
<td>Medial orbital marginb</td>
</tr>
<tr>
<td>Nasion</td>
</tr>
<tr>
<td>Nasionale</td>
</tr>
<tr>
<td>Porionb</td>
</tr>
<tr>
<td>Rhinion</td>
</tr>
<tr>
<td>Sphenopalatinesutureb</td>
</tr>
<tr>
<td>Staphylion</td>
</tr>
<tr>
<td>Zygomatic process root inferiorb</td>
</tr>
<tr>
<td>Zygomatic process root superiorb</td>
</tr>
<tr>
<td>Zygomaxillareb</td>
</tr>
</tbody>
</table>

* All landmarks are defined following White et al. (2012). Definitions and references (if available) are provided for the less common landmarks.

b Paired right and left landmarks.

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reconstruct fragmentary fossil material. Arago 21 required the most extensive reconstruction. A detailed account of this reconstruction and the protocol can be found in Gunz et al. (2009b).

Statistical analyses

To explore the temporal variability in facial morphology among Pleistocene humans, a PCA was performed in shape space. A PCA reduces the dimensionality of high dimensional shape space and provides summaries of large-scale trends within the data (Bookstein, 1991; Rohlf, 1993). We used TPS warping of the Procrustes mean shape along the first two principal components (PCs) to visualize the shape changes (see Gunz and Harvati, 2007; Mitteroecker and Gunz, 2009). Additionally, to identify which individuals are most phenetically similar to one another, nearest neighbors were calculated using inter-individual Procrustes distances. To visualize the morphological similarities shared between nearest neighbors, each of the Middle Pleistocene hominins was superimposed on its nearest neighbor.

In morphometrics, a distinction is made between shape and form. Shape refers to the geometric properties of an object that are independent of its overall size, position and orientation, whereas the form of an object includes both its shape and size (Mitteroecker and Gunz, 2009). Because this study focuses on allometry, the inclusion of size in our statistical analyses is essential. To quantify facial size, we used the variable centroid size, which is computed during the Procrustes superimposition. Following Mitteroecker et al. (2004, 2005), we performed a PCA in Procrustes form space (also called size-shape space) on the Procrustes landmark and semilandmark coordinates. Form space includes the geometric size (as the natural logarithm of centroid size) of each specimen (Mitteroecker et al., 2004) and is valuable because the relationship between shape and size can be readily explored.

In this study, we compute the ontogenetic allometric trajectories as multivariate regressions of the Procrustes shape variables on the natural logarithm of centroid size. As outlined by Mitteroecker et al. (2004, 2005), properties of these trajectories (e.g., length, shape, divergence) can be compared between populations and species. Coincidental ontogenetic trajectories indicate a common pattern of shared development between the groups under investigation. We interpret coincidental growth trajectories for the extant (recent modern humans) and extinct groups (Neanderthals) as a shared pattern of relative growth that also may be truncated or extended. Parallel trajectories reveal that the morphological divergence between groups has already occurred prior to the age of the youngest specimen, and that there is a common pattern of subsequent growth shared between groups. By contrast, divergent trajectories indicate that development further accentuates group differences.

Ontogenetic trajectories were plotted in shape and Procrustes form space for Neanderthals, each of the four modern human populations, and the modern human mean. The modern human mean trajectory was calculated by regressing Procrustes shape coordinates on the natural logarithm of centroid size on the entire modern human sample. Because only adult MPhs faces are included in this study, static, rather than ontogenetic, allometric trajectories were calculated and plotted in Procrustes shape and form space for these hominins.

To see if modern humans and Neanderthals share a common ontogenetic allometric trajectory during postnatal ontogeny, we computed the angle between the Neanderthal and the mean modern human ontogenic allometric vectors. We then tested whether the angle was statistically different from zero using a permutation test (McNulty et al., 2006; Gunz, 2012). We first mean-centered the respective groups and then compared the actual angle with angles obtained from regressions computed for 5000 permutations that randomly reassigned group membership, permuting the entire sample for each iteration. Likewise, the angles between the ontogenetic allometric trajectories of the four modern human populations were calculated and tested to see if they were significantly different from zero. To assess the effects of the small Neanderthal sample size on the computation of the ontogenetic allometric trajectory, we bootstrapped subsamples from the recent modern human sample, simulating the composition of the Neanderthal sample (i.e., one specimen from age group 1, one from age group 2 and six adults).

Developmental simulations and visualization techniques

The aim of the series of developmental simulations was to identify the allometric shape changes that occur when scaling an adult modern human and Neanderthal to the size of a MPh. To do so, we calculated the mean adult modern shape and grew it following the modern human mean ontogenetic allometric trajectory to the size of a) Kabwe, an African MPh that has a particularly inflated infraorbital surface topography for a MPh, and b) Bodo, an African MPh that has the largest face in our sample. Shape changes were visualized by TPS warping of the adult modern human mean shape to the modern human mean grown to the size of Bodo and Kabwe. The same approach was applied to Neanderthals. We warped the surface of La Ferrassie 1 to the mean adult Neanderthal shape, and then grew it following the Neanderthal ontogenetic allometric trajectory to the size of Kabwe and Bodo.

Results

Principal component analyses and permutation tests

To explore temporal trends in facial morphology, a PCA was performed in Procrustes shape space of only the adult individuals (Fig. 2). The first two principal components (PCs) represent 46.9% of the total shape variation, and neither of the PCs correlate with size. There is a clear separation between the modern humans, including...
the early modern and Upper Paleolithic humans, and the archaic humans. Additionally, members of each temporal group cluster together. However, there is some overlap between Middle Pleistocene humans and Neanderthals. The main shape changes that occur along PC 1 are in the curvature of the anterior portion of the frontal bone, browridge projection, width of the nasal aperture and facial prognathism. Middle Pleistocene specimens, such as Bodo and Sima de los Huesos 5, and Neanderthals, such as La Chapelle-aux-Saints, cluster at the extreme positive end of PC 1. These fossils share a more receding anterior frontal bone, anteriorly projecting browridge, wide nasal aperture, and prognathic mid and lower face when compared with recent modern humans, which generally plot at the negative end of PC 1. While several shape changes are shared between PC 1 and PC 2, such as frontal bone curvature, facial prognathism and infraorbital surface topography, PC 2 primarily demonstrates changes in facial length and orientation of the maxillary body (i.e., maxillary body facies). Shanidar 5, Petralona and Kabwe share a superiorly—inferiorly long face and their maxillary body is oriented near vertically. On the opposite end of PC 2, the modern humans express a shorter face and a maxillary body that is oriented down and slightly posteriorly.

Based on pairwise Procrustes distances (PD), Bodo is most similar to Sima de los Huesos 5 (PD = 0.068), Sima de los Huesos 5 is most similar to Arago 21 (PD = 0.06), Arago 21 is most similar to La Chapelle (PD = 0.05), Petralona and Kabwe are most similar to one another (PD = 0.056), and Shanidar 5 is most similar to Petralona (PD = 0.056). To illustrate the resemblances between these specimens, we superimposed each MPh onto its nearest neighbor (Fig. 3a–o). Bodo and Sima de los Huesos 5 share similarly projecting lateral browridges, wide nasal apertures and interorbital breadths. However, Bodo’s glabellar region is more anteriorly projecting and its mid and lower face morphology is especially different from Sima de los Huesos 5 (Fig. 3a–c). For example, Sima de los Huesos 5 has a more prognathic mid and lower face, a slightly more inflated infraorbital surface topography and a more parasagittally oriented midface when compared with Bodo (Fig. 3c: Sima de los Huesos 5 is green and Bodo is bone color). Sima de los Huesos 5 and Arago 21 (Fig. 3d–f) share a similar mid and lower face morphology and diverging upper faces (i.e., browridges). Thus they share a similar infraorbital surface topography, and they exhibit a similar degree of facial prognathism and parasagittal rotation. However, Arago 21 has a more projecting browridge, especially the middle
portion (Fig. 3f: Sima de los Huesos 5 is green). The similarities between Arago 21 and La Chapelle (Fig. 3g–i) are in midfacial prognathism and infraorbital surface topography. La Chapelle has a more anteriorly projecting browridge than Arago 21, except for the lateral portions, its midface is more parasagittally oriented, and its nasal aperture is more anteriorly projecting (Fig. 3i: La Chapelle is red). Kabwe and Petralona (Fig. 3j–l) primarily share similarities in the lateral midface, mainly in zygomatic bone projection. Kabwe has a more anteriorly projecting browridge, and a superiorly—inferiorly longer and more prognathic subnasal region. However, the infraorbital topography of Petralona is more inflated than Kabwe (Fig. 3l: Kabwe is green). Lastly, Shanidar 5 and Petralona (Fig. 3m–o) share a similar degree of mid and lower facial prognathism, infraorbital inflation, and nasal aperture width. The main difference between these two specimens is in the morphology of their browridge. Petralona expresses a more anteriorly projecting browridge and upper face (Fig. 3o: Shanidar 5 is red).

The results of the PCA in Procrustes shape space of the complete sample (i.e., subadult modern humans and Neanderthals) are shown in Fig. 4. The first three PCs were plotted and represent

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**Figure 3.** Procrustes superimposition of each of the Middle Pleistocene hominins on its nearest neighbor in shape space. The Procrustes shape information for each specimen is contained in the landmark and semilandmarks and everything in between these landmarks is interpolated. The landmarks and semilandmarks are color-coded according to the specimen’s surface color (dark yellow is associated with the bone colored surfaces; dark green with the green surfaces; and dark red with the red surfaces). Thus, when two different colored landmarks are exposed this indicates overlapping (i.e., similar) morphology. Different surface morphologies are present when only one landmark color and corresponding surface is visible. Nearest neighbors are indicated by the arrows in Fig. 2. The full names and abbreviations for the fossil specimens are listed in Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
60.0% of total shape variance. PC 1 is correlated with size ($r = -0.79$). The solid lines represent the ontogenetic allometric trajectories for each of the four modern human populations, the Neanderthal and mean modern human ontogenetic allometric trajectories, and the MPh static allometric trajectory. The shaded region represents the 95% single prediction interval of the modern human regressions of shape on the natural logarithm of centroid size. The thin gray lines represent the bootstrapped estimates of the modern human allometric trajectory computed from subsamples that simulate the Neanderthal sample composition.

None of the Neanderthal or recent modern human ontogenetic allometric trajectories coincide. Because each ontogenetic trajectory has a unique starting point, this plot shows that population and species-specific facial morphology is present before permanent teeth erupt. As in Fig. 2, clusters of temporal groups are also apparent when including the entire sample (i.e., all subadults included) although the MPhs and Neanderthals overlap. Apart from Qafzeh 9, the early and Upper Paleolithic modern humans fall within the range of recent human variation.

The variance explained by ontogenetic allometry is 26.0% for recent modern humans and 59.7% for Neanderthals. The angle between the modern human average ontogenetic trajectory and the Neanderthal ontogenetic trajectory in the subspace of the first three PCs is $28.0^\circ$. A permutation test using all dimensions of shape space, however, reveals that the slopes of the Neanderthal and mean modern human (MH) ontogenetic trajectories are not...
significantly different from zero ($p < 0.31$). Therefore, we cannot reject the null hypothesis that the mean modern human and Neanderthal ontogenetic allometric trajectories are parallel.

To further explore the effects of size on facial morphology, we performed a PCA in Procrustes form space (Fig. 5). The first three PCs represent 85.0% of total variance. The Neanderthal and modern human mean ontogenetic trajectories do not coincide. The angle between the two trajectories in the subspace of the first three PCs is $8.8^\circ$. However, a permutation test cannot reject the null hypothesis that these trajectories are parallel ($p < 0.35$). As expected in a form-space analysis, PC 1 is highly correlated with centroid size ($r = 0.99$). The variance explained by ontogenetic allometry in recent modern humans is 80.1% and in Neanderthals it is 92.4%. As in shape space, the shaded region in Fig. 5 represents the 95% single prediction interval of the modern human regressions of form on the natural logarithm of centroid size, and, as in shape space, all Neanderthal and MPh adults fall outside this modern human confidence interval for allometric scaling. The thin lines represent the bootstrapped estimates of the modern human allometric trajectory computed from subsamples that simulate the Neanderthal sample composition.

The Neanderthal infant Pech de L’Azé and the youngest recent MH subadult individuals cluster at the left end of the plot (indicating smaller size) and the individuals with larger faces, e.g., Bodo, Petralona, and Kabwe fall at the opposite end. The MPhs fall at the end of the Neanderthal ontogenetic allometric trajectory and the orientation of the Neanderthal ontogenetic and MPh static trajectories appear similar. The position of the larger MPhs, Kabwe, Petralona and Bodo suggests that allometric scaling along a common trajectory explains some differences in facial morphology between them and Neanderthals. The early MH and Upper Paleolithic humans cluster with the adult recent MH.

Table 5 lists the angles between the ontogenetic allometric trajectories for each of the four modern human populations. The angles were computed in the subspace of the first three PCs to make them easier to interpret. The permutation tests were computed using all dimensions of shape space and Procrustes form space, respectively. The results of the permutation test indicate that in both shape and form space, the trajectories of each of the modern human populations is significantly different from zero (i.e., not parallel). The only exceptions are the angles between the Point Hope and Khoisan populations (shape space: $\angle = 4.3^\circ$, $p < 0.23$; form space: $\angle = 18.5^\circ$, $p < 0.07$).

**Developmental simulations**

To visualize the allometric shape changes that occur in the face of recent modern humans, the modern human mean shape was calculated and grown to the size of Bodo, the largest specimen in our sample, following the modern human mean ontogenetic allometric trajectory. Fig. 6d–f illustrates the allometric shape changes that occur in recent modern humans. Developmental simulations were also performed on Neanderthals using the Neanderthal mean facial shape and its ontogenetic allometric trajectory. These developmental simulations are depicted in Fig. 7d–f. Table 6 lists the facial features affected by allometry in both recent modern humans and Neanderthals. Among the recent modern humans in our sample, the Point Hope group has the largest faces according centroid size. Therefore, to verify that this population was not driving our results, we removed them and recalculated the mean modern human developmental allometric trajectory. The same allometric shape changes occurred in modern humans when the Point Hope sample was not included. The following facial shape changes occur as facial size increases in recent modern humans and Neanderthals: 1) a more receding and narrower frontal bone, 2) a more robust frontal process of the zygomatic, 3) an anterolateral projection of the zygomatic, 4) an anteriorly projecting nasal bone and a more prognathic nasal aperture, 5) a superoinferiorly smaller orbital length, and 6) the subnasal region becomes superoinferiorly elongated and more prognathic. The main differences between recent modern humans and Neanderthals are in the shape of the browridge and nasal aperture. In Neanderthals, the entire browridge becomes more anteriorly projecting, not only the glabellar and lateral regions as in modern humans, and the nasal aperture becomes wider.

Fig. 8 depicts a modern human (in bone color) grown to the size of Kabwe (Fig. 8a, b) and Bodo (Fig. 8c, d), and superimposed on the later two MPhs. Both fossil specimens have a more projecting and laterally expanded browridge, prognathic midface and inflated infraorbital region compared with a modern human grown to their size. Additionally, in the inferior perspective Kabwe's infraorbital plate and zygomatic bone appear to be more sagittally rotated and its nasal aperture is more anteriorly projecting. By contrast, an overgrown modern human has an entirely different facial architecture maintaining two planes: a coronal infraorbital plate combined with sagittally oriented lateral nasal walls, as well as a less projecting nasal aperture. In these features, Bodo also appears to express two midfacial planes like the modern human condition. However, it exhibits a much more projecting nasal aperture and a more inflated infraorbital surface topography than a modern human grown to its size.

Fig. 9 visualizes the mean adult Neanderthal facial shape (in bone color) grown to the size of Kabwe and Bodo, and superimposed on them (Kabwe — a, b — and Bodo — c, d). Kabwe has a more robust and projecting browridge and zygomatic bone when compared with the scaled Neanderthal. Additionally, its zygomatic bone is more anterolaterally projecting and the Neanderthal infraorbital surface topography is more inflated. Despite these differences, however, they share a similar orientation of the infraorbital plate and zygomatic body. The comparisons between Bodo (Fig. 9c, d) and the scaled Neanderthal are similar to those of Kabwe (Fig. 9a, b). The main differences are in the projection of the browridge and the frontal process of the zygomatic. These features are less anteriorly projecting when compared with the scaled Neanderthal. Additionally, Bodo's zygomatic body is more anterolaterally projecting.

**Table 5**

Angles between the ontogenetic allometric trajectories of the four recent modern human populations.$^a$

<table>
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<th>Africa</th>
<th>North America$^b$</th>
<th>Europe</th>
<th>North America$^c$</th>
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<td>North America$^c$</td>
<td>4.3 ($p &lt; 0.23$)</td>
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<td>9.0 ($p &lt; 0.001$)</td>
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$^a$ The angles were calculated in the subspace of the first three PCs in shape (upper) and form space (lower). Significant values are denoted in bold.

$^b$ Canyon del Muerto (Arizona) and Grand Gulch (Utah)

$^c$ Point Hope (Alaska)
Figure 6. Ontogenetic allometric shape changes associated with recent modern humans. The mean adult modern human shape was calculated and grown to the size of Bodo following the mean modern human ontogenetic allometric trajectory. a–c: modern human mean shape in a) anterior; b) lateral; and c) inferior orientations. d–f: scaled modern human mean shape in d) anterior; e) lateral; and f) inferior orientations. The main allometric shape changes in modern humans include a narrowing of the frontal bone, a more anteriorly projecting glabellar region, an anterolateral projection of the zygomatic, a more prognathic nasal region, and changes in subnasal morphology. See text for a more detailed description of shape changes.

Figure 7. Ontogenetic allometric shape changes associated with Neanderthals. The mean adult Neanderthal shape was calculated, warped to the surface of La Ferrassie 1 and grown to the size of Bodo following the Neanderthal ontogenetic allometric trajectory. a–c: Neanderthal mean shape in a) anterior, b) lateral, and c) inferior orientations. d–f: scaled Neanderthal mean shape in d) anterior, e) lateral, and f) inferior orientations. Neanderthals shared many allometric shape changes with modern humans. The main allometric shape differences between Neanderthals and modern humans are in the browridge and nasal aperture morphology (see text and Fig. 6 legend for a more detailed description).
Discussion

The aim of this study was threefold: 1) to explore temporal trends in facial morphology in order to gain a clearer understanding of the polarity of facial features, 2) to describe the allometric patterning of facial shape in archaic and modern humans, and 3) to test the hypothesis that differences in facial shape between archaic and modern humans are attributable to ontogenetic scaling along a common growth allometry.

Temporal trends and evolutionary models

Our PCA results and nearest neighbor calculations illustrate a temporal trend in facial morphology during Pleistocene human evolution. Although MPVs and Neanderthals overlap with one another in Procrustes shape space (Fig. 2), each individual is most similar to a member within its respective group. The main exception to this is Arago 21, which is most similar to La Chapelle-aux-Saints. Additionally, our PCA results show that there is no clear

<table>
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<th>Anatomical region</th>
<th>Recent modern humans</th>
<th>Neanderthals</th>
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<tr>
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<td>Glabellar region and lateral browridge becomes more robust and anteriorly projecting</td>
<td>Entire browridge becomes more anteriorly projecting</td>
</tr>
<tr>
<td></td>
<td>Receding frontal bone</td>
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<tr>
<td></td>
<td>Narrower frontal bone</td>
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</tr>
<tr>
<td>Midface</td>
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<tr>
<td></td>
<td>Anterior and lateral projection of zygomatics</td>
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<td>Prognathic subnasal region</td>
<td>X</td>
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</tbody>
</table>

* Allometric shape changes are described as a comparison between the modern human and Neanderthal mean shape and their respective scaled versions (e.g., the glabellar region and lateral browridge becomes more robust and anteriorly projecting with size when compared with the modern human or Neanderthal mean shape).
* X indicates that the Neanderthal condition is the same as in the modern humans.

Table 6
Recent modern humans and Neanderthal facial features affected by allometry.

Figure 8. Overgrown modern human superimposed on Kabwe and Bodo. The mean adult modern human shape was calculated, grown to the size of Kabwe and to the size of Bodo and superimposed onto them. Modern human is bone color and Kabwe (a, b) and Bodo (c, d) are in transparent purple. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
distinction between African and European MPhs. This is consistent with previous morphometric studies (e.g., Stringer, 1974, 1983; Arsuaga et al., 1997; Rightmire, 1998, 2007, 2008; Mounier et al., 2009; Harvati, 2009a; Harvati et al., 2010). For example, our nearest neighbor calculations support morphological and metric similarities between Petralona and Kabwe (Stringer et al., 1979; Murrill, 1981; Stringer, 1983; Rightmire, 2001; Harvati, 2009a; Friess, 2010; Harvati et al., 2010, 2011), as well as between Bodo and Sima de los Huesos 5 (Arsuaga et al., 1997).

In the PCA in form space, Arago 21 and Sima de los Huesos 5 plot on one end of the MPh static allometric trajectory, and Petralona, Kabwe and Bodo fall on the opposite end, indicating that the latter group of hominins express larger faces. This signal may suggest sexual dimorphism within the MPhs sample, with Arago 21 and Sima de los Huesos 5 being females, and Bodo, Kabwe and Petralona being males. Arago 21, Bodo, Kabwe, and Petralona have been described as males in earlier studies (de Lumley and de Lumley, 1973). However, the sex assignment of Sima de los Huesos 5 is more ambiguous. Compare with other specimens from the SH assemblage, as well as other MPhs and Neanderthals, Arsuaga et al. (1997) notes that the calvarial and cranial base measurements suggest that Sima de los Huesos 5 is either a small male or a large female. On the other hand, Rosas (1997) assigns the Sima de los Huesos 5 mandible to a male. While we cannot rule out the possibility that the size discrepancy between these MPhs is due to sexual dimorphism, the variation seen in these fossils could also be attributed to interpopulation variation, directional trends or diachronic fluctuations.

As noted previously, Arago 21 is most similar to La Chapelle, Sima de los Huesos 5 is most similar to Arago 21, and Shanidar 5 is most similar to Petralona. This latter point could suggest that the European Middle Pleistocene hominins display incipient Neanderthal features, as put forward in the accretion hypothesis. According to our nearest neighbor comparisons and PCA visualizations in shape space, the European Middle Pleistocene hominins share a more parasagittally rotated midface when compared with the African Middle Pleistocene hominins and a slightly more inflated infraorbital surface topography. Both the African and European Middle Pleistocene hominin groups share a wide nasal aperture and midfacial prognathism with Neanderthals. Our results indicate these latter two features are largely influenced by facial size and are most likely symplesiomorphies.

Whether the African and European Middle Pleistocene specimens are conspecific (i.e., *H. heidelbergensis*) or the European MPhs are pre-Neanderthals that look like African *H. rhodesiensis* due to symplesiomorphies cannot be clearly determined based on our data. A more comprehensive analysis including the entire cranium could provide us with greater insight. However, one intriguing alternative possibility is that Arago 21, Sima de los Huesos 5, and possibly Petralona are early members of the Neanderthal lineage and Bodo and Kabwe form a Middle Pleistocene group that is either part of a separate lineage leading to *H. sapiens*, or similar in facial features.
form to the common ancestral species of *H. sapiens* and *H. neanderthalensis*. Under this model, *H. rhodesiensis* is ancestral to *H. sapiens* in Africa. According to this model, substantial levels of genetic drift are responsible for the origins of Neanderthals in Europe and modern humans in Africa (Endicott et al., 2010). The primary problem with this model is the date of the SH material. The SH material clearly exhibits Neanderthal dental and mandibular features (Arsuaga et al., 1997; Rosas, 2001; Martinón-Torres et al., 2007, 2012) and are too derived in the Neanderthal direction for such an early geological date of ca. 600 ka (thousands of years ago) (Endicott et al., 2010; Stringer, 2012). If the taphonomic doubts (see Endicott et al., 2010; Stringer, 2012) concerning the SH material are substantiated and the previous dates of between 200 and 400 ka (Arsuaga et al., 1997; Bischoff et al., 2003) are correct, then this scenario becomes more plausible. Alternatively, Martinón-Torres et al. (2012) propose that more than one hominin lineage may have coexisted during the Middle Pleistocene in Europe. Their comprehensive study on the SH dentition shows that the SH teeth are more Neanderthal-like than any of the other penecontemporaneous Middle Pleistocene samples (e.g., Mauer or Arago), and in some aspects even more derived than Neanderthals. However, the main problem with this interpretation is that the relative ages of Mauer, Arago and the Sima de los Huesos material is highly debated (Hublin, 2009; Endicott et al., 2010).

Our results confirm previous morphometric studies (e.g., Howells, 1973; Stringer, 1974; Weber et al., 2006; Athreya, 2009; Harvati, 2009b; Harvati et al., 2010; Stansfield and Gunz, 2011) showing that modern humans, including the early modern humans, have a facial morphology that is distinct from archaic humans. All of our modern human groups are most similar to one another based on nearest neighbor calculations, reflecting a high degree of homogeneity among these groups, as well as a clear *H. sapiens* lineage separation from archaic humans at this later time period (ca. 200 ka). The similarities in facial morphology between the three temporal groups of modern humans (early, Upper Paleolithic and recent modern humans) in our study indicate that the characterized modern human facial anatomy had already evolved in Jebel Irhoud 1, around 170 ka. This is not the first study to recognize the modern-like morphology of the Jebel Irhoud 1 face (Hublin, 1992; Harvati, 2009b; Harvati and Hublin, 2012). However, the transitional and early modern human specimens, especially Jebel Irhoud 1, express morphologically more primitive frontal bones (Hublin, 1992; Athreya, 2009; Freidline et al., 2012). While Smith (2002) termed the African fossils from the time span of ca. 250 to 160 ka (e.g., Jebel Irhoud 1–4, Florisbad, Ngaloba, Eliye Springs, Guomde and Omo Kibish 2) as the African Transitional Group (ATG), other researchers (Bräuer, 2008; Rightmire, 2009; Gunz et al., 2009a) have proposed that Jebel Irhoud, along with Laetoli 18, Florisbad, Iferet, and several other Late Pleistocene African specimens represent the beginning of the *H. sapiens* lineage. Our results tentatively support this.

### Allometric patterning of facial shape in recent and archaic humans

Our results are consistent with a growing body of evidence demonstrating that taxon-specific craniofacial morphology among hominin species developed prenatally or very early postnatally (e.g., Ponce de León and Zollikofer, 2001; Ackermann and Krovitz, 2002; Lieberman et al., 2002; Strand Viðarsdóttir et al., 2002; Williams et al., 2002; Krovitz, 2003; Bastir and Rosas, 2004; Mitteroecker et al., 2004; McNulty et al., 2006; Gunz et al., 2010, 2011, 2012; Gunz, 2012).

A comparison of the developmental simulations in Figs. 6 and 7 demonstrate that modern humans and Neanderthals share many aspects of ontogenetic allometric patterning in facial shape changes (see Table 6), but they are not identical. Shape changes associated with an increase in size in these two groups include a receding and narrower frontal bone, a more robust frontal process of the zygomatic, an anterolateral projection of the zygomatic, an anteriorly projecting nasal bone and a more prognathic nasal aperture, a superoinferiorly smaller orbit, and the subnasal region becomes superoinferiorly elongated and more prognathic. Strand Viðarsdóttir et al. (2002) also identified many of these features as aspects of ontogenetic allometry shared by a geographically diverse modern human sample including a decrease in relative orbit size, a relative expansion of the zygomatic, and a relative reduction in frontal breadth. The general allometric pattern of robusticity associated with browridge size in Neanderthals and modern humans is not overly surprising. Data from primates indicate that circumorbidital features (e.g., browridge height; Ravosa, 1991) and neurocranial vault thickness (Gauld, 1996) scale with strong positive allometry. Larger anthropoids will have disproportionately larger browridges simply because they are big.

We found localized allometric differences in facial morphology between Neanderthals and modern humans; in particular, details of the nasal aperture and browridge morphology. These results are consistent with several geometric morphometric analyses on human and non-hominin primates that have found that both early postnatal cranial morphology and later postnatal cranial growth contribute to further differentiate populations and species (Richtsmeier et al., 1993; O’Higgins and Jones, 1998; O’Higgins et al., 2001; Strand Viðarsdóttir et al., 2002; Bastir and Rosas, 2004; Cobb and O’Higgins, 2004; Strand Viðarsdóttir and Cobb, 2004; Bastir et al., 2007).

In a recent ontogenetic study examining the relationship between nasal breadth, anterior palatal breadth and facial prognathism, Holton and Franciscus (2008) found that variations in nasal breadth in recent and fossil *Homo* is determined by basion—prosthion length rather than anterior palatal breadth dimensions. Lower facial prognathism, a plesiomorphic retention in Neanderthals (Trinkaus, 1987, 2003), explains their wide nasal aperture. Our results demonstrate that both facial prognathism and nasal aperture breadth are influenced by facial size in Neanderthals. Thus, the broad nasal apertures in the MPWs are most likely due to their large, prognathic faces.

In our study, the Neanderthal and modern human allometric trajectories are not coincident and the ontogenetic trajectories diverge. However, the angular difference between the modern human and Neanderthal allometric trajectories does not reach the level of statistical significance. Therefore, our results cannot reject the null hypothesis that the Neanderthal and modern human postnatal ontogenetic allometric trajectories are parallel. While our results are consistent with other comparative morphometric studies that have reported parallel ontogenetic postnatal trajectories between modern humans and Neanderthals (Ponce de León and Zollikofer, 2001; Williams et al., 2002; Krovitz, 2003), the inability to reject the null hypothesis may be an artifact of our small subadult Neanderthal sample size (see McNulty et al., 2006 for a discussion of this issue). This is an especially strong possibility since we find significant differences between the slopes in three out of the four modern human populations. Due to the small Neanderthal subadult sample size, there is a lot of potential error in its slope (as can be seen by our bootstrap simulations in Figs. 4 and 5), and the position and orientation of the Neanderthal ontogenetic allometric trajectory is strongly influenced by Pech-de-l’Azé and Teshik-Tash. Therefore, we caution against over-interpretation of this particular result. Future studies with a larger sample of Neanderthal subadults would greatly improve the accuracy of these results. Additionally, the discrepancy between our findings and those of previous studies (e.g., Bastir et al., 2007) may be explained.
by differences in the anatomical region analyzed (e.g., neurocranium versus face) or by differing landmark data sets (see Bastir and Rosas, 2004 for further discussion). For example, in their geometric morphometric study on mandibular ontogeny, Bastir et al. (2007) found modern human and Neanderthal postnatal ontogenetic allometric trajectories to be significantly different from one another. They argue that this is strong evidence for divergent postnatal ontogenetic shape changes between modern humans and Neanderthals. Different anatomical regions have different rates and patterns of growth. For example, longitudinal data reveal that among modern humans adult brain size and by extension neurocranial growth is nearly achieved (90–95%) by six years of age, whereas facial growth continues into puberty, especially among males (Bulygina et al., 2006).

The position of the MPHs in shape and form space in conjunction with the position and orientation of their static allometric trajectory suggests that allometric scaling explains large-scale differences in facial morphology between MPHs and Neanderthals. However, scaling cannot explain the morphological differences between the latter two groups and recent modern humans. Lieberman (2008) noted that in many ways MPHs are scaled-up versions of H. erectus with larger brains and faces, and that the evolutionary transformation from a MPH to a modern human involves more complex changes in the underlying cranial architecture. In a morphometric study on cranial development and integration, Lieberman et al. (2002) demonstrated that the main architectual craniofacial differences between archaic and modern humans can be attributed to differences in the length of the middle cranial fossa and cranial base angles, and that these features explain facial retraction in modern humans.

The results of our developmental simulations (Fig. 6 and 7) suggest that the following features that are present in the largest MPH faces (Bodo, Petralona and Kabwe) can be explained by ontogenetic allometric scaling along a shared archaic human trajectory (i.e., MPH and Neanderthal trajectory): narrow and receding frontal bone; wider, more projecting and entirely more robust browridge, especially the lateral portion; robust frontal process of the zygomatic; wide nasal aperture; and overall facial prognathism. There are several facial features that are commonly shared between MPHs, especially the European MPHs, and Neanderthals that cannot entirely be explained by allometry including parasagittally oriented zygomatic bones and infraorbital plate, and flat or inflated infraorbital surface topography. According to the results of our Neanderthal developmental simulations in Fig. 9, these features are less pronounced in the African MPHs when compared with a Neanderthal face, even when size differences are accounted for. Therefore, the degree of their expression can be used to differentiate between Neanderthals and MPHs.

In a recent geometric morphometric study evaluating the accretion hypothesis, Harvati et al. (2010) proposed that a convex and receding infraorbital profile may be the primitive condition for Neanderthals. They found that the infraorbital profile of African and European Middle Pleistocene hominins are nearly indistinguishable and similar, but not as inflated or parasagittally rotated, to the Neanderthal mean configuration. These authors reached a similar conclusion regarding the projection and position of glabella. MPHs, Neanderthals and Jebel Irhoud 1 show an anteroinferior placement of glabella, a condition different from H. erectus and recent modern humans (Harvati et al., 2010). Their results indicate that this morphology is most pronounced in the African MPHs (Harvati et al., 2010). Our study and others (e.g., Rosas and Bastir, 2002; Spoor et al., 2007) demonstrate that there is an allometric relationship between glabellar projection and size. Thus, the large facial sizes of Bodo and Kabwe most likely explain why the African MPHs show the most anteriorly projecting glabellae.

In a recent study testing the effects of evolutionary and static allometry on the midface, Maddux and Franciscus (2009) concluded that differences in infraorbital surface topography across the genus Homo can be explained by allometric scaling. However, we show that a modern human grown to the size of Bodo clearly displays a less inflated infraorbital surface topography than Bodo, and a Neanderthal grown to the size of Bodo expresses greater inflation in this region. This is most likely due to the fundamental differences in their craniofacial architecture. According to our results, features like infraorbital surface depression or inflation can be used to distinguish between modern and archaic populations. One key difference between our studies is that Maddux and Franciscus (2009) scaled against infraorbital region size rather than facial size. This may partly explain the discrepancies between our studies. Future work testing facial integration in MPHs and Neanderthals would provide greater insight to how this feature covaries with the surrounding facial morphology and its taxonomic value.

Conclusion

In this paper, we set out to explore temporal trends in facial morphology among Middle to Late Pleistocene humans to gain a clearer understanding of the polarity of facial features. We identify patterns of allometric shape changes in facial morphology in these hominins, and apply developmental simulations to examine how size affects facial features. Pleistocene humans can be divided into temporal groups according to their facial morphology, however, the boundary between the MPHs and Neanderthals is less obvious. Additionally, our nearest neighbor calculations show that the African and European MPHs share an overall similar facial morphology, although Arago 21, Sima de los Huesos 5 and Petralona exhibit several facial features that are intermediate between the African Middle Pleistocene and Neanderthal condition. These features include an intermediate inflation of the infraorbital surface topography and a parasagittally rotated midface. In line with the predictions of the accretion hypothesis, this could suggest that the European Middle Pleistocene hominins display incipient Neanderthal facial features.

Our findings contribute to a growing body of research that highlights the important role of allometry in hominin craniofacial development and evolution. The results of our growth studies complement previous research showing that the distinctive modern human and Neanderthal facial morphology developed early in ontogeny, by at least two years of age. While both the position of the Neanderthal and recent modern human postnatal ontogenetic trajectories and developmental simulations suggests that they share a similar pattern of ontogenetic allometric scaling, the slopes of three out of four modern human ontogenetic allometric trajectories analyzed in our study are significantly different from one another. This indicates that in modern humans, both prenatal and postnatal ontogeny contributes to further differentiate populations. By extension, this is most likely true for Neanderthals as well. The lack of statistical significance between the Neanderthal and modern human ontogenetic allometric trajectories is probably due to the restricted subadult and adult Neanderthal sample sizes. Further studies with a larger Neanderthal sample size are needed to verify this.

The overall position of the MPHs in shape and form space in conjunction with the direction and orientation of their static allometric trajectory suggests that ontogenetic allometric scaling explains large-scale differences in facial morphology between MPHs and Neanderthals. Features present in the MPHs that are due to allometric scaling include a narrow and receding frontal bone;
a wider, more projecting and entirely more robust browridge, especially the lateral portion; a robust frontal process of the zygomatic; a wide nasal aperture; and overall facial prognathism. Whereas, the parasagittally oriented zygomatic bones and infraorbital plate and flat or inflated infraorbital surface topography present in MPH faces cannot be explained by allometric scaling. Furthermore, ontogenetic allometric scaling does not explain differences between archaic and modern humans. Jebel Irhoud 1 undoubtedly expresses a modern human pattern of facial morphology, reflecting a clear modern human lineage separation at this later time period.

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Appendix A. Supplementary data

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References


