

# Hierarchical Nature of Morphological Integration and Modularity in the Human Posterior Face

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**ABSTRACT** Morphological integration and modularity are important points of intersection between evolution and the development of organismal form. Identification and quantification of integration are also of increasing paleoanthropological interest. In this study, the “posterior face,” i.e., the mandibular ramus and its integration with the associated midline and lateral basicranium, is analyzed in lateral radiographs of 144 adult humans from three different geographic regions. The null hypothesis of homogeneously pervasive morphological integration among “posterior-face” components is tested with Procrustes geometric morphometrics, partial least squares, and singular warps analysis. The results reveal statistically significant differences in integration. Only loose integrative relationships are found between midline and lateral components of the basicranium, which may indicate the presence of at least two different basi-

cranial modules. This modularity can be interpreted in terms of spatiotemporal dissociation in the development of those basicranial structures, and gives support to hypotheses of independent phylogenetic modifications at the lateral and midline basicranium in humans. In addition, morphological integration was statistically significantly stronger between the middle cranial fossa and the mandibular ramus than between the ramus and the midline cranial base. This finding confirms previous hypotheses of a “petroso-mandibular unit,” which could be a developmental consequence of well-known phylogenetic modifications in coronal topology of the posterior face and base in hominoid evolution, related to middle cranial fossa expansion. This unit could be involved in later evolutionary tendencies in the hominid craniofacial system. *Am J Phys Anthropol* 128:26–34, 2005.

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“Modularity allows for evolvability” (Winther, 2001, p. 291) and connects different levels of biological organization (Riedl, 1975; Raff, 1996; Wagner, 1996; von Dassow and Munro, 1999; Klingenberg et al., 2003; Bastir, 2004). Klingenberg et al. (2003, p. 522) recently described modules as units that “are made internally coherent by manifold and strong *interactions* among their component parts, but ... relatively independent from other modules and have relatively weak or few connections with other parts of a system.” Such kinds of interactions characterize also morphological integration (Olson and Miller, 1958; Cheverud, 1982, 1995; Zelditch, 1987; Wagner, 1990; Chernoff and Magwene, 1999; Lieberman et al., 2000a,b; Klingenberg et al., 2001, 2003; Hallgrímsson et al., 2002; Rosas and Bastir, 2004), defined as a “correspondence of patterns of covariation among traits to *a priori* or *a posteriori* hypotheses” (Chernoff and Magwene, 1999, p. 319).

The relative independence among components of morphological structures (associated with modularity and integration) is an important precondition of mosaic evolutionary change, because modifications in one functional system should not impinge on the functional or structural integrity of others (Riedl, 1975; Raff, 1996). If integration were homogeneously pervasive, then morphological evolution

would not occur (Smith, 1996). All parts of a system would be affected in the same degree by a modification of one specific component, unlikely to produce viable biological results (Riedl, 1975, 1977; Wagner and Altenberg, 1996). In order to understand specific processes that lead to the relative independence of morphological units (modularization), it is first essential to identify and delimit modules (Klingenberg et al., 2003).

## EVIDENCE FROM HUMAN CRANIOFACIAL AND PALEO BIOLOGY

Soft tissues such as the brain, muscles, or even functional (empty) spaces were suggested to be

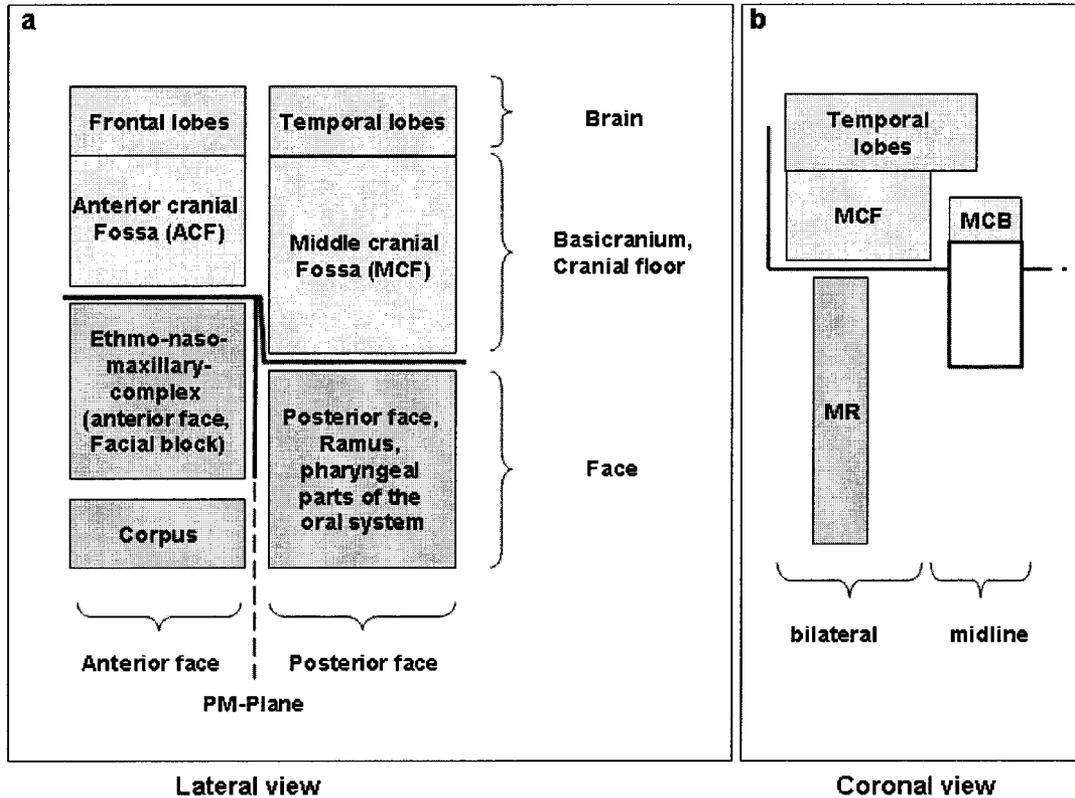
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**Fig. 1.** Anterior and posterior face. **a:** Lateral view of Enlow's growth counterparts drawn in perspective of modularity. Hypothetical relationships between brain and basicranial and facial components of craniofacial system. PM plane delimits modules of anterior and posterior face. **b:** Coronal perspective illustrates spatial relationships of proposed components of posterior face (mandibular ramus) and base (middle cranial fossa, midline cranial base).

morphologically integrated with adjacent skeletal elements, a key idea in the functional matrix hypothesis (Moss, 1962, 1997c,d). Changes in the ontogeny or phylogeny of these soft tissues are hypothesized to control the morphogenesis of skeletal morphology (Moss, 1997a,b). Many different functional cranial components (*sensu* Moss, 1997a,b) are integrated at a higher morphological scale within the framework of Enlow's counterpart analysis (Enlow et al., 1969, 1982; Bhat and Enlow, 1985). Counterpart principles are conceived within the idea of modularity because growth counterparts of the craniofacial system are thought to divide the face into a series of morphogenetically interacting modules (Enlow et al., 1969). These components are divided into an anterior and a posterior region, i.e., the anterior and posterior face, separated by the posterior maxillary (PM) plane (Enlow and Hans, 1996; McCarthy and Lieberman, 2001) (Fig. 1).

The anterior face, Enlow's nasomaxillary complex (Enlow and Hans, 1996), was recently identified as a morphologically integrated "facial block" together with the orbits (Lieberman et al., 2000b; McCarthy and Lieberman, 2001). Also, other studies suggested a relative independence of the positioning of the face with respect to the rest of the skull as a possible reflection of different developmental modules in human faces (McCollum, 1999; Lieberman et al.,

2000a; Zollikofer and Ponce de León, 2002; Bastir and Rosas, 2004), in australopithecines (McCollum, 1999), and in humans and chimpanzees (Bastir and Rosas, 2004; Bastir et al., 2005).

However, modularization at the posterior face and base (Fig. 1) has not yet been proposed, although a series of recent studies might justify this. In a recent analysis of basicranial ontogeny, Lieberman and McCarthy (1999) found that in humans, the adult morphological pattern of the cranial base angle is achieved relatively early in ontogeny, at approximately 2–3 years of age. Other structures of the posterior base, such as the middle cranial fossae (Fig. 1b), attain their mature morphology much later, presumably linked to the development of associated brain regions (Ranly, 1988; Enlow and Hans, 1996; Lieberman et al., 2000b). This kind of spatiotemporal dissociation during ontogenetic maturation of adjacent basicranial structures suggests a relative independence in the development of midline and lateral basicranial structures of the posterior base. Therefore, lower degrees of morphological integration can be expected between both basicranial elements.

In addition, basicranial flexion is phylogenetically correlated with encephalization (Biegert, 1957; Hofer, 1965; Gould, 1977; Ross and Ravosa, 1993). Increasing relative brain volume (encephalization)

leads to increased flexion. Because of functional reasons, Ross and Henneberg (1995) suggested that this flexion is phylogenetically constrained to an angle of  $90^\circ$  (achieved in some australopithecines), but follow-up studies showed that the hypothesis of constraint on basicranial angle is only valid if anterior cranial floor structures are excluded from the analysis (Spoor, 1997; McCarthy, 2001). Also, ontogenetic analyses, which indicated that pure brain expansion in fetal development did not necessarily lead to an increase in flexure in humans and some nonhuman primates (Jeffery and Spoor, 2002; Jeffery, 2003), challenged the mechanistic aspect of the hypothesis of constraint of Ross and Henneberg (1995). Although no discriminatory hypothesis is currently available (Ross et al., 2004), it is clear that from a morphogenetic point of view, a strong morphological integration between midline and lateral basicranial parts in humans would a priori exclude independent evolutionary modifications, and thus the hypothesis of constraint of Ross and Henneberg (1995). Modularity at the posterior base among midline and lateral basicranial elements is a precondition for the hypothesis of constrained flexion.

However, lateral basicranial modifications and encephalization, independent from the idea of constraints on flexion, were suggested early in paleoanthropology by Dabelow (1929, 1931) and Biegert (1957), and have recently been increasingly discussed (Seidler et al., 1997; Spoor et al., 1999; Lieberman et al., 2002; Bastir, 2004). This can be assumed also because bilateral basicranial floor structures share close anatomical relationships with the frontal, temporal, and indirectly even parietal lobes, which are discussed as effectively encephalized structures in human evolution (Semenferi and Damasio, 2000; Rilling and Seligman, 2002; Bruner et al., 2003). Again, such independent phylogenetic modifications at the lateral cranial floor require a basicranium composed of several developmentally autonomous modules.

Finally, a recent study, which analyzed the relationships between mandibular ramus breadth and the PM plane in humans, suggested that the bilateral middle cranial fossa and the mandibular ramus form a morphologically integrated unit (Bastir et al., 2004). Whenever the petrosal temporal was rotated in a backwards-upward position with respect to the PM plane (as a reference structure), the posterior parts of the mandibular ramus were shifted posteriorly, and so increasing the antero-posterior breadth of the mandibular ramus. The tendency of covariation appeared less clear between the ramus and the cranial base at the midline (Bastir et al., 2004). Although this hypothesis has not been tested (it is the second hypothesis of this study), the findings are in line with Sherwood et al. (2002), who showed quantitatively that humans, compared with great apes, differ in the spatial relation between the middle cranial fossae and glenoid fossa (and thus the mandibular

ramus). Middle cranial fossa position in humans can influence the spatial setting of the ramus and consequently its pattern of development (Enlow et al., 1982; Bhat and Enlow, 1985) as a consequence of phylogenetic reduction of the masticatory apparatus and an expansion of the middle cranial fossa (Sherwood et al., 2002; Stedman et al., 2004).

The first hypothesis of this study will test for modularity among basicranial elements of the posterior base, and the second hypothesis for increased integration between the middle cranial fossa and the mandibular ramus, against the null hypothesis of homogeneously integrated components of the posterior face and base.

## MATERIALS AND METHODS

A total sample of 144 adult skulls of European, Japanese, and West African adult modern humans was analyzed. Only in fully developed individuals had all functional systems reached skeletal maturity, and are thus likely to reflect the theoretically relevant patterns of morphological variation and covariation as evidence for underlying developmental mechanisms (Klingenberg, 1998; Klingenberg et al., 2001). Specimens were selected avoiding any cranial or other deformation of the dental arches of the mandibles and maxillae, and controlling for clinically acceptable occlusion. Details of each population and further evaluation criteria are described elsewhere (Bastir et al., 2004; Kuroe et al., 2004).

All 144 skulls were x-rayed laterally, with the mandible fixed in occlusion. An Andrex portable x-ray machine with a cephalostat for dry skull material was used for this study. The focus-to-film distance and the distance from the midsagittal plane of the skull to the film were 150 cm and 15 cm, respectively. Lateral cephalograms were taken at 80 kV, 3 mA, and 60 sec.

The lateral radiographs were digitally scanned, and a set of 17 landmarks was digitized by tpsDIG software (Rohlf, 1997) (Table 1, Fig. 2) that represented the morphology of the middle cranial fossa, the midline cranial base, and the mandibular ramus. The selection of basicranial landmarks respected the three-dimensional (3D) nature of the basicranium, and distinguished between midline and lateral structures. However, paired bilateral landmarks were digitized following standard radiographic averaging methods (Enlow and Hans, 1996), which may imply an increased degree of measurement error. In addition, due to the relatively large sample size, such error may cause increased noise within variation patterns of lateral systems compared with the midline base. Theoretically, this situation is likely to weaken the correlative properties of bilateral structures. However, the measurement error was evaluated by a repeated data recording of 10 specimens on 4 different days and tested by MANOVA. No significant difference was found between the repeated samples (Wilk's

TABLE 1. Landmark definitions<sup>1</sup>

	Count	Landmarks, description
MCB	1	PS, limit between planum sphenoidale and cribriform plate (Ross and Ravosa, 1993)
	2	Posterior limit of planum sphenoidale (Ross and Ravosa, 1993)
	3	Dorsum sellae (Bastir et al., 2004)
	4	Basion
MCF	5	Superiormost point of MCF (spheno-parietal junction)
	6	Anterior vertex of MCF curvature (between landmarks 1 and 3 of MCF)
	7	Inferiormost point of MCF (petrosal part)
	8	Posteriormost point of MCF (temporo-parietal junction)
MR	9	Condylion
	10	Ramus flexion, posterior border of minimal ramus breadth
	11	Gonion
	12	Preangular notch, deepest point
	13	Foramen mandibularis
	14	Mandibular notch
	15	Apex of coronoid process
	16	Anterior ramus, anterior limit of minimal ramus breadth
	17	Posterior alveolus of last molar

<sup>1</sup>MCB, midline cranial base; MCF, middle cranial fossa; MR, mandibular ramus.

$\lambda = 0.00$ ;  $F = 1.78$ ;  $df_{1, 2} = 140, 6.65$ ;  $P = 0.2$ ), indicating that measurement error was smaller than the variation within the samples.

### Geometric morphometrics

In the present study, we used Procrustes geometric morphometry, based on the analysis of landmark coordinates (Table 1) to investigate patterns of morphological covariation. After geometric morphometric standard procedures, such as Procrustes superimposition (Rohlf and Slice, 1990; Bookstein, 1991) and thin-plate spline transformation (Bookstein, 1991) ruling out information of scale, position, and orientation, three different sets of partial warps and uniform component scores resulted (Rohlf, 1996; Rohlf et al., 1996). These scores are the three blocks of shape variables of this study: one block for the middle cranial fossa, one for the midline cranial base, and one for the mandibular ramus.

### Statistical analysis

Partial least squares (PLS) analysis helps to find correlated pairs of linear combinations (singular vectors) between two blocks of variables (Bookstein, 1991; Rohlf and Corti, 2000). The singular vectors are constructed in the form of new, paired "latent" variables (one per block, also called singular warps; Bookstein et al., 2003) that account for as much as possible of the covariation between the two original sets of variables. In a similar sense to a principal components analysis (PCA), the singular value decomposition (SVD) describes the data in terms of scores of each specimen along singular axes, singular values (similar to eigenvalues), and loadings

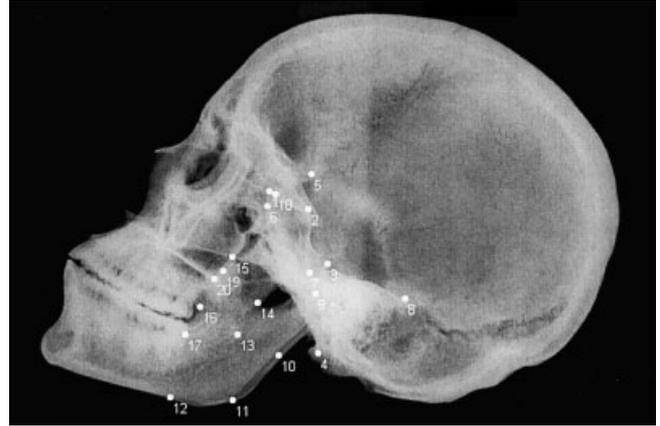


Fig. 2. Digitized landmarks of posterior face and base (see Table 1 for explanation of landmarks 1–17).

(singular vectors, similar to eigenvectors). However, singular value decomposition is applied with a different goal, i.e., to maximize low-dimensional representation of between-block covariance (SVD) vs. maximizing low-dimensional representation of total sample covariance (PCA). The singular warps display the maximal covariance between both the shape variables within-block and with the shape variables of the other block (Bookstein, 1991; Rohlf and Corti, 2000; Bookstein et al., 2003).

The amount of covariance explained by the paired singular vectors (the SVD axes), the correlation "r" of the scores of specimens along the singular axes of the two blocks, and permutations by tpsPLS (Rohlf, 1998) allow statistical assessment of the observed singular values and correlations. This correlation coefficient "r" can be used as a measurement of integration of two blocks of shape variables (Klingenberg et al., 2001; Bookstein et al., 2003). Permutations ( $N = 10,000$ ) were calculated to assess the statistical significance of the singular warp scores correlations. PLS-angle software (Sheets, 2001) (<http://www.canisius.edu/~sheets/morphsoft.htm>) can be used for resampling procedures, in which the 95% confidence intervals of the correlation coefficients between the singular warps are evaluated on the basis of repeated PLS analyses in bootstrapped subsamples. These 95% confidence intervals based on bootstrapping ( $N = 1,000$ ) were used to assess the statistical significance of differences among compared singular warps correlation coefficients.

The tpsPLS software permits the comparison of two sets of shape data. Therefore, three different PLS-analyses were performed, and three correlation coefficients were compared:  $r_1$  quantifies the integration between the midline cranial base and the middle cranial fossa (hypothesis 1);  $r_2$  quantifies the integration between the midline cranial base and the mandibular ramus; and  $r_3$  quantifies the integration between the middle cranial fossa and the mandibular ramus (hypothesis 2). The null hypothesis predicts no difference between the three correlation coefficients ( $r_1 = r_2 = r_3$ ).

TABLE 2. Statistics of PLS analyses (10,000 permutations)

Compared structures	PLS statistics		
	SVD correlations "r"	% higher r-values in permutations	% explained covariation
MCB-MCF ( $r_1$ )	0.27	7.2	54.0
	0.18	20.1	38.3
	0.06	71.2	6.2
	0.06	9.4	1.6
MCB-MR( $r_2$ )	0.04	0.1	64.8
	0.29	10.3	21.5
	0.21	33.0	12.0
	0.01	66.1	1.7
MCF-MR ( $r_3$ )	0.62	0.0	94.4
	0.32	2.6	4.3
	0.19	48.5	0.7
	0.22	6.0	0.6

## RESULTS

Three PLS analyses yielded different correlation coefficients between singular warps of the middle cranial fossae, the midline cranial base, and the mandibular ramus (Table 2). The three first singular warps were analyzed in more detail. A large number of permutations (10,000) (tpsPLS software; Rohlf, 1998) revealed that no statistical significance was found for the low correlation between the middle cranial fossa and the midline cranial base ( $r = 0.27$ ,  $P = 0.07$ ). Only two pairs of shape data were statistically significantly correlated, i.e., the midline cranial base with the mandibular ramus ( $r = 0.4$ ;  $P = 0.0001$ ), and the mandibular ramus and the middle cranial fossa ( $r = 0.62$ ;  $P = 0.0000$ ).

The 95% confidence intervals evaluated by bootstrapping of the singular warp correlations are shown in Table 3. They indicate that the mandibular ramus and middle cranial fossae are significantly more highly integrated than the midline base and ramus (Fig. 3). The results show that the null hypothesis of homogenous integration among all three components should be rejected.

## DISCUSSION

In the present study, modularity and morphological integration among the midline cranial base, bilateral middle cranial fossae, and mandibular ramus were investigated (Enlow et al., 1969; Smith and Josell, 1984; Enlow and Hans, 1996; Lieberman et al., 2000b; McCarthy and Lieberman, 2001; Bastir et al., 2004). Partial least squares analyses of Procrustes superimposed shape data (Bookstein, 1991; Rohlf and Corti, 2000) and permutation analyses (Zelditch et al., 2000; Bastir et al., 2005) were used to assess and compare correlation coefficients of principal patterns of shape covariation (singular warps) (Bookstein et al., 2003). These analyses were used to test a null hypothesis that predicted no difference in correlation coefficients between the singular warps of all three compared anatomical structures. The results indicate that the null hypothesis should be rejected.

TABLE 3. First singular warp correlations and confidence intervals (1,000 permutations)

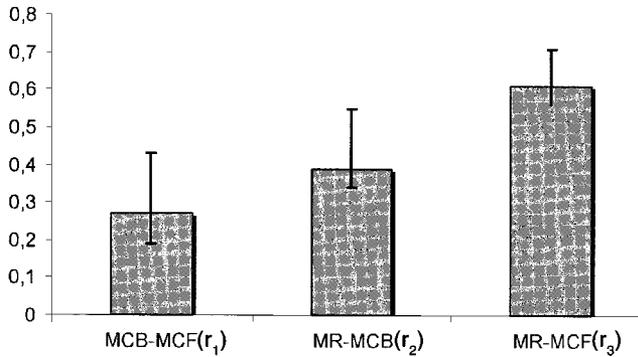
Compared structures	r	Lower 95% CI	Upper 95% CI	Standard error
MCB-MCF ( $r_1$ )	0.27	0.19	0.43	0.061
MR-MCB ( $r_2$ )	0.39	0.34	0.55	0.057
MR-MCF ( $r_3$ )	0.61	0.56	0.71	0.039

Modularity in primate skulls was addressed in different aspects (Lieberman et al., 2000b; McCarthy and Lieberman, 2001; Zollikofer and Ponce de León, 2002; Bastir and Rosas, 2004; Bastir et al., 2005). All of these analyses address morphological integration of the nasomaxillary complex, but the "posterior face" has not been analyzed. This area is nevertheless of specific interest in various ontogenetic and phylogenetic perspectives.

A recent comparative ontogenetic analysis (Lieberman and McCarthy, 1999) showed that angular measurements of midline basicranial flexion in ontogenetic series attain mature values relatively early (2 years), while the development of the cerebrum and associated parts of the basicranium continue their maturation for a much longer period, still modifying their morphology (Moss and Young, 1960; Ranly, 1988; Lieberman et al., 2000b). The relatively low and statistically nonsignificant correlations ( $r_1 = 0.27$ ) between the first singular warps of the middle cranial fossa and the midline cranial base can be interpreted as a result of this spatiotemporal divergence in maturation. Longer postnatal development of the middle cranial fossae is possibly related to the morphological maturation of the developing temporal lobes (Dabelow, 1931; Enlow and Hans, 1996; Lieberman et al., 2000b). It was suggested that the temporal lobes and middle cranial fossa yield their mature morphology several years later than the frontal lobes and the anterior cranial fossa (fully grown at approximately 6–7 years) (Enlow and Hans, 1996; Lieberman et al., 2000b), and considerably later than the angulation of the midline cranial base (Lieberman and McCarthy, 1999). Independent maturation might possibly be reflected by independent patterns of morphological variation.

It remains to be analyzed whether the lack of correlation between midline and lateral structures in this study is due to general differences in variability (one structure less variable than the other) or to simply uncorrelated patterns of shape variation. Recent investigation of the ontogeny of basicranial flexure, although for a limited prenatal ontogenetic period, indicated also a certain resistance of the midline cranial base angle to mechanic stimuli such as pure brain expansion (Jeffery and Spoor, 2002; Jeffery, 2003), which may favor an interpretation of reduced or stabilized morphological variation at midline basicranial elements.

However, decreased interdependence can also be associated with the different functional and struc-



**Fig. 3.** Correlation coefficients of singular warp (SW) scores.  $r_1$ , SW correlations between midline cranial base (MCB) and middle cranial fossa (MCF);  $r_2$ , SW correlations between midline cranial base (MCB) and mandibular ramus (MR);  $r_3$ , SW correlations between middle cranial fossa (MCF) and mandibular ramus (MR).

tural roles of midline and lateral basicranial components. The midline cranial base is located at the interface of at least two different functional systems. On its exocranial part, the midline base provides the surface for the attachment of pharyngeal structures. It is thus part of the respiratory system (Moss, 1962; Moss and Salentijn, 1969; Enlow and Hans, 1996), and may be involved in sexual dimorphism (Rosas and Bastir, 2002) and speech (Lieberman and McCarthy, 1999; Lieberman et al., 2001). On its internal surface, the midline base is associated with neural structures, such as the brain stem, the hypophyseal system, and particularly at its lateral part to the before-mentioned developmental aspects of the middle cranial fossae and possibly the temporal lobes (Dabelow, 1931; Enlow and Hans, 1996; Lieberman et al., 2000a). However, Lieberman et al. (2000b) suggested that a possible morphogenetic association between temporal lobe morphology and middle cranial fossa development (Enlow and Hans, 1996) as a functional matrix system (Moss and Young, 1960; Moss, 1962) needs to be tested explicitly before a direct relationship can be inferred. This seems particularly important in the light of the findings of Jeffery and Spoor (2002; see also Jeffery, 2003), who showed that brain development alone is not exclusively relevant for fetal morphogenesis of the midline basicranium.

However, the low integration between midline and lateral basicranial elements is also important in different phylogenetic perspectives (Dabelow, 1929, 1931; Biegert, 1957; Hofer, 1957, 1965; Ross and Ravosa, 1993; Ross and Henneberg, 1995; Lieberman et al., 2000b, 2002; McCarthy, 2001; Strait, 2001; Ross et al., 2004). It is currently under discussion whether hominid evolution may or may not be characterized by constrained variation on midline basicranial flexure (Ross and Ravosa, 1993; Ross and Henneberg, 1995; Spoor, 1997; Jeffery and Spoor, 2002; Jeffery, 2003; Ross et al., 2004). From a methodological perspective, much of this debate depends on the inclusion of basicranial

elements of the anterior cranial floor (McCarthy, 2001; Ross et al., 2004) and the identification of genetic and/or epigenetic control of basicranial flexure (Jeffery and Spoor, 2002; Jeffery, 2003). The current state of the discussion indicates that hypotheses favoring or against phylogenetic constraints of basicranial flexure cannot be “discriminated at present” (Ross et al., 2004).

The findings of a relative independence of lateral and midline basicranial elements, shown in the present study by the low singular warp correlations (Table 2), contribute to this debate insofar as they indicate that lateral encephalization of frontal and temporal lobes, morphogenetically independent from midline structures, is principally possible (Bastir, 2004). This modularity inferred by the lack of strong morphological integration (Klingenberg et al., 2003) allows generally for independent (mosaic) evolutionary changes in lateral basicranial regions, which need not be related to constraints at the midline. Lateral encephalization was suggested with respect to various cerebral structures: the frontal lobes (Dabelow, 1929; 1931; Hofer and Tigges, 1963; Hofer, 1965), the temporal lobes (Semendeferi and Damasio, 2000; Rilling and Seligman, 2002), and the parietal lobes (Bruner et al., 2003). Also, modifications of anterior cranial fossa morphology (Seidler et al., 1997; Lieberman, 1998; Spoor et al., 1999) and middle cranial fossa morphology (Seidler et al., 1997; Spoor et al., 1999; Lieberman et al., 2002; Bastir, 2004) were associated with possible encephalization of bilateral structures.

### Basicranial and mandibular relationships

One key idea of the counterpart analysis principle is that the structural function of the ramus is to bridge the pharyngeal space and to provide occlusion (Enlow et al., 1982; Bhat and Enlow, 1985; Enlow and Hans, 1996). This hypothesis was corroborated previously (Smith and Josell, 1984), and the moderate correlation in this study (Table 2) between the midline base and ramus is likely a further indication of this structural function of the ramus.

However, the new findings of this study provide support for the second hypothesis that predicted that lateral basicranial elements are more strongly integrated with the mandible than are midline basicranial elements (Bastir et al., 2004). This interpretation is evident from the high singular warp correlations between middle cranial fossa and mandibular ramus shape variation (Tables 2 and 3). It is possible to discuss higher lateral integration within the same structural and functional perspectives. In humans, the inferior part of the middle cranial fossa carries the temporomandibular joint. Any modification of middle cranial fossa position is directly related to a modification of the ramus position. It was recently shown that ramus breadth variation is located almost exclusively at the posterior part of the ramus with respect to the

PM plane (Bastir et al., 2004). This supports the functional aspects of the counterpart principles of Enlow (Enlow et al., 1969, 1982; Smith and Josell, 1984; Bhat and Enlow, 1985; McCarthy and Lieberman, 2001). The present findings are complementary and lend additional support to these ideas, indicating that the lateral basicranium is in particular the morphogenetically relevant structure, more than the midline basicranial flexure. It is interesting to note that the importance of the "lateral portions of the cranial floor" was mentioned in a footnote (Enlow et al., 1971, p. 166), but never explicitly tested.

The importance of the lateral basicranium for human ramus shape may be the consequence of evolutionary modifications of the topology of the posterior face, both in larger and smaller phylogenetic scales. The larger scale was recently investigated by Sherwood et al. (2002), who showed with CT data that the coronal spatial relationships between the temporomandibular joint and the middle cranial fossa changed during human evolution. While in great apes the glenoid fossa is lateral to the middle cranial fossae, in humans it is located below. Similar spatial relationships were recently related to specific genetic modifications (Stedman et al., 2004).

The increased integration in the lateral system in the present data can be interpreted as a consequence of the derived spatial situation in humans. However, further study should compare the integrative relations between the ramus and middle cranial fossae in great apes, as they could indicate a specific example in hominoid skulls of a more general principle, according to which phylogenetic reorganization of modularity would participate in the organization of phylogenetic trends in morphological variation. Based on the present data, and the observations of Sherwood et al. (2002), decreased levels of morphological integration should be expected between the middle cranial fossa and mandibular ramus in hominoids. Preliminary results apparently support this hypothesis (unpublished data).

The lower evolutionary scale implies that phylogenetic modifications of alignment and the size of the middle cranial fossae (and possibly temporal lobes) in hominids (Seidler et al., 1997; Spoor et al., 1999; Lieberman et al., 2002; Bastir, 2004) would be reflected in phylogenetic modifications of mandibular ramus breadth (Rosas, 1998; Bastir et al., 2002). It seems that the relatively strongly integrated components of the lateral middle cranial fossae and mandibular ramus provide a substrate for a series of interconnected structural and functional relationships. In connecting the "lateral basicranium" with the posterior face (Enlow et al., 1971; Enlow and McNamara, 1973) as traditionally defined, this integration provides a mechanism for changes in the middle cranial fossae associated with temporal lobe evolution to affect the masticatory system, and vice versa.

The present study showed that in humans, morphological integration at the posterior face and cranial base is hierarchically organized. Low levels of integration characterized the modularity of midline and lateral basicranial elements. Significantly higher integration was found between the middle cranial fossa and mandibular ramus. Future studies should expand this approach to study endocranial and facial 3D data in great apes, and should also include fossil hominid skulls in order to complement the understanding of the evolution of morphological integration and modularity and their relationships to the morphogenesis of this important region of the human skull.

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## LITERATURE CITED

- 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 Neanderthals. Structural and systemic factors of morphology in the hominid craniofacial system. Doctoral dissertation, Autonomous University of Madrid.
- 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, Kuroe K. 2002. Morphogenetic determinants of mandibular ramus breadth: a test in modern human populations. *Am J Phys Anthropol* 115:40–41.
- 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, Rosas A, Sheets DH. 2005. The morphological integration of the hominoid skull: a partial least squares and PC analysis with morphogenetic implications for European Mid-Pleistocene mandibles. In: Slice D, editor. *Modern morphometrics in physical anthropology*. New York: Kluwer Academic/Plenum. (In press.)
- Bhat M, Enlow DH. 1985. Facial variations related to headform type. *Angle Orthod* 55:269–280.
- Biegert J. 1957. Der Formwandel des Primatenschädels und seine Beziehungen zur ontogenetischen Entwicklung und den phylogenetischen Spezialisierungen der Kopforgane. *Gegenbaurs Morphol Jahrb* 98:77–199.
- Bookstein FL. 1991. *Morphometric tools for landmark data*. Cambridge: Cambridge University Press.
- Bookstein FL, Gunz P, Mitteroecker P, Prossinger H, Schaefer K, Seidler H. 2003. Cranial integration in *Homo*: singular warps analysis of the midsagittal plane in ontogeny and evolution. *J Hum Evol* 44:167–187.

- 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.
- Chernoff B, Magwene PM. 1999. Afterword. In: Olson EC, Miller PL, editors. *Morphological integration*. Chicago: University of Chicago. p 319–353.
- Cheverud JM. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. *Evolution* 36:499–516.
- Cheverud JM. 1995. Morphological integration in the saddle-backed tamarin (*Saguinus fuscicollis*). *Am Nat* 145:63–89.
- Dabelow A. 1929. Über Korrelationen in der phylogenetischen Entwicklung der Schädelform I. Die Beziehungen zwischen Rumpf und Schädelform. *Gegenbaurs Morphol 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. *Gegenbaurs Morphol Jahrb* 67:84–133.
- Enlow DH, Hans MG. 1996. *Essentials of facial growth*. Philadelphia: W.B. Saunders Co.
- Enlow DH, McNamara JAJ. 1973. The neurocranial basis for facial form and pattern. *Am J Orthod Dentofacial Orthop* 43:256–270.
- Enlow DH, Moyers RE, Hunter WS, McNamara JA Jr. 1969. A procedure for the analysis of intrinsic facial form and growth. *Am J Orthod Dentofacial Orthop* 56:6–23.
- Enlow DH, Kuroda T, Lewis AB. 1971. The morphological and morphogenetical basis for craniofacial form and pattern. *Angle Orthod* 41:161–188.
- Enlow DH, Pfister C, Richardson E, Kuroda T. 1982. An analysis of Black and Caucasian craniofacial patterns. *Angle Orthod* 52:279–287.
- Gould SJ. 1977. *Ontogeny and phylogeny*. Cambridge, MA: Harvard University Press.
- Hallgrímsson B, Willmore K, Hall BK. 2002. Canalization, developmental stability, and morphological integration in primate limbs. *Yrbk Phys Anthropol* 45:131–158.
- Hofer H. 1957. Zur Kenntnis der Kyphosen des Primatenschädels. *Verh Anat Ges* 54:54–76.
- Hofer H. 1965. Die morphologische Analyse des Schädels des Menschen. In: Heberer G, editor. *Menschliche Abstammungslehre, Fortschritte der Anthropogenie, 1863–1964*. Stuttgart: Gustav Fischer Verlag. p 145–226.
- Hofer H, Tigges J. 1963. Studien zum Problem des Gestaltwandels des Schädels der Säugetiere insbesondere der Primaten: III. Zur Kenntnis der Hirnkyphosen. *Z Morphol Anthropol* 54:115–126.
- 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. 2002. Brain size and the human cranial base. *Am J Phys Anthropol* 118:324–340.
- Klingenberg CP. 1998. Heterochrony and allometry: the analysis of evolutionary change in ontogeny. *Biol Rev Cambridge Philosophic Soc* 73:79–123.
- Klingenberg CP, Badyaev AV, Sowry SM, Beckwith NJ. 2001. Inferring developmental modularity from morphological integration: analysis of individual variation and asymmetry in bumblebee wings. *Am Nat* 157:11–23.
- Klingenberg CP, 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.
- Lieberman DE. 1998. Sphenoid shortening and the evolution of modern human cranial shape. *Nature* 393:158–162.
- Lieberman DE, McCarthy RC. 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 DE, McCarthy RC, Hiiemae KM, Palmer JB. 2001. Ontogeny of postnatal hyoid larynx descent in humans. *Arch Oral Biol* 46:117–128.
- Lieberman DE, Pearson OM, Mowbray KM. 2000a. Basicranial influence on overall cranial shape. *J Hum Evol* 38:291–315.
- Lieberman DE, Ross C, Ravosa MJ. 2000b. The primate cranial base: ontogeny, function, and integration. *Yrbk Phys Anthropol* 43:117–169.
- Lieberman DE, McBratney BM, Krovitz G. 2002. The evolution and development of cranial form in *Homo sapiens*. *Proc Natl Acad Sci USA* 99:1134–1139.
- McCarthy R. 2001. Anthropoid cranial base architecture and scaling relationships. *J Hum Evol* 40:41–66.
- McCarthy R, Lieberman DE. 2001. Posterior maxillary (PM) plane and anterior cranial architecture in primates. *Anat Rec* 264:247–260.
- McCollum M. 1999. The robust australopithecine face: a morphogenetic perspective. *Science* 284:301–305.
- Moss M. 1962. The functional matrix. In: Kraus B, Reidel R, editors. *Vistas in orthodontics*. Philadelphia: Lea and Febiger. p 85–98.
- Moss M. 1997a. The functional matrix hypothesis revisited. 1. The role of mechanotransduction. *Am J Orthod Dentofacial Orthop* 112:8–11.
- Moss M. 1997b. The functional matrix hypothesis revisited. 2. The role of an osseous connected cellular network. *Am J Orthod Dentofacial Orthop* 112:221–226.
- Moss M. 1997c. The functional matrix hypothesis revisited. 3. The genomic thesis. *Am J Orthod Dentofacial Orthop* 112:338–342.
- Moss M. 1997d. The functional matrix hypothesis revisited. 4. The epigenetic antithesis and the resolving synthesis. *Am J Orthod Dentofacial Orthop* 112:410–417.
- Moss M, Salentijn L. 1969. The capsular matrix. *Am J Orthod Dentofacial Orthop* 56:474–490.
- Moss M, Young RW. 1960. A functional approach to craniology. *Am J Phys Anthropol* 45:281–292.
- Olson EC, Miller RL. 1958. *Morphological integration*. Chicago: University of Chicago Press.
- Raff RA. 1996. *The shape of life. Gene, development, and the evolution of animal form*. Chicago: University of Chicago Press.
- Ranly DM. 1988. *A synopsis of craniofacial growth*. Norwalk, CT: Appleton & Lange.
- Riedl R. 1975. *Die Ordnung des Lebendigen. Systembedingungen der Evolution*. Hamburg: Paul Parey Verlag.
- Riedl R. 1977. A systems-analytical approach to macro-evolutionary phenomena. *Q Rev Biol* 52:351–370.
- Rilling JK, Seligman RA. 2002. A quantitative morphometric comparative analysis of the primate temporal lobe. *J Hum Evol* 42:1–29.
- Rohlf FJ. 1996. Morphometric spaces, shape components and the effects of linear transformations. In: Marcus LF, editor. *Advances in morphometrics*. New York: Plenum Press. p 117–128.
- Rohlf F. 1997. *tpsDIG*. New York: Department of Ecology and Evolution, State University, Stony Brook.
- Rohlf F. 1998. *tpsPLS*. New York: Department of Ecology and Evolution, State University, Stony Brook.
- Rohlf FJ, Corti M. 2000. The use of two-block partial least-squares to study covariation in shape. *Syst Zool* 49:740–753.
- Rohlf FJ, Slice D. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Syst Zool* 39:40–59.
- Rohlf FJ, Loy A, Corti M. 1996. Morphometric analysis of Old World Talpidae (Mammalia, Insectivora) using partial warp scores. *Syst Biol* 45:344–362.
- Rosas A. 1998. Modelos de crecimiento en mandíbulas fósiles de homínidos. Atapuerca, un nuevo paradigma. In: Aguirre E, editor. *Atapuerca y la evolución humana*. Madrid: Fundación Ramón Areces. p 239–275.
- 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, Bastir M. 2004. Geometric morphometric analysis of allometric variation in the mandibular morphology from the hominids of Atapuerca, Sima de los Huesos site. *Anat Rec* 278:551–560.
- 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 CF, Ravosa MJ. 1993. Basicranial flexion, relative brain size, and facial kyphosis in nonhuman primates. *Am J Phys Anthropol* 91:305–324.
- Ross CF, Henneberg M, Ravosa MJ, Richard S. 2004. Curvilinear, geometric and phylogenetic modeling of basicranial flexion: is it adaptive, is it constrained? *J Hum Evol* 46:185–213.
- Seidler H, Falk D, Stringer C, Wilfing H, Muller GB, zur Nedden D, Weber GW, 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.
- Semendeferi K, Damasio H. 2000. The brain and its main anatomical subdivisions in living hominoids using magnetic resonance imaging. *J Hum Evol* 38:317–332.
- Sheets HD. 2001. IMP, integrated morphometric package: <http://www.canisius.edu/~sheets/morphsoft.html>; Sheets, David H.
- Sherwood RJ, Rowley RB, Ward SC. 2002. Relative placement of the mandibular fossa in great apes and humans. *J Hum Evol* 43:57–66.
- Smith KK. 1996. Integration of craniofacial structures during development in mammals. *Am Zool* 36:70–79.
- Smith RJ, Josell SD. 1984. The plan of the humans face: a test of three general concepts. *Am J Orthod Dentofacial Orthop* 85:103–108.
- 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 DE. 1999. Anterior sphenoid in modern humans. *Nature* 397:572.
- Stedman H, Kozyak BW, Nelson A, Thesier DM, Su LT, Low DW, Bridges CR, Shrager JB, Minugh-Purvis N, Mitchell MA. 2004. Myosin gene mutation correlates with anatomical changes in the human lineage. *Nature* 428:415–418.
- Strait DS. 2001. Integration, phylogeny, and the hominid cranial base. *Am J Phys Anthropol* 114:273–297.
- von Dassow G, Munro E. 1999. Modularity in animal development and evolution: elements of a conceptual framework for EvoDevo. *J Exp Zool* 285:307–325.
- Wagner G. 1996. Homologues, natural kinds and the evolution of modularity. *Am Zool* 36:36–43.
- Wagner GP. 1990. A comparative study of morphological integration in *Apis mellifera* (Insecta, Hymenoptera). *Z Syst Evol* 28: 48–61.
- Wagner GP, Altenberg L. 1996. Complex adaptation and the evolution of evolvability. *Evolution* 50:967–976.
- Winther R. 2001. Varieties of modules: kinds, levels, origins, and behaviors. *J Exp Zool (Mol Dev Evol)* 291:116–129.
- Zelditch ML. 1987. Evaluating models of developmental integration in the laboratory rat using confirmatory factor analysis. *Syst Zool* 36:368–380.
- Zelditch ML, Sheets DH, Fink WL. 2000. Spatiotemporal reorganization of growth rates in the evolution of ontogeny. *Evolution* 54:1363–1371.
- Zollikofer CPE, Ponce de León MS. 2002. Visualizing patterns of craniofacial shape variation in *Homo sapiens*. *Proc R Soc Lond [Biol]* 269:801–807.