



Effects of brain and facial size on basicranial form in human and primate evolution

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ABSTRACT

Understanding variation in the basicranium is of central importance to paleoanthropology because of its fundamental structural role in skull development and evolution. Among primates, encephalisation is well known to be associated with flexion between midline basicranial elements, although it has been proposed that the size or shape of the face influences basicranial flexion. In particular, brain size and facial size are hypothesized to act as antagonists on basicranial flexion. One important and unresolved problem in hominin skull evolution is that large-brained Neanderthals and some Mid-Pleistocene humans have slightly less flexed basicrania than equally large-brained modern humans. To determine whether or not this is a consequence of differences in facial size, geometric morphometric methods were applied to a large comparative data set of non-human primates, hominin fossils, and humans ($N = 142$; 29 species). Multiple multivariate regression and thin plate spline analyses suggest that basicranial evolution is highly significantly influenced by both brain size and facial size. Increasing facial size rotates the basicranium away from the face and slightly increases the basicranial angle, whereas increasing brain size reduces the angles between the sphenoccipital clivus and the presphenoid plane, as well as between the latter and the cribriform plate. These interactions can explain why Neanderthals and some Mid-Pleistocene humans have less flexed cranial bases than modern humans, despite their relatively similar brain sizes. We highlight that, in addition to brain size (the prime factor implicated in basicranial evolution in *Homo*), facial size is an important influence on basicranial morphology and orientation. To better address the multifactorial nature of basicranial flexion, future studies should focus on the underlying factors influencing facial size evolution in hominins.

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Introduction

Craniofacial evolution in higher vertebrates (birds, mammals, and particularly primates) is characterized by pronounced changes in the basicranium (Dabelow, 1929, 1931; Hofer, 1952; Starck, 1952; Biegert, 1957; Enlow, 1990; Ross and Ravosa, 1993; Marugán-Lobón and Buscalioni, 2006; Hallgrímsson and Lieberman, 2008). Basicranial variation is also of central importance to paleoanthropology, because variation in basicranial morphology can modify the spatial relations between facial and neurocranial skull elements. An understanding of the factors influencing basicranial variation will

improve comprehension of morphological variation and evolution of the entire skull (Biegert, 1957, 1963; Enlow, 1990; Ross and Ravosa, 1993; Lieberman et al., 2000).

Basicranial variation has traditionally been investigated in the midline, although variation in more lateral basicranial morphology is increasingly well studied (Dean and Wood, 1982; Seidler et al., 1997; Holloway et al., 2004; Bastir et al., 2008; Bastir and Rosas, 2009). Still, the evolutionary factors impacting midline cranial base morphology are far from clear. For example, from a phylogenetic perspective, it has been shown that encephalisation, the increase of relative brain size, is a key factor influencing basicranial flexion in the midline (Ross and Ravosa, 1993; Spoor, 1997; Strait, 1999; Lieberman et al., 2000; McCarthy, 2001; Ross et al., 2004). These studies (among others) indicate that larger relative brain size is generally associated with a smaller basicranial angle. Thus,

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basicranial flexion has been interpreted as a mechanism for spatial packing.

However, from an ontogenetic perspective, Jeffery and Spoor (2002) have shown that pure physical cerebral expansion alone does not sufficiently explain basicranial flexion in humans. Between the 10th and 29th week of intrauterine ontogeny, increase of brain volume accompanied decreased basicranial flexure (retro-flexion), rather than by the expected increase in flexure. While their results on prenatal basicranial flexion aligned with previous observations in prenatal humans (Virchow, 1857; Kummer, 1952; Sperber, 1989), these findings also indicate a need for additional explanations (Jeffery, 2002; Jeffery and Spoor, 2002; Jeffery, 2003).

It has long been speculated that one potentially important factor in midline cranial base evolution in *Homo* might be the size or shape of the face (Biegert, 1957; Ross and Ravosa, 1993; Bastir et al., 2006; Rosas et al., 2006; Bastir, 2008; Lieberman et al., 2008). Dabelow (1929, 1931) hypothesised that facial and/or body size interacts with basicranial morphology, but it was Biegert (1957) who first quantitatively analysed these interactions in several primate species and a few hominin fossils. Biegert compared ontogenetic and phylogenetic data from a wide range of non-human primates and humans and found that in non-human primates basicranial flexion decreased as facial size increased postnatally. This trend was different in humans, in which postnatal brain size increased much stronger or faster than facial size and was accompanied by increased basicranial flexion. Biegert's ontogenetic observations were confirmed in chimpanzees and humans in more detail by Lieberman and McCarthy (1999).

On the basis of his ontogenetic and phylogenetic analyses, Biegert (1957) formulated a hypothesis according to which “bi-directional” factors have to be taken into account when analysing basicranial flexion. Biegert's “bi-directional” hypothesis predicts that an increase of facial size relative to brain size is associated with a reduction in basicranial flexion (retro-flexion *sensu* Jeffery and Spoor, 2002). This would have an opposite effect on basicranial flexion than that caused by the evolutionary increase of brain size relative to facial size, which increases basicranial flexion. More specifically, Biegert (1957) hypothesised that the extreme basicranial flexion in modern humans is a result of (1) the evolution of an enlarged brain, and (2) a reduced masticatory apparatus (for reviews see Bastir, 2004, 2008). Biegert's underlying rationale invoked mechanic-static (structural) reasons of “spatial packing” (defined by Ravosa, 1988; Ross and Ravosa, 1993) and functional aspects related to jaw mechanics and masticatory movement.

Ross and Ravosa (1993) tested the bi-directional aspect of Biegert's hypothesis in a comparative anatomical context among primates, but while their findings provide some support for platyrrhines, they failed to support the hypothesis for other suborders. Moreover, they used palatal length as an indicator of facial size, but did not quantify other dimensions of facial size, such as vertical or transverse dimensions, which are equally important *sensu* Biegert (1957).

In contrast to the findings of Ross and Ravosa (1993), postnatal ontogenetic data in modern humans suggest that larger faces are associated with less flexed cranial bases (Rosas et al., 2006). Prenatal ontogenetic data can also be interpreted in this sense (Jeffery and Spoor, 2004). Jeffery and Spoor's (2004) study on cross sectional fetal variation at the mid-sagittal cranial base found significant associations between increasing fetal size and basicranial retro-flexion (extension).

Recently, experimental data from mouse models have demonstrated that mice with larger faces have less flexed basicranial angles compared with genetic strains of smaller faces, which show slightly reduced basicranial angles (Hallgrímsson and Lieberman, 2008; Lieberman et al., 2008). These studies have coined the term

“facial” packing hypothesis. Also, genetically engineered mice with larger brains have downwardly flexed cribriform plates (Lopez et al., 2008).

Although ontogenetic studies support Biegert's hypothesis (Jeffery and Spoor, 2004; Rosas et al., 2006; Hallgrímsson and Lieberman, 2008; Lieberman et al., 2008; Lopez et al., 2008), it cannot be ruled out that morphological changes simply co-vary in time due to developmental modularity without having any causal relations. This kind of relationship would be best analyzed on a broad comparative sample (Ross and Ravosa, 1993; Ross and Henneberg, 1995).

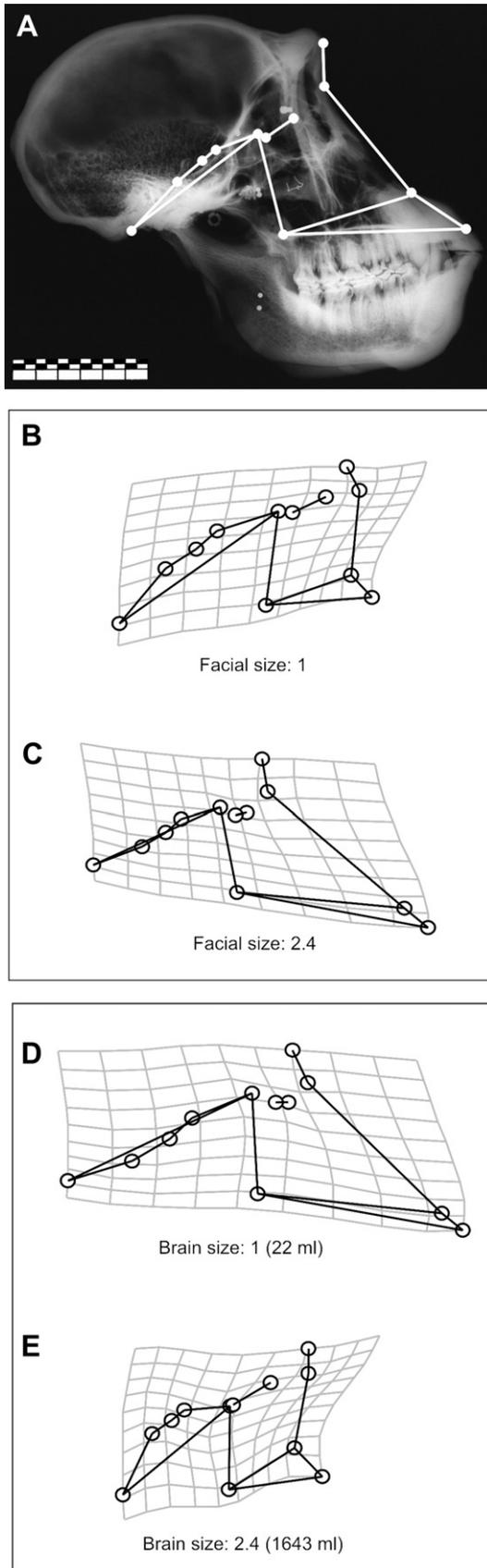
Facial reduction and brain size increase represent general evolutionary trends in hominins (Stringer, 2002; Lieberman et al., 2002; Trinkaus, 2003), so they provide an ideal context for testing this hypothesis. In particular, despite large cranial capacities in both *H. sapiens*, Neanderthals and some Mid-Pleistocene humans, it has been suggested that the latter have slightly less flexed cranial bases in the midline than modern humans (Lieberman et al., 2000). Because facial size is different in these human species (Rosas and Bermúdez de Castro, 1998; Trinkaus, 2003; Bastir et al., 2007), the basicranial antagonism hypothesis directly applies. Also, in the light of opposite evolutionary tendencies of brain size (Ruff et al., 1997) and facial size (Trinkaus, 2003) in Early and Middle Pleistocene *Homo*, quantitative support for Biegert's hypothesis could provide crucial information relevant to better understanding these general trends in human craniofacial evolution.

Thus far, no study has addressed this important question by simultaneously analysing both facial size and brain size in the comparative context of primates and hominins. A methodological difficulty with testing this hypothesis is that basicranial angles, traditionally used to quantify basicranial flexion, span many different anatomical structures. One cranial base angle (CBA) measures the flexion between the pre-sellar sphenoid and the sphenoccipital clivus (CBA4 [Landzert, 1866; Lieberman and McCarthy, 1999]). This is the angle Biegert (1957) measured originally, while another commonly used angle (CBA1 [Spoor, 1997; Lieberman and McCarthy, 1999]) measures flexion between basion, sella, and the foramen caecum associated with the cribriform plate of the ethmoid. This latter angle thus spans three different midline basicranial and facial elements (i.e., the ethmoid). Each angle evaluates different bony elements, and similar angular relationships can be attributable to very different anatomical factors. This implies that such angles may not be biologically comparable and spatial proportions are not quantified at all. Our study provides an overall anatomical comparison of these structures by applying geometric morphometric techniques to analyse midline basicranial morphology of homologous landmarks. This enables us to evaluate variation in flexion and to also consider evolutionary changes in spatial proportions of each basicranial element and its relation to the face in terms of shape.

This paper tests Biegert's bi-directional hypothesis of antagonistic effects of brain size and facial size on basicranial flexion assessed from geometric morphometrics and statistical analysis of interactions between shape and robust descriptors of facial size and brain size across a broad comparative anatomical dataset of human and non-human primates.

Material and methods

Biegert's hypothesis, that relative facial size increased with decreased basicranial flexion and relative brain volume increased with increased basicranial flexion, was tested at several levels with geometric morphometrics (Bookstein, 1991; Zelditch et al., 2004). We measured seven standard midline landmarks of the cranial base



and the face to capture those anatomical relationships that are relevant to the hypothesis. One problem in previous comparative studies has been that *foramen caecum* within the anterior cranial base is located superior to the anterior end of the cribriform plate in hominins, while in non-human primates it is located anterior to the plate. Thus, angles measured using *foramen caecum* in non-human primates do not reflect the orientation of the anterior cranial base the way they do in humans, introducing difficulties of interpretation of interspecific comparisons. Using landmarks at the anterior and posterior limits of the cribriform plate avoids this problem (Ross and Ravosa, 1993; Ravosa and Shea, 1994; Spoor, 1997). We measured anterior and posterior limits of the cribriform plate, the anterior border (or highest point) of *planum sphenoidum*, the posterior edge of *planum sphenoidum*, *sella*, *dorsum sellae*, and *basion* (following standard definitions) (Ross and Ravosa, 1993; Ravosa and Shea, 1994). These landmarks enable us to (1) analyse shape variation of the most important midline basicranial structures and (2) to calculate the traditional angles. For a better overall shape assessment we measured five additional landmarks on the face (glabella, nasion, anterior and posterior nasal spines, prosthion) (Fig. 1A) from lateral x-rays and midsagittal CT-scans of a large sample ($N = 142$, Table 1) of adult anthropoid primates (Ross and Ravosa, 1993), modern humans, and hominin fossils (Sts5, KNM-ER 3733, Bodo, Broken Hill, Guattari 1, Forbes' Quarry 1).

Shape data consisted of partial warps (Rohlf et al., 1996; Zelditch et al., 2004) obtained from thin plate splines (TPS) of Procrustes superimposed landmark configurations and Procrustes shape coordinates. Brain and facial size were obtained independently. Brain size was measured consistently by one researcher (MJR) by filling dry crania with mustard seeds (Ross and Ravosa, 1993) or obtained from the literature (Holloway et al., 2004; Ankel-Simons, 2007). Facial size (in mm) was calculated as the centroid size of the facial landmarks.

To account for differences in absolute ranges of the variables and to reduce dimensionality, brain volume (1.8 ml to 1600 ml) was converted to its cube root. Brain size and facial size were both log-transformed to remove correlations between means and standard deviations due to variations in absolute body size among species and to provide homoscedasticity (Sokal and Rohlf, 1998). After these transformations (Table 2), both facial size and brain size had similar ranges of variation (facial size: min. = 0.5, max. = 2.7, mean = 1.7, std. dev. = 0.52; brain size: min. = 0.43, max. = 2.5, mean = 1.5, std. dev. = 0.43).

First, we used multiple multivariate regressions with brain size and facial size as the independent variables (tpsReg, Rohlf, 1998–2008) to test Biegert's hypothesis statistically. For each shape variable this analysis performs a multiple regression onto the independent variables and reports an R^2 value and a probability. Wilks' lambda indicates the overall multivariate test of significance. This partitions the variance into shape factors related to either facial size or brain size and visually presents it as TPS grid transformations of craniofacial landmark configurations, from which the basicranial part can be compared with the predictions of Biegert's model. The transformation grid visualises differences between the mean shape and the regression prediction and can visually test Biegert's hypothesis. Second, we predicted basicranial morphologies (i.e., landmark configurations) for given (log) values of facial

Figure 1. Basicranial and facial morphologies predicted by the multiple multivariate regressions. (A) X-ray of chimpanzee with landmark configuration; scale bar is 6 cm long. (B) shape with facial size 1; (C) shape with facial size 2.4; (D) shape with brain size 1; and (E) shape with brain size 2.4. Facial size co-varies with basicranial flexion, the orientation of the cranial base with respect to the posterior face, as well as the vertical position of the cribriform plate. Brain size is associated with basicranial flexion and the orientation of the cribriform plate.

Table 1
Species and sample sizes (and composition)

| Groups | Species | Source ^a | N (males + females) | |
|-------------------------------|--|-----------------------------|---------------------------------|-----------|
| Cebidae | <i>Pithecia pithecia</i> | FMNH | 6 (3 + 3) | |
| | <i>Chiropotes satanas</i> | FMNH | 6 (3 + 3) | |
| | <i>Alouatta belzebul</i> | FMNH | 6 (2 + 4) | |
| | <i>Cebus apella</i> | FMNH | 6 (3 + 3) | |
| | <i>Saimiri sciureus</i> | FMNH | 6 (3 + 3) | |
| | <i>Ateles fusciceps</i> | FMNH | 6 (3 + 3) | |
| | <i>Lagothrix lagotricha</i> | FMNH | 6 (3 + 3) | |
| | Callitrichidae | <i>Callithrix argentata</i> | FMNH | 6 (3 + 3) |
| | | <i>Saguinus fuscicollis</i> | FMNH | 6 (3 + 3) |
| <i>Leontopithecus rosalia</i> | | FMNH | 1 (1 + 0) | |
| Cercopithecidae | <i>Cercopithecus aethiops</i> | FMNH | 6 (3 + 3) | |
| | <i>Miopithecus talapoin</i> | FMNH | 2 (+ 1) | |
| | <i>Macaca fascicularis</i> | FMNH | 6 (3 + 3) | |
| | <i>Macaca nigra</i> | FMNH | 3 (3 + 0) | |
| | <i>Papio anubis</i> | FMNH | 6 (3 + 3) | |
| | <i>Theropithecus gelada</i> | FMNH | 3 (3 + 0) | |
| | <i>Colobus guereza</i> | FMNH | 6 (3 + 3) | |
| | <i>Semnopithecus entellus</i> | FMNH | 6 (3 + 3) | |
| | <i>Trachypithecus cristata</i> | FMNH | 5 (3 + 2) | |
| | <i>Pygathrix nemaeus</i> | FMNH | 3 (1 + 2) | |
| | <i>Hylobates moloch</i> | FMNH | 6 (3 + 3) | |
| Hylobatidae | <i>Pongo pygmaeus</i> | MNCN | 8 (5 + 3) | |
| | <i>Pan troglodytes</i> | FMNH, MNCN | 8 (3 + 5) | |
| Great apes | <i>Gorilla gorilla</i> | FMNH, MNCN | 7 (3 + 4) | |
| | <i>H. sapiens</i> | MNCN | 6 (3 + 3) | |
| Hominins | <i>A. africanus</i> | MNCN | Sts 5 | |
| | <i>H. ergaster/erectus</i> | MNCN | KNM-ER 3733 | |
| | <i>H. heidelbergensis/rhodesiensis</i> | MNCN | Bodo, Broken Hill | |
| | <i>H. neanderthalensis</i> | MNCN | Forbes' Quarry 1, Guattari 1 | |
| | <i>H. sapiens</i> | MNCN | 6 (3 + 3) | |

^a FMNH (Field Museum of Natural History, Chicago); MNCN (Museo Nacional de Ciencias Naturales, Madrid).

size and brain size from this regression model in order to measure and calculate both cranial base angles (CBA1, CBA4) and compare them with the prediction of Biegert's hypothesis.

Finally, we constructed an empirical morphospace (Rosas and Bastir, 2002) using Partial Least Squares (PLS) analysis and a biplot to explore and visualise the relationships between the interaction of the independent variables (brain size, face size) and shape variation. The biplot is a single diagram that projects two separate scatter plots on the same pair of axes (Marcus, 1993; Rohlf, 1998–2008; Rohlf and Corti, 2000). PLS computes the covariation among the independent variables, between the independent variables and the shape variables, and among the shape variables. The TPS grids of the PLS vectors can be used to explore and visualize the interplay of brain size and facial size with respect to craniofacial shape evolution in *Homo*.

Because phylogenetic relatedness can influence the interactions between basicranial morphology, brain and facial size, we performed all analyses also using the comparative method of independent contrasts (Garland et al., 2005). The phylogeny on which the contrasts were built and the branching times of the nodes were taken from Ross et al., (2004). The mapping of the analyses (multiple multivariate regressions, PLS) on phylogeny was performed using MorphoJ (Klingenberg, 2009). Permutation tests (N = 10000) tested the null hypothesis of independence.

Results

Multiple multivariate regression analysis suggests that basicranial evolution is highly significantly influenced by both brain and facial size (Wilks' Lambda = 0.0028; F = 107.077, df = 1; 240; 240.0; $p < 0.0001$; explained variance = 58.6%). Independent contrasts

Table 2
Means and standard errors of independent data (*data from literature)

| species | logbrain | std. err. | logface | std. err. |
|--------------------------------|----------|-----------|---------|-----------|
| Sts5* | 2.06 | | 2.17 | |
| KNM-ER 3733* | 2.25 | | 2.34 | |
| Bodo* | 2.38 | | 2.38 | |
| Broken Hill* | 2.40 | | 2.33 | |
| Forbes Quarry* | 2.36 | | 2.26 | |
| Guattari 1* | 2.38 | | 2.38 | |
| <i>Homo sapiens</i> | 2.40 | 0.01 | 2.10 | 0.04 |
| <i>Alouatta belzebul</i> | 1.31 | 0.01 | 1.86 | 0.04 |
| <i>Ateles fusciceps</i> | 1.56 | 0.01 | 1.65 | 0.04 |
| <i>Callithrix argentata</i> | 0.71 | 0.01 | 0.65 | 0.04 |
| <i>Cebus apella</i> | 1.38 | 0.01 | 1.52 | 0.04 |
| <i>Chiropotes satanas</i> | 1.34 | 0.01 | 1.43 | 0.04 |
| <i>Chlorocebus aethiops</i> | 1.38 | 0.01 | 1.63 | 0.04 |
| <i>Colobus guereza</i> | 1.44 | 0.01 | 1.77 | 0.04 |
| <i>Gorilla gorilla</i> * | 2.05 | 0.01 | 2.63 | 0.04 |
| <i>Hylobates moloch</i> | 1.49 | 0.01 | 1.61 | 0.04 |
| <i>Lagothrix lagotricha</i> | 1.52 | 0.01 | 1.58 | 0.04 |
| <i>Leontopithecus rosalia</i> | 0.83 | 0.03 | 0.89 | 0.10 |
| <i>Macaca fascicularis</i> | 1.38 | 0.01 | 1.91 | 0.04 |
| <i>Macaca nigra</i> | 1.52 | 0.02 | 2.15 | 0.06 |
| <i>Miopithecus talapoin</i> | 1.24 | 0.02 | 1.36 | 0.07 |
| <i>Pan troglodytes</i> * | 1.98 | 0.01 | 2.37 | 0.04 |
| <i>Papio anubis</i> | 1.70 | 0.01 | 2.47 | 0.04 |
| <i>Pithecia pithecia</i> | 1.17 | 0.01 | 1.41 | 0.04 |
| <i>Pongo pygmaeus</i> * | 2.01 | 0.01 | 2.32 | 0.04 |
| <i>Pygathrix nemaeus</i> | 1.44 | 0.02 | 1.66 | 0.06 |
| <i>Saguinus fuscicollis</i> | 0.72 | 0.01 | 0.73 | 0.04 |
| <i>Saimiri sciureus</i> | 1.05 | 0.01 | 1.07 | 0.04 |
| <i>Semnopithecus entellus</i> | 1.48 | 0.01 | 1.71 | 0.04 |
| <i>Theropithecus gelada</i> | 1.65 | 0.02 | 2.34 | 0.06 |
| <i>Trachypithecus cristata</i> | 1.39 | 0.02 | 1.61 | 0.05 |

indicate the same results (58.8% expl. variance, $p < 0.0001$). Figure 1B–E shows the associated morphological changes that were basically identical when corrected for phylogenetic relatedness (not shown). The TPS grids clearly show that variation in facial size is related to angle and orientation of the basicranium and the proportions and position of the cribriform plate. The basicranium in smaller-faced taxa is more flexed between the presphenoid and the sphenoccipital clivus. In addition, the entire sphenoccipital complex (that is, pre- and basisphenoid plus basioccipital clivus, *os tribasilaris* [Hofer, 1952]) is rotated antero-inferiorly, approximating the base and the posterior border of the face (posterior nasal spine). The cribriform plate is shifted relatively anterior. In turn, larger faces are associated with retroflexed basicrania, which are also rotated postero-superiorly, increasing the relative distance between basion and posterior nasal spine. The cribriform plate becomes relatively short and substantially shifted into an inferior and posterior position. Variation in facial size was not associated with the orientation of the cribriform plate.

Shape changes purely associated with brain size relate to the basicranial angle as well as the relative size and orientation of the cribriform plate (Fig. 1). Small-brained individuals show a retroflexed cranial base. The cribriform plate is relatively short and in a horizontal orientation. The presphenoid is rotated downwards with respect to the posterior face. Larger-brained individuals show a highly flexed basicranium with a relatively large cribriform plate and a strong superior rotation. The presphenoid meets the posterior face at approximately 90°. The palate shows the same orientation. Thus, regression analysis of shape data supports Biegert's hypothesis of bidirectional interactions between basicranial morphology and facial and brain size on the other.

When basicranial angles are calculated from configurations predicted by the regression model, it is possible to assess them as they change due to pure variation in either facial or brain size (Fig. 2). When angles are predicted by the previous regression

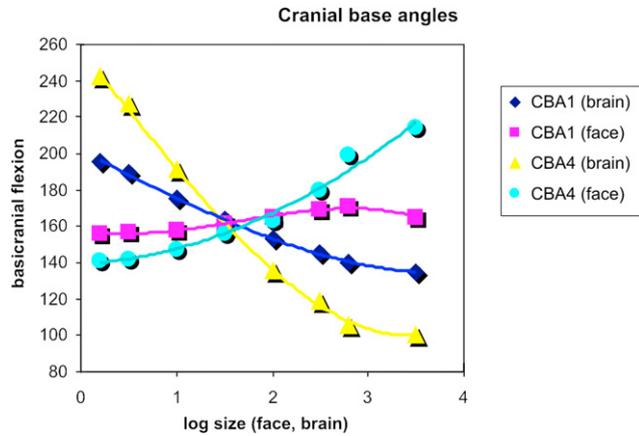


Figure 2. Predicted angles of basicranial flexion along standardized brain and facial size (3rd order polynomial curves for visualization). Note the clear trend towards reduction of both angles as the cube root of brain size increases (CBA1 [brain], CBA4 [brain]). Note that both angles flatten out towards large brain size. Both cranial base angles show complex trajectories with increase of facial size (CBA1 [face]; CBA4 [face]). CBA1 driven by facial size can give identical values for animals with intermediate and very large faces. CBA4 shows an unequivocal, curvilinear trend towards increase.

model for specific values of facial and brain size, then increase of facial size reveals that CBA1 is low with small faces, higher with intermediate faces, and lower again with larger faces. This non-linear trend contradicts Biegert's hypothesis. However, CBA4, which is predicted by facial size, follows a different trend, with a positively exponential trajectory that supports Biegert's hypothesis, because the angle is small in small faces and large in larger faces. Each angle quantifies different anatomies.

With respect to increasing brain size, both angles clearly decrease, with CBA4 decreasing more drastically than CBA1. These results support Biegert's hypothesis. Also, the curves of both angles seem to flatten out as brain size increases.

Finally, the PLS analysis shown in Fig. 3 indicates how size variation of both brains and faces interact during the evolution of the associated craniofacial configurations. PLS1 accounts for 97.1% of variance and PLS2 for 2.9%; both are highly and significantly correlated with the shape factors (PLS1: $r = 0.9$; $p < 0.01$; PLS2: $r = 0.8$; $p < 0.01$). The PLS analysis of the independent contrast gave similar results (PLS1: $r = 0.94$; expl. var. = 96.1%, PLS2: $r = 0.84$; expl. var. = 3.8%). Permutation tests against the null hypothesis of independence also indicated statistical significance ($p < 0.0001$).

The morphospace (Fig. 3) shows that facial size can be large due to either strong forward projection (cercopithecines) or increased vertical height (great apes, hominins). These facial sizes combine with brain sizes to form different craniofacial shapes. Sts5 plots closely to the chimpanzee sample but with a slightly smaller face, a slightly larger brain, and a more flexed basicranium. KNM-ER 3733 represents early *Homo* with a large face and a small brain relative to later humans. African Middle Pleistocene fossils (Bodo, Broken Hill) are similar to Neanderthals (Forbes' Quarry 1, Guattari 1) in their proportions and show flexed basicrania, although more distant relative to the face, which projects antero-inferiorly. These shapes are separated from modern humans, who have large brains, specifically small faces, and extreme basicranial flexion. This latter result clearly supports the specific aspect of Biegert's hypothesis regarding modern human basicranial flexion.

Discussion

The angles predicted by the regression models clearly fit with the well established hypothesis that between taxa brain size increase is related to increase in basicranial flexion (Hofer, 1952;

Biegert, 1957, 1963; Ross and Ravosa, 1993; Ross and Henneberg, 1995; Lieberman et al., 2000). Our data also show that in primates, larger faces sometimes have opposite effects on basicranial flexion, thus supporting both the brain and facial size component of Biegert's hypothesis. In addition, we demonstrated that an increase in facial size rotates the entire base away from the posterior face. These are new findings not captured by traditional basicranial angles and have not been identified before.

Our results also indicate that the relationship between facial size and basicranial angles is more complex than between basicranial angles and brain size (Fig. 2). Along positive increments of facial size, we observed positive, negative, and also no changes of basicranial angle depending on which measurement was used. Analyses of CBA4 (the angle Biegert measured originally) support the hypothesis, because smaller faces are associated with smaller angles than larger faces. This increase in angles is smaller in faces of low to intermediate size and becomes much larger with larger facial sizes. CBA1, in turn, shows a very slight increase within small faces, which becomes slightly more accentuated in enlarging faces (i.e., supports Biegert's hypothesis), while in large faces it decreases (i.e., rejects Biegert's hypothesis). This non-monotonic behaviour is because increments of facial size rotate the entire spheno-occipital complex into a superior position, along with an inferior shift of the cribriform plate (Fig. 1). At very large facial sizes, this effect causes a "secondary" decrease of CBA1. Furthermore, it implies that Biegert's hypothesis for CBA1 is only valid for small to intermediate sized faces. These values are close to the relevant ones for understanding human evolutionary changes. It should be noted that the effect of facial size on basicranial angle is considerably weaker than that of brain size. These results confirm the view that, in human evolution, brain size is an important factor in basicranial evolution (Ross and Ravosa, 1993; Ross and Henneberg, 1995; Spoor, 1997; Lieberman et al., 2000), but that facial size has the potential to "fine-tune" basicranial morphology in the midline. The complex interplay between facial size, brain size, and evolution of the craniofacial complex is best understood by looking at human evolution and considering all variables together. Regression analysis (Fig. 1) revealed that facial size acts strongly on basicranial orientation with respect to the posterior face, and slightly on the angle of the spheno-occipital complex, while brain size acts strongly on the spheno-occipital angle, but also strongly on the base-face orientation. Putting this information together (Fig. 3) suggests that the differences in basicranial angles between Mid-Pleistocene humans (e.g., Broken Hill, Bodo) and Neanderthals (e.g., Guattari 1, Forbes' Quarry 1), and modern humans, are related to the effect of facial size on the orientation of the entire cranial base. This is intuitive because brain size is roughly similar (Fig. 3), while facial size decreased during the Middle Pleistocene (Rosas and Bermúdez de Castro, 1998; Trinkaus, 2003; Bastir et al., 2004, 2007). The biplot of the figures also orders hominin fossils grossly in categories of large faces and small brains (early *Homo*), large faces and larger brains (later *Homo*), and large brains and small faces (modern humans).

All these interactions did not change when phylogenetic relatedness is taken into account. This result, together with similar observations in phylogenetically distant organisms (Dabelow, 1929; 1931; Hallgrímsson and Lieberman, 2008; Lieberman et al., 2008), favours interpretations in terms of functional factors.

However, what could the underlying factors be? Biegert (1957) suggested that basicranial retro-flexion in larger-faced primates provides vertical facial height, which is necessary for grinding masticatory movements in primates. In other mammals (e.g., mice), there has been speculation about a basicranial "packing" mechanism ("facial packing"), spatially accommodating the face (Hallgrímsson and Lieberman, 2008; Lieberman et al., 2008).

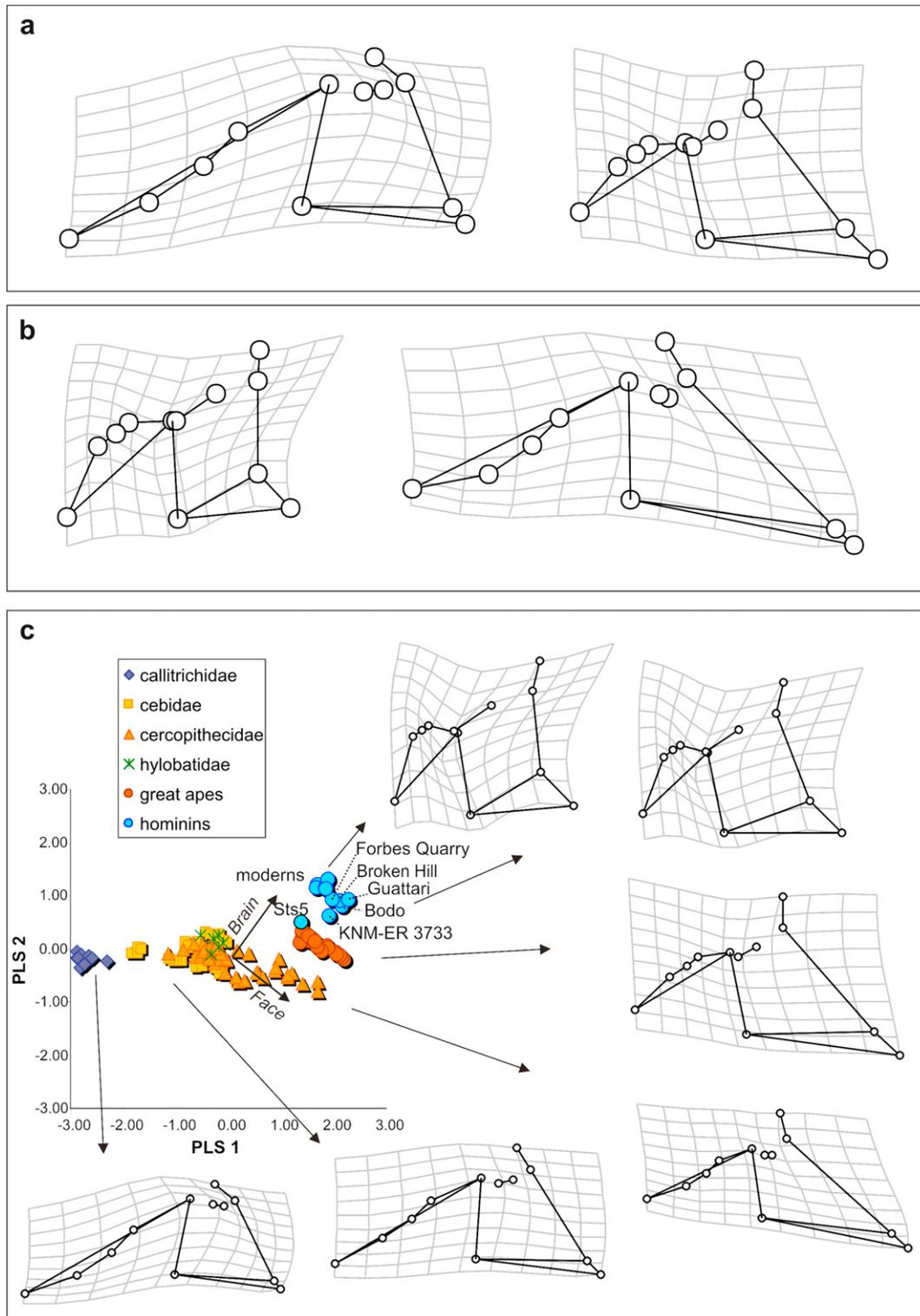


Figure 3. This morphospace shows how brain and facial size interact with basicranial and facial morphology as indicated by the PLS vectors. (a) Pure shape effect of PLS 1; (b) Pure shape effect of PLS 2; (c) Morphospace combination of PLS 1 and PLS 2 and biplot of the sizes of the face and the brain on common origin (0,0). The main effect of increased facial size (toward the arrow) is a backwards and upwards orientation of the entire sphenoccipital bone, while the main effect of increased brain size (toward the arrow) is basicranial flexion. Both factors together show that, in larger-brained hominins, an increasingly flexed basicranium is backwardly rotated due to increase in facial size. This influences basicranial angles that involve the ethmoid (CBA1), but not CBA4.

Besides masticatory biomechanics and facial packing, maintenance of respiratory function may underlie the effect of larger facial size on the backwards extension of the total cranial base from the face. The area between basion and the posterior nasal spine is

occupied by pharyngeal structures of the posterior face (Bastir and Rosas, 2005). Larger faces (Trinkaus, 2003) likely imply larger airway dimensions (Rosas and Bastir, 2002; Hall, 2005; Bastir et al., 2009) as a consequence of body energetics (Churchill, 2006). The

space for these structures would be provided by a backwards rotation of the entire cranial base from the face (Biegert, 1963). Support for such an interpretation comes also from more recent ontogenetic and clinical studies (Trenouth and Timms, 1999; Jeffery, 2005). Thus, respiratory, metabolic and energetic factors (Churchill, 2006) could indirectly contribute to the basicranial morphologies observed in larger-faced Mid- and Late Pleistocene humans due to physiological integration within the respiratory apparatus (Bastir, 2008). However, it remains to be seen whether these effects are always important or are only important at morphological extremes (Ross and Henneberg, 1995).

With respect to human evolution, our findings point to the face as important in determining the overall orientation of the midline cranial base, a factor that has not previously been isolated quantitatively and visually. However, some fossil hominins such as Sangiran 17, OH-5, and OH-9 (Ross and Henneberg, 1995; Spoor, 1997; McCarthy, 2001), show higher basicranial flexion than expected for their brain size. Following Biegert's model, small faces could explain this, yet Sangiran 17 and OH-5 have large faces, as was likely the case for OH-9. Such deviations could be due to issues of reconstruction of missing basicranial data because all of these fossils are broken and possibly distorted (McCarthy, 2001). Another possibility is natural variation in relationships between facial size and basicranial flexion, or simply the need for identification of further, additional factors (Lieberman et al., 2000). The latter has been suggested already because previous research has shown that relative encephalisation leaves 64% of variance in basicranial flexion unexplained (Lieberman et al., 2000). Our regression model accounts for 58% of variance, which leaves 42% unexplained. Although these numbers cannot be directly compared because of methodological differences, they still indicate that, while brain size and facial size are important for human basicranial evolution, basicranial morphogenesis is likely multi-factorial in nature (Spoor, 1997; Spoor et al., 1999; Lieberman et al., 2000; Ross et al., 2004). Brain shape may be one factor (Seidler et al., 1997; Bruner, 2004; Bastir et al., 2008) and intrinsic (genetic) factors might contribute (Jeffery and Spoor, 2002), but it is clearly necessary to improve our models about these complex issues.

Ross and Ravosa (1993) tested Biegert's hypothesis on the same data, using palate length as a facial size measurement, and found only limited support. Our results (Fig. 3) show that facial shape is an important feature to bear in mind when quantifying facial size, because cercopithecines, great apes, and hominins (e.g., KNM-ER-3733, Guattari 1, Bodo) can have essentially identical facial sizes with very different degrees of facial projection, which is what palate length likely quantifies. Great ape and hominin faces with shorter palates would appear as "smaller," thus obscuring the actual covariation between basicranial morphology and facial size. This might contribute to the non-significant relations between facial size and basicranial angle in their samples (Ross and Ravosa, 1993).

Finally, when basicranial angles are predicted by brain size using our regression model (which corrects for the influence of facial size), there is support for the hypothesis of constraint on basicranial flexion. Both curves of CBA1 and CBA4 flatten out as brain size increases (Fig. 2). Ross and Henneberg (1995) suggested that basicranial flexion likely never surpasses the threshold of 90° degrees, possibly because of functional reasons related to respiratory physiology. When facial size is corrected for, basicranial flexion beyond 90° can only be expected for very (biologically unlikely) large cranial capacities (Fig. 2).

Conclusions

This study has shown that the sizes of the brain and the face interact significantly with basicranial morphology in primate and

human evolution. While an increase of brain size is associated with a decrease in basicranial angles, an increase of facial size has an opposite effect. These findings support the hypothesis of Biegert (1957) and can explain why large faced Neanderthals and some Mid-Pleistocene humans have less basicranial flexion than similarly encephalised but smaller faced modern humans (Ruff et al., 1997; Trinkaus, 2003). Our shape analysis also shows that quantification of the complex patterns of basicranial morphology by a single angle necessarily implies an oversimplification which has been commented on earlier (Bastir et al., 2006; Lieberman et al., 2008). It must be mentioned, however, that while simultaneous consideration of brain size and facial size improves previous models in primate and human evolution (Lieberman et al., 2000), it still leaves 42% of variation in shape unexplained. This might reflect hominins that do not follow that trend and indicates a more complex picture of basicranial evolution implying the need for improved models. Beyond size as studied here, brain shape, facial shape and intrinsic (genetic) factors (Jeffery and Spoor, 2002) might further contribute to the variation. Also, more comparative ontogenetic study is necessary in different species to test for homology in processes of angulation at the basicranial synchondroses.

Future study should analyse 3D aspects of the basicranium and the face and take these factors into consideration. Respiratory system and dental size are possible factors in basicranial evolution. Only the consideration of all facial organ systems will provide insight into the complex and intriguing evolutionary changes in the craniofacial system in the genus *Homo*.

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jhevol.2010.03.001

References

- Ankel-Simons, F., 2007. Primate Anatomy: An Introduction. Academic Press, Orlando.
- 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. Doctoral Dissertation, 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., 2005. Hierarchical nature of morphological integration and modularity in the human posterior face. *Am. J. Phys. Anthropol.* 128, 26–34.
- 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., 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., 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., O'Higgins, P., 2006. Craniofacial levels and the morphological maturation of the human skull. *J. Anat.* 209, 637–654.
- Bastir, M., O'Higgins, P., Rosas, A., 2007. Facial ontogeny in Neanderthals and modern humans. *Proc. Roy. Soc. B.* 274, 1125–1132.
- Bastir, M., García-Taberner, A., Rosas, A., 2009. Geometric morphometrics of the human nasal cavity. *Paleontol. i evol.* 3, 25–26.
- Biegert, J., 1957. Der Formwandel des Primatenschädels und seine Beziehungen zur ontogenetischen Entwicklung und den phylogenetischen Spezialisierungen der Kopfgorgane. *Gegenbr. Morph. Jahrb.* 98, 77–199.
- Biegert, J., 1963. The evaluation of characteristics of the skull, hands and feet for primate taxonomy. In: Washburn, S.L. (Ed.), *Classification and Human Evolution*. Aldine Publishing Co., Chicago, pp. 116–145.
- Bookstein, F.L., 1991. *Morphometric Tools for Landmark Data*. Cambridge University Press, Cambridge.
- Bruner, E., 2004. Geometric morphometrics and paleoneurology: brain shape evolution in the genus *Homo*. *J. Hum. Evol.* 47, 279–303.
- 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.
- Dabelow, A., 1929. Über Korrelationen in der phylogenetischen Entwicklung der Schädelform I. Die Beziehungen zwischen Rumpf und Schädelform. *Gegenbr. Morph. Jahrb.* 63, 1–49.
- Dabelow, A., 1931. Über Korrelationen in der phylogenetischen Entwicklung der Schädelform II. Die Beziehungen zwischen Gehirn und Schädelbasisform bei den Mammaliern. *Gegenbr. Morph. Jahrb.* 67, 84–133.
- Dean, M.C., Wood, B.A., 1982. Basicranial anatomy of Plio-Pleistocene hominids from East and South Africa. *Am. J. Phys. Anthropol.* 59, 157–174.
- Enlow, D.H., 1990. *Facial Growth*. W.B. Saunders Company, Philadelphia.
- Garland Jr., T., Bennett, A.F., Rezende, E.L., 2005. Phylogenetic approaches in comparative physiology. *J. Exp. Biol.* 208, 3015–3035.
- Hall, R.L., 2005. Energetics of nose and mouth breathing, body size, body composition, and nose volume in young adult males and females. *Am. J. Hum. Biol.* 17, 321–330.
- Hallgrímsson, B., Lieberman, D.E., 2008. Mouse models and the evolutionary developmental biology of the skull. *Int. Comp. Biol.* 48, 373–384.
- Hofer, H., 1952. Der Gestaltwandel des Schädels der Säugetiere und der Vögel, mit besonderer Berücksichtigung der Knickungstypen und der Schädelbasis. *Verh. Anat. Ges.* 99, 102–126.
- Holloway, R., Broadfield, D.C., Yuan, M.S. (Eds.), 2004. *The Human Fossil Record, Brain Endocasts: The Paleoneurological Evidence*. John Wiley & Sons, New Jersey.
- Jeffery, N., 2002. Differential regional brain growth and rotation of the prenatal human tentorium cerebelli. *J. Anat.* 200, 135–144.
- Jeffery, N., Spoor, F., 2002. Brain size and the human cranial base. *Am. J. Phys. Anthropol.* 118, 324–340.
- Jeffery, N., 2003. Brain expansion and comparative prenatal ontogeny of the non-hominoid cranial base. *J. Hum. Evol.* 45, 263–284.
- Jeffery, N., Spoor, F., 2004. Ossification and midline shape changes of the human fetal cranial base. *Am. J. Phys. Anthropol.* 123, 78–90.
- Jeffery, N., 2005. Cranial Base angulation and growth of the human fetal pharynx. *Anat. Rec.* 284A, 491–499.
- Klingenberg, C.P., 2009. Morphometric integration and modularity in configurations of landmarks: tools for evaluating a priori hypotheses. *Evol. Dev.* 11, 405–421.
- Kummer, B., 1952. Untersuchungen über die ontogenetische Entwicklung des menschlichen Schädelbasiswinkels. *Ztschr. Morphol. Anthropol.* 43, 331–360.
- Landzert, T., 1866. Der Sattelwinkel und sein Verhaeltnis zur Pro- und Orthognathie. *Abh. Senck. Nat. Ges.* 6, 19–165.
- 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.
- Lieberman, D.E., McBratney, B.M., Krovitz, G., 2002. The evolution and development of cranial form in *Homo sapiens*. *Proc. Natl. Acad. Sci.* 99, 1134–1139.
- Lieberman, D.E., Ross, C., Ravosa, M.J., 2000. The primate cranial base: ontogeny, function, and integration. *Yrbk. Phys. Anthropol.* 43, 117–169.
- 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.
- Lopez, E.K.N., Stock, S.R., Taketo, M.M., Chenn, A., Ravosa, M.J., 2008. A novel transgenic mouse model of fetal encephalization and craniofacial development. *Int. Comp. Biol.* 48, 360–372.
- Marcus, L.F., 1993. Some aspects of multivariate statistics for morphometrics. In: Marcus, L.F., Bello, E., Valdecasas-García, A. (Eds.), *Contributions to Morphometrics*, Museo Nacional de Ciencias Naturales. Consejo Superior De Investigaciones Científicas, Madrid, pp. 95–130.
- Marugán-Lobón, J., Buscalioni, Á.D., 2006. Avian skull morphological evolution: exploring exo- and endocranial covariation with two-block partial least squares. *Zoology*, 109, 217–230.
- McCarthy, R., 2001. Anthropoid cranial base architecture and scaling relationships. *J. Hum. Evol.* 40, 41–66.
- Ravosa, M.J., 1988. Browridge development in Cercopithecidae: a test of two models. *Am. J. Phys. Anthropol.* 76, 535–555.
- Ravosa, M.J., Shea, B.T., 1994. Patterns in craniofacial biology: evidence from the old world monkeys (Cercopithecidae). *Int. J. Primatol.* 15, 801–822.
- Rohlf, F.J., 1998–2008. tpsSeries: Ecology, Evolution. SUNY at Stony Brook. <http://life.bio.sunysb.edu/morph/>.
- Rohlf, F.J., Corti, M., 2000. The use of two-block partial least-squares to study covariation in shape. *Syst. Zool.* 49, 740–753.
- Rohlf, F.J., Loy, A., Corti, M., 1996. Morphometric analysis of old world Talpidae (Mammalia, Insectivora) using partial warp scores. *Syst. Biol.* 45, 344–362.
- 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., Bermúdez de Castro, J.M., 1998. The Mauer mandible and the evolutionary significance of *Homo heidelbergensis*. *Geobios*, 31, 687–697.
- Rosas, A., Bastir, M., Martínez-Maza, C., García-Taberner, A., Lalueza-Fox, C., 2006. Inquiries into Neanderthal cranio-facial development and evolution: 'Accretion' vs 'organismic' models. In: Harvati, K., Harrison, T. (Eds.), *Neanderthals Revisited*. Springer Verlag, New York, pp. 38–69.
- 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 nonhuman 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.
- Seidler, H., Falk, D., Stringer, C., Wilfing, H., Müller, G.B., zur Nedden, D., Weber, G.W., Reicheis, W., Arsuaga, J.-L., 1997. A comparative study of stereolithographically modelled skulls of Petralona and Broken Hill: implications for future studies of middle Pleistocene hominid evolution. *J. Hum. Evol.* 33, 691–703.
- Sokal, R.R., Rohlf, F.J., 1998. *Biometry*. W.H. Freeman and Company, New York.
- 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.
- Starck, D., 1952. Form und Formbildung der Schädelbasis bei Chiropteren. *Verh. Anat. Ges.* 99, 114–121.
- Strait, D., 1999. The scaling of basicranial flexion and length. *J. Hum. Evol.* 37, 701–719.
- Stringer, C., 2002. Modern human origins: progress and prospects. *Phil. Trans. R. Soc. Lond. B.* 357, 563–579.
- Sperber, G.H., 1989. *Craniofacial Embryology*. Wright, London, Boston, Singapore, Sydney, Toronto, Wellington.
- Trenouth, M.J., Timms, D.J., 1999. Relationship of the functional oropharynx to craniofacial morphology. *Angle Orthod.* 69, 419–423.
- Trinkaus, E., 2003. Neandertal faces were not long; modern human faces are short. *Proc. Natl. Acad. Sci.* 100, 8142–8145.
- Virchow, R., 1857. Untersuchung über die Entwicklung des Schädelgrundes im gesunden und krankhaften Zustande und über den Einfluß derselben auf Schädelform, Gesichtsbildung und Gehirnbau. Reimer, G., Berlin.
- Zelditch, M.L., Swiderski, D.L., Sheets, H.D., Fink, W.L., 2004. *Geometric Morphometrics for Biologists: A Primer*. Elsevier Academic Press, San Diego.