Cranial base topology and basic trends in facial evolution of *Homo*.

Markus Bastir* and Antonio Rosas

Paleoanthropology Group, Museo Nacional de Ciencias Naturales, CSIC. J. G. Abascal 2; 28006
Madrid, Spain.

Keywords: Facial projection, Prognathism, Orthognathism, Sphenoid, Integration

***Corresponding author**

E-mail address: mbastir@mncn.csic.es (M. Bastir)

Abstract

Facial prognathism and projection are important characteristics in human evolution but their three-dimensional (3D) architectonic relationships to basicranial morphology are not clear. We used geometric morphometrics and measured 51 3D-landmarks in a comparative sample of modern humans ($N = 78$) and fossil Pleistocene hominins ($N = 10$) to investigate the spatial features of covariation between basicranial and facial elements. The study reveals complex morphological integration patterns in craniofacial evolution of Middle and Late Pleistocene hominins. A downwards-orientated cranial base correlates with alveolar maxillary prognathism, relatively larger faces, and relatively larger distances between the anterior cranial base and the frontal bone (projection). This upper facial projection correlates with increased overall relative size of the maxillary alveolar process. Vertical facial height is associated with tall nasal cavities and is accommodated by an elevated anterior cranial base, possibly because of relations between the cribriform and the nasal cavity in relation to body size and energetics. Variation in upper and midfacial projection can further be produced by basicranial topology in which the midline base and nasal cavity are shifted anteriorly relative to retracted lateral parts of the base and the face. The zygomatics and the middle cranial fossae act together as bilateral vertical systems that are either projected or retracted relative to the midline facial elements, causing either midfacial flatness or midfacial projection correspondingly. We propose that facial flatness and facial projection reflect classical principles of craniofacial growth counterparts, while facial orientation relative to the basicranium as well as facial proportions reflect the complex interplay of head-body integration in the light of encephalization and body size decrease in Middle to Late Pleistocene hominin evolution. Developmental and evolutionary patterns of integration may only partially overlap morphologically, and traditional concepts taken from research on two-dimensional (2D)

lateral X-rays and sections have led to oversimplified and overly mechanistic models of basicranial evolution.

Introduction

The form of the face is of major interest in human evolution (Tobias, 1972; Bilsborough and Wood, 1988; Bermúdez de Castro et al., 1997; Lieberman, 1998; Leakey et al., 2012; Lordkipanidze et al., 2013). The most important factors of evolutionary variation in the facial skeleton of *Homo* include i) prognathism, which is the angular relationship between the face and the cranial base, and ii) facial projection, which describes the degree to which the facial profile projects out anteriorly (Bilsborough and Wood, 1988; Lieberman, 1998).

Early hominins are very prognathic (Bilsborough and Wood, 1988) though some show particularly flat (Leakey et al., 2012) or even concave (“dished”; Tobias, 1972; Lordkipanidze et al., 2013) midfacial profiles. In later human evolution, prognathism is reduced (orthognathism) but variation in facial projection and size is still considerable (Trinkaus, 1987; Lieberman, 1998; Trinkaus, 2003; Bastir et al., 2007; Maddux and Franciscus, 2008; Freidline et al., 2012). These variations have been interpreted from very distinct perspectives (Rak, 1983, 1986; Trinkaus, 1987; Ponce de León and Zollikofer, 2001; Weaver, 2009; Lieberman, 2011).

From an adaptive point of view, factors triggering the evolution of hominin facial form have been associated with its functional performance. In particular, adaptation to masticatory (or para-masticatory) biomechanics (e.g., “anterior dental loading hypothesis”; Rak, 1986; Spencer and Demes, 1993; Lieberman, 2011) as well as respiration and its related functions (e.g., humidity and temperature control) have been suggested (Franciscus and Trinkaus, 1988; Holden, 1999; Mlynski et al., 2001; Churchill et al., 2004). These approaches have been also used to investigate

the enigmatic but distinctive and recognizable face of Neandertals. However, hypotheses of biomechanics and respiratory models accounting for distinctive facial morphology are not supported by recent quantitative analyses (O'Connor et al., 2005; Holton and Franciscus, 2008; Rae et al., 2011), and random processes (e.g., genetic drift) have been suggested as ultimate causes of Neanderthal craniofacial form (Weaver, 2009).

As alternatives to functional adaptations or random changes, models of evolutionary and developmental integration have been developed that link large-scale evolutionary changes in size and position of the face to developmental shifts of the brain and/or cranial base topology and embryological brain-face interactions (Enlow, 1990; Rosas, 1992; Ross and Ravosa, 1993; Ross et al., 2004; Lieberman, 2011; Marcucio et al., 2011). According to this perspective, evolutionary brain expansion is a primary agent affecting underlying cranial base topology and this in turn, would have modified facial form via developmental cascades, because the face is physically attached to the external cranial base (physical “knock-on” effects) (Biegert, 1957; Enlow, 1990; Rosas, 1992; Lieberman et al., 2000a, b; 2001; Lieberman, 2011; Marcucio et al., 2011; Martínez-Abadías et al., 2012).

The basicranium plays a key role as the interface between the brain and face. In particular, the angle of the cranial base has long been assumed to link evolutionary brain size increase with facial reorientation and reduction (Enlow, 1990; Lieberman et al., 2000b, 2002; Jeffery and Spoor, 2002; Bastir and Rosas, 2009; Bastir et al., 2010). However, even though this is grossly true at the level of the order Primates (Ross and Ravosa, 1993; Ross and Henneberg, 1995; Ross et al., 2004), within hominins neither intra- nor interspecifically clear quantitative evidence is available for such relations (Bastir and Rosas, 2009). This is in part due to different measurement protocols (Ross and Henneberg, 1995; Spoor, 1997; Lieberman and McCarthy, 1999), as well as to conceptual differences between basicranial orientation and flexion (Kuroe et al., 2004; Rosas et al., 2008), and

also because no study has yet quantified the three-dimensional (3D) anatomy of the cranial base and the face together.

Previous studies, based on 2D x-ray dataset, have proposed that shortening of the anterior sphenoid in the midline is linked with evolutionary reduction of facial projection in humans (Enlow, 1990; Lieberman, 1998) based on ontogenetic correlations between anterior sphenoid and midfacial length. However, no convincing evidence has been produced at the level of evolutionary anatomy. Indeed, Spoor et al. (1999) showed that anterior sphenoid length may even be smaller in strongly projecting and prognathic faces of Mid-Pleistocene hominins and Neandertals. Also, the “facial block rotation model” links decrease in facial prognathism and projection with encephalization, middle cranial fossa length, and basicranial flexion, which causes a (brain size-driven) rotation of the facial block (orbits, anterior cranial base, ethmomaxillary complex [Lieberman, 2000; Lieberman et al., 2000b; McCarthy and Lieberman, 2001]). The basic hypothesis of this two-dimensional model is that the posterior maxillary (PM)-plane (defined in x-rays by the anteriormost point of the greater sphenoid wings and the posteriormost points of the maxillary alveolar tubercle, both projected into the midline) is tightly aligned 90 degrees with the orbits. The orbits are part of the anterior cranial base and cranial base flexion affects the angle between the anterior and the posterior cranial base. Therefore, during human evolution basicranial flexion increased and rotated the PM-plane (and the orbits/anterior cranial base = facial block) below the anterior cranial base, thereby reducing projection and prognathism (Lieberman, 2000, 2011).

However, only 3D analyses can capture the complex spatial relationships between basicranial and facial morphology. As an example, it has been suggested recently that basicranial flexion (in the sagittal plane) has remained stable among hominins (Ross and Henneberg, 1995; Ross et al., 2004; Bastir and Rosas, 2009), while lateral cranial base elements continue to accommodate increasing size of the brain lobes (Bastir and Rosas, 2009; Bastir et al., 2011b).

Further studies have emphasized the 3D complexity of basicranial anatomy, suggesting that lateral base configurations are relevant for facial evolution, thus drawing attention to new structural relationships and potential interactions (Bastir and Rosas, 2006; Bastir et al., 2006, 2011b; Gkantidis and Halazonetis, 2011; Neaux et al., 2013a). In the light of this, it is still unclear how evolutionary basicranial changes relate to basic facial features such as prognathism and projection in hominins (Jeffery and Spoor, 2002; Ross et al., 2004; Bastir and Rosas, 2006, 2009; Lieberman, 2011; Neaux et al., 2013).

In this paper, we address the hypothesis of integration between the cranial base and the face. We use geometric morphometrics to analyze 51 3D landmarks of the internal and external cranial base and the face in fossil early *Homo*, Mid-Pleistocene hominins, Neandertals, and modern humans. It is expected that cranial base topology is tightly correlated with facial prognathism and projection because of anatomical proximity, developmental timing, and interactions (Enlow, 1990; Rosas, 1992; Lieberman et al., 2000b; Bastir et al., 2006; Marcucio et al., 2011).

Materials and methods

Computed tomographic (CT) scans of 78 adult recent humans, representing geographic variation from Africa (N = 27), Asia (N = 26), and Europe (N = 25), and ten fossil Pleistocene humans (Table 1) were reconstructed and computer models of their 3D endocranial and facial surfaces were generated in Amira 4.1 software (Mercury Inc. USA). A set of 51 3D landmarks was digitized on the endo- and exocranial surface of the cranial base (Bastir et al., 2011b) and on the face on the 3D reconstructions (Table 2). These landmark sets required the least amount of missing data estimation in the fossils and defined the most important features of basicranial and

facial architecture. Landmark data of the fossil basicrania were taken from a previous study (Bastir et al., 2011b), where missing landmarks were estimated geometrically using densely-spaced 3D semilandmarks in the vicinity of the missing data (Mitteroecker and Gunz, 2009). For the present study, we used only the true basicranial landmarks of Bastir et al. (2011b). Missing data of facial structures in the fossil hominins were reconstructed using bilateral symmetry and multiple multivariate regressions (Mitteroecker and Gunz, 2009). Landmark digitizing error was small and within acceptable limits, as reported previously (Bastir et al., 2008, 2011b).

Statistical analyses

Generalized Procrustes Analysis (GPA) was performed to generate shape data (Mitteroecker and Gunz, 2009). Hypotheses of shape integration were tested by Two-Block Partial Least Squares Analysis (PLS) within the full landmark configuration, following Gunz and Harvati (2007). This method allows for the visual assessment of the PLS shape covariation patterns in the context of the full landmark configuration within the same shape space. That was important to assess prognathism, defined as facial orientation relative to the base in the full craniofacial context, and facial projection relative to the cranial base. Partial Least Squares analysis is an ordination method that maximizes the covariation between the basicranial and the facial block and quantifies that with a correlation between scores along corresponding PLS vectors of each block (Bastir et al., 2005; Mitteroecker and Gunz, 2009). In addition, an overall correlation coefficient is provided, known as RV-coefficient (Klingenberg et al., 2003). The PLS analyses were performed and the statistical significance assessed by permutation tests ($N = 10000$) in MorphoJ geometric morphometric software (Klingenberg, 2011). Finally, the EVAN-toolkit (EVAN-Society, 2010) was used for calculation and visualization of specifically located thin-plates splines (TPS) of

warped mean shapes along their respective PLS vectors. These splines are registration-independent interpolations between two landmark configurations and thus the preferable way of visualization (Bastir et al., 2011b). The TPS grids were used to pinpoint features of shape covariation.

Results

Table 3 shows the results of the PLS analysis. The RV-coefficient between the basicranial and the facial block was 0.67 ($p < 0.0001$). The first three PLS dimensions accounted for approximately 88% of total covariance, with highly correlated patterns of shape covariation (Fig. 1). The first dimension (PLS1) accounts for 60.7% of total covariance (Fig. 2). Towards the negative scores, cranial bases have wide and elongated middle cranial fossae and a wide anterior cranial fossa base with a relatively elongated anterior cranial floor. These basicranial configurations correlate with relatively smaller faces that are mediolaterally narrower and retracted and with a reduced alveolar prognathism (orthognathism; $R = 0.95$; $p < 0.0001$; Fig. 2). Towards the positive PLS1 scores, the cranial bases are narrower, with relatively shorter middle cranial fossae and a shorter anterior cranial floor that correlates with wider, relatively larger, projecting faces with increased alveolar prognathism. Upper facial projection is also evident by the larger relative distance between the nasion and foramen caecum (Fig. 2). Similar slopes of fossil and recent human groups in the associated PLS1 scatterplot indicate roughly shared integration patterns among human species (Fig. 1a). While modern humans and Neandertals overlap on positive PLS1 scores, the Mid-Pleistocene hominins plot towards the extreme of the positive scores (Fig. 1a).

The second PLS dimension (PLS2) accounts for 22.8% of total covariance ($R = 0.85$, $p < 0.0003$). Figure 3 indicates that towards the negative scores (left column of Fig. 3) the cranial bases

are elevated in the midline relative to the lateral parts of the greater sphenoid wings, and the anterior cranial fossae and the cribriform plates are shortened. The elevation of the midline anterior cranial floor is part of a cranial base that is rotated entirely counter-clockwise relative to the face and associated with tall internal nasal cavities within tall faces (Fig. 3). This is seen also in frontal view where both the midline base within the nasal roof is slightly elevated in the midline (superior TPS grid of Figure 3) and the anterior facial height is relatively larger reflecting the tall faces. Lateral views also show a downward declined nasal floor. In the axial view, the widths of the middle cranial fossae are relatively reduced (Fig 3). Towards positive PLS2 scores (right column of Fig. 3) the entire cranial base is rotated clockwise and associated with a reduced relative vertical height of the face. The entire anterior cranial fossae and cribriform plate are relatively longer and wider at the base of the frontal lobes (axial view). In lateral view, the nasal floor is more horizontally oriented. Again, similar covariation patterns are observed in the scatterplots in different hominin groups (Fig. 1b) but, importantly, Neandertals display smaller facial PLS scores suggesting a grade-shift towards taller nasal cavities and faces.

The third PLS dimension (PLS3) accounts for 5.6% of total covariance ($R = 0.77$, $p < 0.0001$; Table 3) and is depicted in Figure 4. Towards negative scores (left column, Fig. 4) it shows narrow basicrania in which axial views display an anteriorly shifted, midline base relative to posteriorly retracted bilateral sphenoid wings (Fig. 4). The midline cranial base is only weakly flexed between the anterior sphenoid and the spheno-occipital clivus. The projecting anterior cranial floor in the midline is correlated with upper and midfacial projection (glabella, foramen caecum, nasion, rhinion) and a forward extension of the nasal cavity relative to the retracted zygomatic bones. In contrast, towards positive PLS3 scores (right column, Fig. 4) the anterior midline cranial floor is retracted relative to bilaterally projecting sphenoid wings. Sphenoid wing projection is accompanied by a projection and reorientation of the zygomatics. The midline cranial base is

strongly flexed between the anterior sphenoid and the spheno-occipital clivus, and this basicranial pattern is associated with upper and midfacial flatness and a retracted nasal cavity. The scatterplots of PLS3 (Fig. 1c) show a trend whereby Mid-Pleistocene hominins and Neandertals have greater midfacial projection than do modern humans (except Bodo plotting as an outlier, possibly in relation to uncertainties in its reconstruction; Fig. 1c).

The PLS analyses show a clear statistical signal of morphological integration, both at the general level (RV-coefficient) as well as at more specific levels along the individual PLS vectors. The results also demonstrate that different components of the craniofacial system present specific patterns of covariation and illustrate particular features of variation that reflect nasal cavity and facial size (PLS2; Fig. 1b) and upper-midfacial projection (PLS3; Fig. 1c).

Discussion

The present study analyzed the 3D morphological covariation between the cranial base and the face in modern humans, Mid-Pleistocene hominins, and Neandertals. Integration between the base and the face has been proposed based on anatomical proximity, developmental timing, and early developmental interactions (Enlow, 1990; Lieberman et al., 2000b; Bastir et al., 2006; Lieberman, 2011; Marcucio et al., 2011). Our results provide clear statistical evidence for interactions between the base and the face across hominins and illustrate major evolutionary covariation trends in the *Homo* craniofacial system that manifested as encephalization and facial reduction (Lieberman et al., 2002; Bruner et al., 2003; Gunz et al., 2010). The results further confirm that brain size increase in the last 500,000 years is associated with important basicranial and facial modifications.

Figure 1 shows that PLS1 orders Mid-Pleistocene hominins, Neandertals, and modern humans along a shared evolutionary gradient. At the level of the cranial base, this figure shows that the angle between the spheno-occipital clivus and the anterior sphenoid varies only little (Ross et al., 2004; Bastir and Rosas, 2009). In contrast, the relative lengths of anterior cranial base segments (sphenoid plane, cribriform plate), as well as the lateral middle cranial fossae, vary more strongly and probably reflect features related to encephalization at the level of the frontal, temporal, and parietal lobes (Bruner et al., 2003; Bastir et al., 2008, 2011b; Bruner and Holloway, 2010). Covariation between these basicranial features and alveolar prognathism and facial proportions, such as reflected by PLS1, may well be a shared primitive structural relationship in the hominin skull.

Figures 2 and 5a, b show that the anterior sphenoid in the midline is relatively longer in modern humans compared to Neandertals and Mid-Pleistocene hominins, which supports the findings of Spoor et al. (1999) and challenges Lieberman's (1998) proposition that sphenoid shortening correlates with (and causes) facial retraction in modern humans. Also, the relative length of the spheno-occipital clivus is considerably shorter in Mid-Pleistocene hominins than in modern humans. This has been shown before (Spoor et al., 1999) and may reflect negative scaling between non-cortical brain and body mass, as suggested by Strait (1999). Body mass in Mid-Pleistocene hominins and Neandertals is estimated much larger than in modern humans (Ruff et al., 1997) and could thus account for the smaller posterior cranial base length. Basicranial variation patterns are highly correlated with facial modifications. Facial reduction shown towards negative PLS1 scores occurs in height, length, and width (Fig. 2) and implies reduced facial projection (relative distance between nasion and foramen caecum) and reduced alveolar prognathism (relative alveolar arcade length).

Decrease in facial prognathism and projection has been linked with encephalization, middle cranial fossa length, and basicranial flexion via the “facial block rotation model” (Lieberman, 2000, 2011; Lieberman et al., 2000b; McCarthy and Lieberman, 2001). However, PLS1 shows that the evolutionary relations between basicranial flexion, middle cranial fossa length, as well as facial projection and prognathism, are far more complex than when inferred from 2D (x-ray) driven data analysis. While facial block “rotation” can be actually identified in lateral view (SOM Movie 1 in lateral transparent view, SOM Movie 2 in supero-lateral view), the angle of basicranial flexion remains fairly stable, although the overall orientation of the cranial base changes. Expansion of anterior cranial floor length may alter angle values when measurements include foramen caecum, but flexion between anterior and posterior basicranial elements is not strongly modified. However, the overall orientation of the base relative to the face is altered (Enlow and McNamara, 1973; Enlow et al., 1982; Kuroe et al., 2004; Rosas et al., 2008; Bastir et al., 2010). Because of this, the facial block rotation model cannot easily explain a reorientation of the face that is associated with reduction in facial width and height. In addition, this different overall orientation affects the architecture of the posterior face via a reduction of mandibular ramus breadth and pharyngeal space (Smith and Josell, 1984; McCarthy and Lieberman, 2001; Bastir et al., 2002, 2004; Bastir and Rosas, 2005). However, rather than rotating, the maxilla decreases in its overall alveolar proportions relative to the cranial base, which changes its proportions in response to increased brain size and globularity (Lieberman et al., 2002; Bruner et al., 2003; Bruner and Holloway, 2010; Gunz et al., 2010; Bastir et al., 2011b).

Our data indicate, therefore, that what appears as “rotation of the facial block and PM-plane” (Lieberman et al., 2000b; McCarthy and Lieberman, 2001), characteristic of modern human facial architecture, is in fact the combined result of i) an elongation of the bilateral middle cranial fossae and temporal lobes (Bastir et al., 2008, 2011b) with ii) an elongation of the anterior

sphenoid (Spoor et al., 1999), both of which define the cranial reference of the PM plane, and iii) an elongation of the posterior base (Strait, 1999) together with iv) a counterclockwise rotation of the entire base (Enlow et al., 1982; Kuroe et al., 2004; Rosas et al., 2008; Bastir et al., 2010; see SOM Movies 1 and 2). It is possible that basicranial flexion between the anterior sphenoid and the spheno-occipital clivus is far less important than previously assumed (Ross and Henneberg, 1995; Ross et al., 2004), at least in the evolution of *Homo*. Changes in basicranial orientation relative to the face are (necessarily) expressed by variations in facial orientation.

Along PLS2, the basicranial orientation is associated with the height of the nasal cavity and the face, and the orientation of the nasal floor and lower maxilla. Taller faces (e.g., Neandertals and Mid-Pleistocene humans) show also more klinorhynch (downwards oriented lower maxillae) relative to the posterior base (Hofer, 1957, 1960; Shea 1985; Ross and Ravosa, 1993; Ross and Henneberg, 1995; Bastir and Rosas, 2004). It is important to note a grade shift along PLS2 scores for block 2 (the face) in fossil *Homo* (Fig. 1b). This implies that, while sharing a similar integration pattern (represented by the slope), modern humans have shorter nasal cavities and faces and less klinorhynch (as evident from the intercept; Ross and Henneberg, 1995). Neandertals and Mid-Pleistocene humans thus have taller nasal cavities and faces than modern humans, a fact that is reflected well in other studies of facial and mandibular evolutionary anatomy (Rosas, 1997, 2001; Trinkaus, 2003; Bastir et al., 2007; Maddux and Franciscus, 2008; Bastir et al., 2010).

Recent research on the underlying factors of facial size seem to indicate the importance of the respiratory apparatus and its functional constraints on the cranial airway dimensions (Rosas and Bastir, 2002; Bastir, 2008; Yokley et al., 2009; Bastir et al., 2011a; Bastir and Rosas, 2011, 2013; Holton et al., 2013). All these studies support the hypothesis that the greater body mass of Middle and Late Pleistocene hominins (Ruff et al., 1997; Churchill, 2006) and its associated energetic demands require larger cranial airways for oxygen supply, which are housed in taller

faces. This coincidence leads us to suggest that for reasons related to the respiratory system and body energetics, postcranial and facial features are probably correlated for systemic (non-random) reasons (Bastir, 2004, 2008; Rosas et al., 2006; Yokley et al., 2009; Holton et al., 2013) and are reflected in covariation patterns related to PLS1 and PLS2. Frontal views in Figure 3 show that the elevated anterior cranial base provides the space for increased nasal cavity size. We suggest that facial variation along PLS 2 is thus likely related to somatic rather than to brain and basicranial factors (Rosas and Bastir, 2002; Bastir, 2004, 2008; Rosas et al., 2006; Yokley et al., 2009; Bastir and Rosas, 2013).

The covariation of basicranial and facial shape illustrated by PLS3 (Fig. 4) shows basicranial variations related to upper and midfacial projection or flatness. The architectonic background of these patterns is best understood in a 3D perspective, looking at the axial views of the cranial base and the lateral views of the associated face. This combination illustrates that i) the projection of the sphenoid wings, ii) a retraction of the midline anterior cranial floor, and iii) a posterior expansion of the cribriform plate results in upper and midfacial flatness (see also SOM Movie 3). The PLS3 scatterplots indicate that Mid-Pleistocene hominins and particularly Neandertals show a strong upper and midfacial projection, expressed by the relative distance between foramen caecum and nasion (Fig. 4, SOM Movie 3). This feature is important as it indicates that the position of the sphenoid body relative to the sphenoid wings, and not its length, contributes to facial projection. This is because the shape distances between the posterior sphenoid and the posterior cribriform landmarks barely change along PLS3 scores. Yet, the position (topology) of the sphenoid body in basicranial shapes that plot towards negative PLS3 scores is shifted forwards, and those that plot towards positive PLS3 scores are retracted backwards (Fig. 4, SOM Movie 3). Midfacial length in projecting faces is longer than in flat faces as shown previously (Lieberman, 2000, 2011). The shared anterior shift of lateral base and face supports previous suggestions of lateral

integration between basicranial and facial elements, independent of midline elements (Bastir et al., 2004; Bastir and Rosas, 2005, 2006; Gkantidis and Halazonetis, 2011). Its relevance for interpretations of evolutionary morphology can be recognized both within and between species (Fig. 1c) and this integration pattern is likely involved in the craniofacial variation of early hominins with “dished” faces (Tobias, 1972; Lordkipanidze et al., 2013). Whenever the lateral middle cranial fossae project forwards (intra- and interspecific factors), the zygomatics will project forwards (SOM Movie 3). Figures 4–6 illustrate the importance of this finding that could be important in the context of the facial architecture of *Homo antecessor* (Fig. 6; Bermúdez de Castro et al., 1997; Gibbons, 1997; Freidline et al., 2013), as well as Neandertals and modern humans (Rak, 1986; Trinkaus, 1987; Rosas, 1992). Our results illustrate that the large face of Neandertals shows midfacial projection due to an anteriorly placed sphenoid body relative to retracted sphenoid wings, zygomatics [and probably the mandibular rami (Bastir and Rosas, 2005)]. This provides the basicranial template (“sphenoid wings retreat”) of the Neandertal “*zygomatic retreat*” suggested by Trinkaus (1987), and most likely also the high frequency of a retromolar space (Franciscus and Trinkaus, 1995); a hypothesis that needs to be tested in the future.

The spatial relation between midline and lateral elements of basicranial topology are established relatively early postnatally (Neubauer et al., 2009), and later facial growth on such a basicranial template will not modify a given facial projection. This could explain why postnatal ontogeny does not modify facial morphology substantially in growth simulation studies of *H. antecessor* (Freidline et al., 2013).

It is very difficult to assess the direction of evolutionary and developmental causes and effects of covariation between basicranial and facial morphology. A spatiotemporal gradient of ontogenetic maturation suggests that earlier maturing basicranial structures will spatially influence the adjacent facial parts that attain adult morphology later. This phenomenon is

described in Enlow's "counterpart analysis" (Enlow, 1990) and has been supported quantitatively by morphometric analyses of longitudinal data of human craniofacial ontogeny (Bastir et al., 2006). However, translating this ontogenetic spatiotemporal principle to an evolutionary framework is not straightforward. Although it is likely that the spatiotemporal gradient of postnatal ontogenetic maturation known for modern humans also applies to the ontogeny of other hominin species, early developmental modifications of craniofacial morphogenesis clearly act on basicranial and facial relations before postnatal craniofacial growth. Growth might only translate early patterning into an observable grade shift in the morphology of adults.

Recently it has been suggested that craniofacial evolution in Middle and Late Pleistocene hominins is compatible with a model of genetic drift and random morphological evolutionary trends, which contrasts with postcranial signals that clearly reflect evolutionary adaptations and selection (Weaver, 2009). Although our study is methodologically not comparable, the present findings indicate that at the level of integration between the head and the body, non-random evolutionary trends are likely. Climate- and activity pattern-related body size in Mid-Pleistocene hominins becomes reduced during evolution towards modern humans (Weaver, 2009). The trend of facial reduction from Middle Pleistocene towards modern humans seen here and noted previously, e.g., by Trinkaus (2003), seems to follow the trend of postcranial gracilization (Weaver, 2009).

Our results further suggest that the orientation of the base relative to the face is one of the most important factors of evolutionary integration in the hominin head and interacts with major facial proportions (Bastir et al., 2010). The question of whether encephalization and brain-base shape "cause" these phenomena requires combining experimental research designs with 3D morphometrics (Hallgrímsson and Lieberman, 2008; Lieberman et al., 2008) and is outside the scope of the present study.

Conclusions

Research on craniofacial evolutionary integration in human evolution may have over-interpreted the role of basicranial flexion and thus over-simplified actual 3D morphological complexity of basicranial anatomy. The findings of this study suggest important interactions between the head and the body in relation to scaling, body mass, and energetics (Biegert, 1957; Bastir, 2004, 2008; Rosas et al., 2006; Yokley et al., 2009; Holton et al., 2013). Developmental integration factors, based on spatial proximity and basicranio-facial attachment, can influence facial variation in antero-posterior and medio-lateral dimensions. Some features of facial projection are related to facial size and prognathism, while features of upper- and midfacial projection are also related to the topology of middle cranial fossae and sphenoid body. Overall basicranial orientation and proportions of anterior and posterior base lengths are more clearly associated with trends in facial evolution than basicranial flexion between the anterior sphenoid and the spheno-occipital clivus (Enlow, 1990).

Acknowledgments

We thank two anonymous reviewers and the editor for helpful suggestions on previous drafts. This research has been funded by CGL2012-37279 and CGL2012-36682 (MINECO, Spain).

References

- Bastir, M., 2004. A geometric morphometric analysis of integrative morphology and variation in human skulls with implications for the Atapuerca-SH hominids and the evolution of Neandertals. Structural and systemic factors of morphology in the hominid craniofacial system PhD-dissertation, Department of Anthropology. Autonoma University of Madrid, Madrid.
- Bastir, M., 2008. A systems-model for the morphological analysis of integration and modularity in human craniofacial evolution. *J. Anthropol. Sci.* 86, 37–58.
- Bastir, M., Rosas, A., 2004. Facial heights: Evolutionary relevance of postnatal ontogeny for facial orientation and skull morphology in humans and chimpanzees. *J. Hum. Evol.* 47, 359–381.
- Bastir, M., Rosas, A., 2005. Hierarchical nature of morphological integration and modularity in the human posterior face. *Am. J. Phys. Anthropol.* 128, 26–34.
- Bastir, M., Rosas, A., 2006. Correlated variation between the lateral basicranium and the face: A geometric morphometric study in different human groups. *Arch. Or. Biol.* 51, 814–824.
- Bastir, M., Rosas, A., 2009. Mosaic evolution of the basicranium in *Homo* and its relation to modular development. *Evol. Biol.* 36, 57–70.
- Bastir, M., Rosas, A., 2011. Nasal form and function in Midpleistocene human facial evolution. A first approach. *Am. J. Phys. Anthropol.* 144, 83.
- Bastir, M., Rosas, A., 2013. Cranial airways and the integration between the inner and outer facial skeleton in humans. *Am. J. Phys. Anthropol.* 152, 287–293.
- Bastir, M., Rosas, A., Kuroe, K., 2002. Morphogenetic determinants of mandibular ramus breadth. A test in modern human populations. *Am. J. Phys. Anthropol.* S115, 40–41.
- Bastir, M., Rosas, A., Kuroe, K., 2004. Petrosal orientation and mandibular ramus breadth: Evidence of a developmental integrated petroso-mandibular unit. *Am. J. Phys. Anthropol.* 123, 340–350.
- Bastir, M., O'Higgins, P., Rosas, A., 2007. Facial ontogeny in Neanderthals and modern humans. *Proc. Roy. Soc. B* 274, 1125–1132.
- Bastir, M., Rosas, A., Lieberman, D.E., O'Higgins, P., 2008. Middle cranial fossa anatomy and the origins of modern humans. *Anat. Rec.* 291, 130–140.
- Bastir, M., Rosas, A., Stringer, C., Cuétara Pastor, J.M., Kruszynski, R., Weber, G.W., Ross, C.F., Ravosa, M.J., 2010. Effects of brain and face size on basicranial form in human and primate evolution. *J. Hum. Evol.* , 424–431.
- Bastir, M., Godoy, P., Rosas, A., 2011a. Common features of sexual dimorphism in the cranial airways of different human populations. *Am. J. Phys. Anthropol.* 146, 414–422.
- Bastir, M., Rosas, A., Gunz, P., Pena-Melian, A., Manzi, G., Harvati, K., Kruszynski, R., Stringer, C., Hublin, J.-J., 2011b. Evolution of the base of the brain in highly encephalized human species. *Nature Commun* 2, 588.
- Bermúdez de Castro, J.M., Arsuaga, J.L., Carbonell, E., Rosas, A., Martínez, I., Mosquera, M., 1997. A Hominid from the Lower Pleistocene of Atapuerca, Spain, Possible Ancestor to Neandertals and Modern Humans. *Science* 276, 1392–1395.
- Biegert, J., 1957. Der Formwandel des Primatenschädels und seine Beziehungen zur ontogenetischen Entwicklung und den phylogenetischen Spezialisierungen der Kopforgane. *Gegenb. Morphol. Jahrb.* 98, 77–199.
- Bilsborough, A., Wood, B., 1988. Cranial Morphometry of Early Hominids: Facial Region. *Am. J. Phys. Anthropol.* 76, 6–86.
- Bruner, E., Holloway, R.L., 2010. A bivariate approach to the widening of the frontal lobes in the genus *Homo*. *J. Hum. Evol.* 58, 138–146.

- Bruner, E., Ripani, M., 2008. A quantitative and descriptive approach to morphological variation of the endocranial base in modern humans. *Am. J. Phys. Anthropol.* 137, 30-40.
- Bruner, E., Manzi, G., Arsuaga, J.-L., 2003. Encephalization and allometric trajectories in the genus *Homo*. Evidence from the Neanderthal and modern lineages. *Proc. Natl. Acad. Sci. USA* 100, 15335–15340.
- Churchill, S.E., 2006. Bioenergetic perspectives on Neanderthal thermoregulatory and activity budgets. In: Harvati, K., Harrison, T. (Eds.), *Neanderthals revisited*. Springer Verlag, New York City, pp. 113–156.
- Churchill, S.E., Shackelford, L.L., Georgi, J.N., Black, M.T., 2004. Morphological variation and airflow dynamics in the human nose. *Am. J. Hum. Biol.* 16, 625–638.
- Enlow, D.H., 1990. *Facial Growth*, 3rd ed. W.B. Saunders Company, Philadelphia.
- Enlow, D.H., McNamara, J.A.J., 1973. The Neurocranial Basis for Facial Form and Pattern. *Am. J. Orthod.* 43, 256–270.
- Enlow, D.H., Moyers, R.E., Hunter, W.S., McNamara Jr., J.A., 1969. A procedure for the analysis of intrinsic facial form and growth. *Am. J. Orthod.* 56, 6–23.
- Enlow, D.H., Pfister, C., Richardson, E., Kuroda, T., 1982. An Analysis of Black and Caucasian Craniofacial Patterns. *Ang. Orthodont.* 52, 279–287.
- Franciscus and Trinkaus, 1995. Determinants of retromolar space presence in Pleistocene *Homo* mandibles. *J. Hum. Evol.* 28, 577–595.
- Franciscus, R.G., Trinkaus, E., 1988. Nasal morphology and the emergence of *Homo erectus*. *Am. J. Phys. Anthropol.* 75, 517–527.
- Freidline, S.E., Gunz, P., Harvati, K., Hublin, J.-J., 2012. Middle Pleistocene human facial morphology in an evolutionary and developmental context. *J. Hum. Evol.* 63, 723–740.
- Freidline, S.E., Gunz, P., Harvati, K., Hublin, J.-J., 2013. Evaluating developmental shape changes in *Homo* antecessor subadult facial morphology. *J. Hum. Evol.* 65, 404–423.
- Gibbons, A., 1997. A New Face For Human Ancestors. *Science* 276, 1331–1333.
- Gkantidis, N., Halazonetis, D.J., 2011. Morphological integration between the cranial base and the face in children and adults. *J. Anat.* 218, 426–438.
- Gunz, P., Harvati, K., 2007. The Neanderthal "chignon": Variation, integration, and homology. *J. Hum. Evol.* 53, 732–746.
- Gunz, P., Neubauer, S., Maureille, B., Hublin, J.-J., 2010. Brain development after birth differs between Neanderthals and modern humans. *Current biology* 20, R921–R922.
- Hallgrímsson, B., Lieberman, D.E., 2008. Mouse models and the evolutionary developmental biology of the skull. *Int. Comp. Biol.* 48, 373–384.
- Hofer, H., 1957. Zur Kenntnis der Kyphosen des Primatenschädels. *Verh. Anat. Ges.* 54, 54–76.
- Hofer, H., 1960. Studien zum Problem des Gestaltwandels des Schädels der Säugetiere insbesondere der Primaten, I. Die medianen Krümmungen des Schädels und ihre Erfassung nach der Methode von Landzert. *Z. Morphol. Anthropol.* 50, 299–316.
- Holden, C., 1999. A New Look Into Neandertals' Noses. *Science* 285, 31–33.
- Holton, N.E., Franciscus, R.G., 2008. The paradox of a wide nasal aperture in cold-adapted Neandertals: a causal assessment. *J. Hum. Evol.* 55, 942–951.
- Holton, N.E., Yokley, T.R., Froehle, A.W., Southard, T.E., 2013. Ontogenetic scaling of the human nose in a longitudinal sample: Implications for genus *Homo* facial evolution. *Am. J. Phys. Anthropol.* 153, 52–60.
- Jeffery, N., Spoor, F., 2002. Brain Size and the Human Cranial Base. *Am. J. Phys. Anthropol.* 118, 324–340.

- Klingenberg, C.P., Mebus, K., Auffray, J.-C., 2003. Developmental integration in a complex morphological structure: how distinct are the modules in the mouse mandible? *Evol. Dev.* 5, 522–531.
- Kuroe, K., Rosas, A., Molleson, T., 2004. Variation in the cranial base orientation and facial skeleton in dry skulls sampled from three major populations. *Eur. J. Orthod.* 26, 201–207.
- Leakey, M.G., Spoor, F., Dean, M.C., Feibel, C.S., Anton, S.C., Kiarie, C., Leakey, L.N., 2012. New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early Homo. *Nature* 488, 201–204.
- Lieberman, D.E., 1998. Sphenoid shortening and the evolution of modern human cranial shape. *Nature* 393, 158–162.
- Lieberman, D.E., 2000. Ontogeny, homology, and phylogeny in the hominid craniofacial skeleton: the problem of the browridge. In: O'Higgins, P., Cohn, M.J. (Eds.), *Development Growth and Evolution. Implications for the study of hominid skeleton*. Academic Press, San Diego, London, pp. 86–122.
- Lieberman, D.E., 2011. *The evolution of the human head*. Belknap Press of Harvard University Press, Cambridge.
- Lieberman, D.E., McCarthy, R.C., 1999. The ontogeny of cranial base angulation in humans and chimpanzees and its implication for reconstructing pharyngeal dimensions. *J. Hum. Evol.* 36, 487–517.
- Lieberman, D.E., Pearson, O.M., Mowbray, K.M., 2000a. Basicranial influence on overall cranial shape. *J. Hum. Evol.* 38, 291–315.
- Lieberman, D.E., Ross, C., Ravosa, M.J., 2000b. The primate cranial base: ontogeny, function, and integration. *Yrbk. Physiol. Anthropol.* 43, 117–169.
- Lieberman, D.E., McBratney, B.M., Krovitz, G., 2002. The evolution and development of cranial form in Homo sapiens. *Proc. Natl. Acad. Sci. USA* 99, 1134–1139.
- Lieberman, D.E., Hallgrímsson, B., Liu, W., Parsons, T.E., Jamniczky, H.A., 2008. Spatial packing, cranial base angulation, and craniofacial shape variation in the mammalian skull: testing a new model using mice. *J. Anat.* 212, 720–735.
- Lordkipanidze, D., Ponce de León, M.S., Margvelashvili, A., Rak, Y., Rightmire, G.P., Vekua, A., Zollikofer, C.P.E., 2013. A Complete Skull from Dmanisi, Georgia, and the Evolutionary Biology of Early Homo. *Science* 342, 326–331.
- Maddux, S.D., Franciscus, R.G., 2008. Allometric scaling of infraorbital surface topography in Homo. *J. Hum. Evol.* 56, 161–174.
- Marcucio, R.S., Young, N.M., Hu, D., Hallgrímsson, B., 2011. Mechanisms that underlie co-variation of the brain and face. *Genesis* 49, 177–189.
- Martínez-Abadías, N., Esparza, M., Sjøvold, T., González-José, R., Santos, M., Hernández, M., Klingenberg, C.P., 2012. Pervasive genetic integration directs the evolution of human skull shape. *Evolution* 66, 1010–1023.
- McCarthy, R., Lieberman, D.E., 2001. Posterior Maxillary (PM) Plane and Anterior Cranial Architecture in Primates. *Anat. Rec.* 264, 247–260.
- Mlynski, G., Grützmacher, S., Plontke, S., Mlynski, B., 2001. Correlation of nasal morphology and respiratory function. *Rhinology* 39, 197–201.
- Neubauer, S., Gunz, P., Hublin, J.-J., 2009. The pattern of endocranial ontogenetic shape changes in humans. *J. Anat.* 215, 240–255.
- O'Connor, C.F., Franciscus, R.G., Holton, N.E., 2005. Bite force production capability and efficiency in Neandertals and modern humans. *Am. J. Phys. Anthropol.* 127, 129–151.
- Ponce de León, M., Zollikofer, C., 2001. Neandertal cranial ontogeny and its implications for late hominid diversity. *Nature* 412, 534–538.

- Rae, T.C., Koppe, T., Stringer, C.B., 2011. The Neanderthal face is not cold adapted. *J. Hum. Evol.* 60, 234–239.
- Rak, Y., 1983. *The Australopithecine Face*. Academic Press, New York.
- Rak, Y., 1986. The Neandertal: A new Look at an Old Face. *J. Hum. Evol.* 15, 151–164.
- Rosas, A. 1992. Ontogenia y Filogenia de la mandíbula en la evolución de los homínidos. Aplicación de un modelo a las mandíbulas fósiles de la Sima de los Huesos (Atapuerca). PhD-dissertation, Complutense University of Madrid, Madrid.
- Rosas, A., 1997. A gradient of Size and Shape for the Atapuerca sample and Middle Pleistocene hominid variability. *J. Hum. Evol.* 33, 319–331.
- Rosas, A., 2001. Occurrence of Neanderthal Features in Mandibles From the Atapuerca-SH Site. *Am. J. Phys. Anthropol.* 114, 74–91.
- Rosas, A., Bastir, M., 2002. Thin-Plate Spline Analysis of Allometry and Sexual Dimorphism in the Human Craniofacial Complex. *Am. J. Phys. Anthropol.* 117, 236–245.
- Rosas, A., M. Bastir, C. Martínez-Maza, García-Tabernero, A., Lalueza-Fox, C., 2006. Inquiries into Neanderthal cranio-facial development and evolution: ‘accretion’ vs ‘organismic’ models. In: Harrison, T., Harvati, K. (Eds.), *Neanderthals Revisited*. Springer Verlag, New York University, pp. 38–69.
- Rosas, A., Bastir, M., Alarcón, J.A., Kuroe, K., 2008. Thin-plate spline analysis of the cranial base in African, Asian and European populations and its relationship with different malocclusions. *Arch. Or. Biol.* 291, 130–140.
- Ross, C., Henneberg, M., 1995. Basicranial flexion, relative brain size, and facial kyphosis in *Homo Sapiens* and some fossil hominids. *Am. J. Phys. Anthropol.* 98, 575–593.
- Ross, C.F., Ravosa, M.J., 1993. Basicranial flexion, relative brain size, and facial kyphosis in non-human Primates. *Am. J. Phys. Anthropol.* 91, 305–324.
- Ross, C.F., Henneberg, M., Ravosa, M.J., Richard, S., 2004. Curvilinear, geometric and phylogenetic modeling of basicranial flexion: is it adaptive, is it constrained? *J. Hum. Evol.* 46, 185–213.
- Ruff, C.B., Trinkaus, E., Holliday, T.W., 1997. Body mass and encephalization in Pleistocene Homo. *Nature* 387, 173–176.
- Shea, B (1985). On aspects of skull form in african apes and orangutans, with implications for hominoid evolution. *American Journal of Physical Anthropology*, 68: 329-342.
- Smith, R.J., Josell, S.D., 1984. The plan of the humans face: a test of three general concepts. *Am. J. Orthod.* 85, 103–108.
- Spencer, M.A., Demes, B., 1993. Biomechanical Analysis of Masticatory System Configuration in Neandertals and Inuits. *Am. J. Phys. Anthropol.* 91, 1–20.
- Spoor, F., 1997. Basicranial architecture and relative brain size of Sts5 (*Australopithecus africanus*) and other Plio-Pleistocene hominids. *S. Afr. J. Sci.* 93, 182–186.
- Spoor, F., O’Higgins, P., Dean, C., Lieberman, D.E., 1999. Anterior sphenoid in modern humans. *Nature* 397, 572.
- Strait, D., 1999. The scaling of basicranial flexion and length. *J. Hum. Evol.* 37, 701–719.
- Tobias, P.V., 1972. "Dished Faces", Brain Size and Early Hominids. *Nature* 239, 468–469.
- Trinkaus, E., 1987. The Neandertal face: Evolutionary and functional perspectives on a recent hominid face. *J. Hum. Evol.* 16, 429–443.
- Trinkaus, E., 2003. Neandertal faces were not long; modern human faces are short. *Proc. Natl. Acad. Sci. USA* 100, 8142–8145.
- Weaver, T.D., 2009. The meaning of Neandertal skeletal morphology. *Proc. Natl. Acad. Sci. USA* 106, 16028–16033.

Yokley, T., Holton, N.E., Franciscus, R.G., Churchill, S.E., 2009. The role of body mass in the evolution of the modern human nasofacial skeleton, Paleoanthropology Society, Chicago, pp. A39-40.

Table 1. Fossil sample

Fossil	Species
Forbes Quarry	<i>H. neanderthalensis</i>
Guattari 1	<i>H. neanderthalensis</i>
La Ferrassie 1	<i>H. neanderthalensis</i>
La Chapelle aux Saints 1	<i>H. neanderthalensis</i>
KNM-ER 3733	<i>H. ergaster</i>
Kabwe	<i>H. heidelbergensis s.l.</i>
Bodo	<i>H. heidelbergensis s.l.</i>
Petralona	<i>H. heidelbergensis s.l.</i>
Mladec 1	<i>H. sapiens</i>
Skuhl 5	<i>H. sapiens</i>

Table 2. Landmarks, definitions and anatomical regions.

Landmarks	Definitions	Region
Foramen caecum		base
Left anterior cribriform	Antero-lateral border of cribriform plate	base
Left posterior cribriform	Foramen of posterior sphenoid vessels	base
Posterior midcribriform	in the midline	base
Posterior sphenoid	at the level of the orbital canals	base
Pituitary		base
Dorsum sellae		base
Basion		base
Ophistion		base
Left spheno-parietal junction (ACF-MCF limit)	(Bastir et al., 2011b)	base
Left petro-parietal junction (MCF-PCF limit)	(Bruner and Ripani, 2008)	base
Left internal acoustic porus	Antero-lateral vertex	base
Left petrosal apex		base
Left forame ovale	Medial	base
Left foramen rotundum	Medial	base
Left anterior MCF point	Bastir et al., 2008	base
Left orbital foramen	Antero-lateral vertex	base
Right anterior cribriform	Antero-lateral border of cribriform plate	base
Right posterior cribriform	Foramen of posterior sphenoid vessels	base
Right spheno-parietal junction (ACF-MCF limit)	(Bastir et al., 2011b)	base
Right petro-parietal junction (MCF-PCF limit)	(Bruner and Ripani, 2008)	base
Right internal acoustic porus	Antero-lateral vertex	base
Right petrosal apex		base
Right foramen ovale	Medial	base
Right foramen rotundum	Medial	base
Right anterior MCF point	(Bastir et al., 2008)	base
Right orbital foramen	Antero-lateral vertex	base
Left porion		face
Left temporo-mandibular joint (TMJ)	Most lateral and superior point	face
Right porion		face
Right TMJ		face
Vomero-sphenoid junction	(Rosas and Bastir, 2002)	face
Glabella		face
Nasion		face
Rhinion		face
Anterior nasal spine		face
Prosthion		face
Left fmo		face
Left zygomax sup		face

Left zygomax inf	face
Left zygmomatic root	face
Left infra-orbital fm	face
Left posterior alveolar border	face
Left canine alveolus	face
Right fmo	face
Right zygomax sup	face
Right zygomax inf	face
Right zygmomatic root	face
Right infra-orbital fm	face
Right posterior alveolar border	face
Right canine alveolus	face

Table 3. Partial Least Squares analysis.^a

	Singular value	<i>p</i> -value (perm.)	% total Covariatio n	Correlation	<i>p</i> -value (perm.)
PLS1	0.000616	0 < 0.001	60.728	0.94555	0 < 0.0001
PLS2	0.000377	0 < 0.001	22.779	0.85323	0 < 0.0003
PLS3	0.000187	0 < 0.001	5.602	0.76532	0 < 0.0001

^acommon Procrustes registration; 10000 permutations [perm].

Figure Legends

Figure 1. Scatterplots showing correlations of PLS1 scores (a), PLS2 scores (b), and PLS3 scores (c). Fossil abbreviations: B = Bodo, K = Kabwe, P = Petralona, E = KNM ER 3733, C = La Chapelle aux Saints, Fe = La Ferassie 1, Fo = Forbe's Quarry, G = Guattari 1, S = Skuhl 5, M = Mládec 1.

Figure 2. Shape changes along PLS1 in frontal, axial, and right lateral views. Arrows indicate shapes associated with the corresponding loadings of PLS1 scores.

Figure 3. Shape changes along PLS2 in frontal, axial, and right lateral views. Arrows indicate shapes associated with the corresponding loadings of PLS2 scores.

Figure 4. Shape changes along PLS3 in frontal, axial, and right lateral views. Arrows indicate shapes associated with the corresponding loadings of PLS3 scores.

Figure 5. Specific features between sphenoid morphology and facial shape. a) PLS1 positive scores show a short anterior sphenoid associated to a large and prognathic face; b) PLS2 negative scores show increased relative anterior sphenoid length associated to reduced, orthognathic face; c) midsagittal section in consensus shape; d) consensus deformed along PLS3 positive scores indicating the retraction of the midline anterior cranial floor relative to the lateral sphenoid wings causing a flat face; e) consensus deformed along PLS3 negative scores showing retracted lateral sphenoid wings relative to projected midline anterior cranial floor produce upper and midfacial projection.

Figure 6. Sphenoid and facial morphology along PLS3 in external cranial views illustrating the effect of sphenoid wing and body topology on the position and shape of the zygomatic bone. a) PLS3 positive: more coronally oriented infraorbital plane and sharply angled zygomatics as a consequence of anterior projected middle cranial fossa position. b) PLS3 negative: more sagittally oriented infra-orbital plane and weakly angled zygomatics associated with retracted position of the middle cranial fossae.

- PLS1 +

- PLS2 +

- PLS3 +

a

b