

# Allometries Throughout the Late Prenatal and Early Postnatal Human Craniofacial Ontogeny

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## ABSTRACT

Craniofacial shape changes throughout the late prenatal and early postnatal ontogeny (32–47 weeks of gestational age) were explored. The purpose was to evaluate whether the skull follows an allometric growth pattern, as was observed in other ontogenetic periods, and to assess shape variation patterns for the cranial vault, cranial base, and face. Thirty three-dimensional landmarks were registered in 54 skulls. Wire-frames were built with landmarks to observe shape variation in the following cranial components: anteroneural, midneural, posteroneural, optic, respiratory, masticatory, and alveolar. The landmark configurations were subjected to generalized Procrustes analyses, and the shape coordinates obtained were subjected to Principal Components Analyses. Multivariate regression of the shape variables (the principal components) on the size vector (the centroid size) was performed to assess allometries. Transformation grids were constructed to identify how cranial components interact across ontogeny. Results indicated that highly significant shape changes depend on size changes. Important shape variation in the vault, small variation in the cranial base, and no variation in the face were observed. Brain growth is proposed to be the major influence on craniofacial shape change, which produces a relative elongation and compression of midneural and posteroneural components. The cranial base elongates by intrinsic factors and affects position of the face. Ontogenetically, the cranial base seems to be independent with respect to brain growth, in contrast to what has been suggested in comparisons at higher taxonomic levels. *Anat Rec*, 290:1112–1120, 2007. © 2007 Wiley-Liss, Inc.

**Key words: ontogenetic allometry; modularity; geometric morphometrics; brain growth**

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Ontogenetic allometry is the size-related shape variation in growing individuals (Cheverud, 1982b; Klingenberg, 1998). It is accepted that, postnatally, the craniofacial skeleton in primates and humans grows allometrically (e.g., Buschang et al., 1983; Corner and Richtsmeier, 1992; Enlow and Hans, 1996; Humphrey, 1998; O'Higgins and Jones, 1998; Strand Vidarsdottir et al., 2002; Bastir and Rosas, 2004; VandeBerg et al., 2004; Bastir et al., 2006). Prenatally, it has been suggested that, after organogenesis, craniofacial growth is mainly characterized by volume increases (Enlow and Hans, 1996); however, shape variation across the second

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**TABLE 1. Distribution of sample across gestational age (weeks)**

Weeks	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
n	1	3	1	4	2	6	7	5	3	7	9	1	1	1	1	2

**TABLE 2. Landmarks and definitions (see Figure 1)**

<i>Landmark</i>	<i>Code</i>	<i>Definition</i>
Glabella	1	Most anterior point of the frontal bone at the sagittal plane
Bregma	2	Intersection of coronal and sagittal sutures
Vertex	3	Most superior point of the vault at the sagittal plane
Lambda	4	Intersection of the sagittal and lambdoidal sutures
Opisthocranium	5	Most posterior point of the skull at the sagittal plane
Opisthion	6	Midline point on the posterior margin of the foramen magnum
Basion	7	Midline point on the anterior margin of the foramen magnum
Hormion	8	Most posterior midline point of the vomer
Pterion	9	Region where the frontal, parietal, sphenoid and temporal joint
Euryon	10	Most lateral point of the vault at the parietal bone
Asterion	11	Intersection of lambdoidal, perimastoid and occipitomastoid sutures
Lesser wing of the sphenoid	12	Midpoint of the septum between the optic foramen and the superior orbital fissure
Dacryon	13	Point where the lacrimomaxillary suture joins the frontal bone
Ectoconchion	14	Most lateral point of the orbital margin
Supraorbital	15	Most superior point of the orbital margin
Orbitale	16	Most inferior point of the orbital margin
Nasion	17	Intersection of internasal and frontonasal sutures
Subspinale	18	Deepest point of the subspinale concavity
Posterior nasal spine	19	Most posterior point of palatal bones
Right alare	20	Most lateral point of the right side of the nasal aperture
Left alare	21	Most lateral point of the left side of the nasal aperture
Zigomaxilare	22	Lowest point of the zygomaticomaxillary suture
Inferior zygotemporal	23	Lowest point of the zygotemporal suture
Glenoid	24	Most posterior point of the glenoid fossa
Sphenotemporal	25	Most external point of the sulcus located forward of the sphenotemporal crest
Stephanion	26	Intersection between the coronal suture and the inferior temporal line
Prostion	27	Most anterior point of the alveolar processes of the maxillae
Ectomolare	28	Most lateral point of the outer table of the alveolar margin
Posterior alveolar	29	Most posterior limit of the maxillary alveolar arch
Palate	30	Intersection of the palatine and maxillary bones

and third trimesters of gestation has been reported (e.g., Trenouth, 1984; Mandarin-de-Lacerda and Alves, 1992; Plavcan and German, 1995; Jeffery, 2002, 2003; Jeffery and Spoor, 2002; Zumpano, 2002; Zumpano and Richtsmeier, 2003).

According to Mossiman and Gould (Klingenberg, 1998), allometry is some shape change associated with some change in size. As individuals change in size, cranial shape changes mainly because different structures present different growth patterns. Cranial morphological traits that are functionally and developmentally connected tend to co-vary among themselves and to be quite independent from other traits due to the modular organization of the craniofacial skeleton (Cheverud, 1982a, 1995, 1996; Lieberman et al., 2000b; Schilling and Thorogood, 2000). A module can be defined as an array of traits that exhibit strong interactions within themselves and weak interactions with other modules (Cheverud, 1982a, Klingenberg et al., 2003). At the evolutionary level, the relative independence of different modules enables morphologic evolution to occur through independent processes (Wagner et al., 2005).

The mammalian skull is composed of, at least, two semi-independent modules: neurocranium and face (Cheverud, 1982a, 1995). Ontogenetically, they are characterized by differences in their embryological origins and

they are subject to different functional and developmental constraints. The neurocranium can be subdivided into the vault and the cranial base. The bones of the vault form through intramembranous ossification with bone expansion occurring at the sutures. The bones in the vault expand in response to extrinsic factors (Opperman et al., 2005), with brain growth being the primary stimulus (Delattre, 1951; Moss and Young, 1960; Michejda, 1975; Sirianni, 1985; Hartwig, 1995). By contrast, the bones in the cranial base form by endochondral ossification and expansion is produced by intrinsic growth potential of the synchondroses rather than by the influence of adjacent functional matrices (Opperman et al., 2005). Facial structures ossify intramembranously from the mesenchymal structures placed in the pharyngeal arches (Sperber, 2001). The development of airways, teeth, and the muscular loadings are the main factors that, through sutural growth (Opperman et al., 2005), influence facial shape (Enlow and Hans, 1996; Herring, 1993). Phylogenetically, some developmental shifts in craniofacial modules can explain morphologic diversity of mammals (Smith, 1996; Schilling and Thorogood, 2000) as well as modern humans with respect to other primates (Lieberman et al., 2004).

Even though both prenatal and postnatal craniofacial growth patterns have been studied independently, cra-

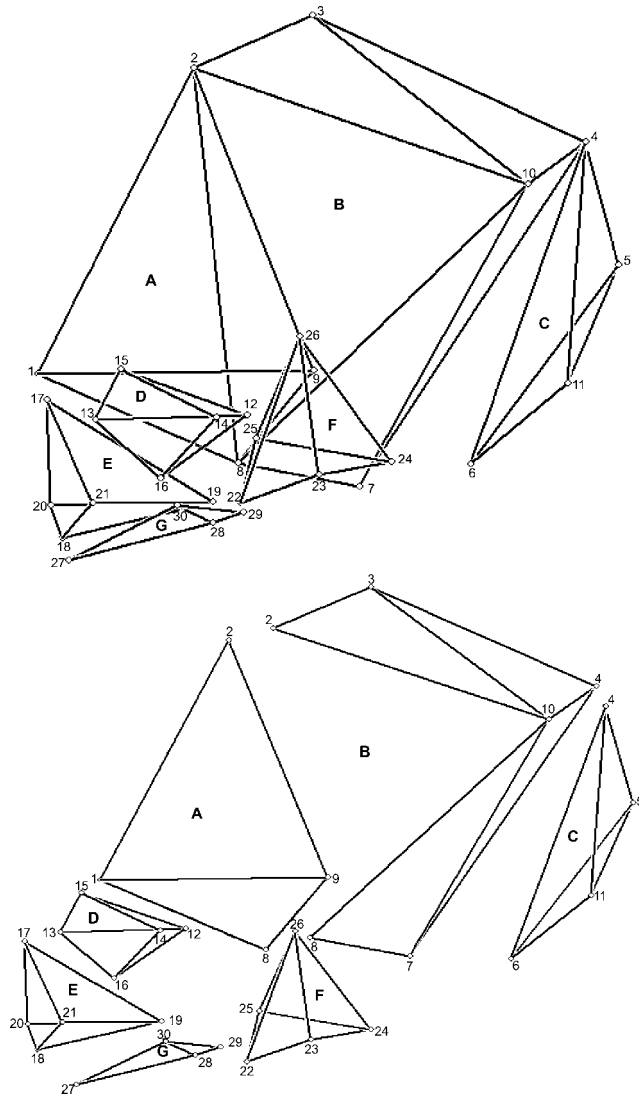


Fig. 1. **a:** Frontolateral view of wire-frames constructed from landmarks defined in Table 2. **b:** Illustration of three-dimensional cranial components.

niofacial morphology across the transition between these stages of individual life history are less well known. This study presents a cross-sectional analysis of morphological changes in the human skull throughout the late prenatal and the early postnatal period. The hypothesis to be tested is that the skull follows an allometric growth pattern as has been observed across prenatal and postnatal ontogeny. If the hypothesis is not rejected, then ontogenetic allometries may be explained by modularity of the craniofacial skeleton; that is, different kinds of changes are expected to be observed in major craniofacial modules.

## MATERIAL AND METHODS

The study used a cross-sectional sample of human dry skulls ( $n = 54$ ) from 32 to 47 weeks of gestational age

TABLE 3. Components defined by wire-frames

Component	Code (see Fig. 1)	Landmarks used for wire-frames
Anteroneural	A	1, 2, 8, 9
Midneural	B	2, 3, 4, 7, 8, 10
Posteroneural	C	4, 5, 6, 11
Optic	D	12, 13, 14, 15, 16
Respiratory	E	17, 18, 19, 20, 21
Masticatory	F	22, 23, 24, 25, 26
Alveolar	G	27, 28, 29, 30

(Table 1), housed at the Musée de l'Homme (Paris, France). Chronological age was estimated for most of the individuals by the method of Guihard-Costa (1988). For this, measurements of skull and postcranial skeleton were compared against reference individuals with a known age at death (Guihard-Costa, 1988).

Thirty three-dimensional (3D) landmarks, located in the vault, basicranium, and face (Table 2; Fig. 1) were registered with Microscribe on the left side of the skull by one of the authors (M.L.S.). In those skulls where the left side was affected by some overlapping of bones, the right side was registered. Because fontanels do not permit the localizations of some landmarks, such as the bregma or asterion, the sutures were extended onto the surface of membranous fontanels and the landmark was located in the intersection of these lines.

Wire-frames were built with landmarks using different cranial components (Table 3; Fig. 1). Functional cranial theory provides the analytical framework for dividing the skull in cranial components and for considering interactions among them (Moss and Young, 1960; Moss, 1973; 1997). Each cranial component is composed of the functional matrix and the skeletal unit (Moss, 1973). All soft tissues and functional spaces compose the functional matrix, while the hard tissues (bone and cartilage) and other connective tissues (tendon and ligaments) that give biomechanical support to the functional matrix compose the skeletal unit. The functional analysis proposes that the skeletal unit is epigenetically modified by the growth of its associated functional matrix (Moss, 1973; 1997).

Components were defined according to previous studies (e.g., Pucciarelli et al. 1990; Dressino and Pucciarelli, 1999; Ramírez Rozzi et al., 2005; Sardi and Ramírez Rozzi, 2005; Sardi et al., 2006) to gain insight on the potential influence of functional matrices on bone morphology, regardless of whether landmarks that define a given component were located in the neurocranium or face. The skull was divided in the following components: anteroneural (neural structures related to the anterior cranial fossa and anterior lobes, and the frontal sinus), midneural (neural structures related to middle and part of posterior cranial fossae and the most part of the brain hemispheres), posteroneural (cerebellum), optic (ocular globe and optic muscles), respiratory (cavity for respiration and smell), masticatory (temporal and part of masseter muscles), and alveolar (teeth, tongue, and palate; Table 3; Fig. 1). Basicranial landmarks were considered being either part of neural or facial components. This is because the cranial base serves as a structural boundary between the vault and face and it was not possible to

**TABLE 4. Eigenvalues of principal components that explain at least 90% of variation**

PC	Eigenvalue	Proportion	Cumul. prop.
1	0.000876	0.190	0.190
2	0.000610	0.132	0.322
3	0.000531	0.115	0.437
4	0.000373	0.081	0.518
5	0.000231	0.050	0.568
6	0.000213	0.046	0.614
7	0.000180	0.039	0.653
8	0.000158	0.034	0.688
9	0.000135	0.029	0.717
10	0.000133	0.029	0.746
11	0.000097	0.021	0.767
12	0.000095	0.021	0.788
13	0.000088	0.019	0.807
14	0.000074	0.016	0.823
15	0.000067	0.014	0.837
16	0.000064	0.014	0.851
17	0.000058	0.012	0.864
18	0.000057	0.012	0.877
19	0.000048	0.010	0.887
20	0.000046	0.010	0.897
21	0.000041	0.009	0.906

attribute an independent functional matrix other than matrices that are shared with other components.

After obtaining raw 3D data, geometric morphometrics were applied. In this context, shape was defined as the residual geometric information remaining once differences due to location, scale, and rotational effects were removed (Rohlf and Slice, 1990; Bookstein, 1991). All individual landmark configurations were subject to generalized Procrustes analysis (GPA; Rohlf and Slice, 1990). All configurations were scaled according to the centroid size (the square root of the sum of square distances from each landmark to the specimen's centroid; Bookstein, 1991; O'Higgins and Jones, 1998). After Procrustes transformation, the coordinates were projected in the tangent space to Kendall's shape space and the resulting shape information was subject to Principal Components Analysis (PCA; Dryden and Mardia, 1998; O'Higgins and Jones, 1998; O'Higgins, 2000). The morphometric analyses were performed in Morphologika (O'Higgins and Jones, 1998).

The principal components (PCs) of tangent coordinates represent axes of maximal shape variation. Only those PCs whose eigenvalues sum at least 90% of the variation were retained for further analysis. Multivariate regression of the shape variables (the principal components) on the size vector (the centroid size) was performed to assess allometries. To establish the localization of size-related shape variation, transformation grids were performed with the first PC, which shows the maximal shape transformation, and with those PCs that show the greatest slopes. The reference and the target were placed according with the regression line: the mean of smallest individuals was used as the reference, and the mean of largest individuals was used as the target.

## RESULTS

The 90% of shape variation was explained by the first 21 PCs (Table 4). The multivariate regression performed

**TABLE 5. Multivariate regression of the first 21 principal components vs. centroid size**

<i>Multivariate Statistics</i>					
Wilks' Lambda	<i>F</i>	Probability			
0.262	4.295	0.000			
<i>Univariate Statistics</i>					
Effect	SS	df	MS	<i>F</i>	Probability
PC 1	0.006	1	0.006	7.979	0.007
error	0.040	52	0.001		
PC 2	0.000	1	0.000	0.744	0.392
error	0.032	52	0.001		
PC 3	0.001	1	0.001	0.965	0.330
error	0.028	52	0.001		
PC 4	0.002	1	0.002	4.530	0.038
error	0.018	52	0.000		
PC 5	0.000	1	0.000	0.097	0.757
error	0.012	52	0.000		
PC 6	0.001	1	0.001	4.323	0.043
error	0.010	52	0.000		
PC 7	0.001	1	0.001	3.203	0.079
error	0.009	52	0.000		
PC 8	0.000	1	0.000	0.726	0.398
error	0.008	52	0.000		
PC 9	0.001	1	0.001	8.720	0.005
error	0.006	52	0.000		
PC 10	0.000	1	0.000	1.930	0.171
error	0.007	52	0.000		
PC 11	0.000	1	0.000	0.003	0.955
error	0.005	52	0.000		
PC 12	0.000	1	0.000	3.845	0.055
error	0.005	52	0.000		
PC 13	0.000	1	0.000	0.231	0.633
error	0.005	52	0.000		
PC 14	0.000	1	0.000	0.476	0.494
error	0.004	52	0.000		
PC 15	0.000	1	0.000	0.834	0.365
error	0.004	52	0.000		
PC 16	0.000	1	0.000	0.555	0.460
error	0.003	52	0.000		
PC 17	0.000	1	0.000	0.459	0.501
error	0.003	52	0.000		
PC 18	0.000	1	0.000	0.009	0.927
error	0.003	52	0.000		
PC 19	0.000	1	0.000	0.002	0.967
error	0.003	52	0.000		
PC 20	0.000	1	0.000	2.177	0.146
error	0.002	52	0.000		
PC 21	0.000	1	0.000	0.260	0.612
error	0.002	52	0.000		

with the first 21 PCs indicated that highly significant shape changes depend on size change (Table 5). Individually, most of the PCs showed nonsignificant slopes, and they explain a low proportion of variation (Table 5). Thus, transformation grids were performed with PC 1 and with PC 9, which showed the largest *F* value ( $P < 0.001$ ). Because deformation was subtle, the reference and the target were placed outside the range of variation of the centroid size to exaggerate and better visualize shape variations (Figs. 2, 3).

The PC 1 accounts for 19% of the variation. The transformation grids indicate that principal changes were located in the neurocranium, involving the midneural and posteroneural components (Fig. 2): Bregma and vertex were located more posteriorly. Lambda and opisthocranium were located more superiorly and euryon more inferiorly, all of which produce the elongation and com-

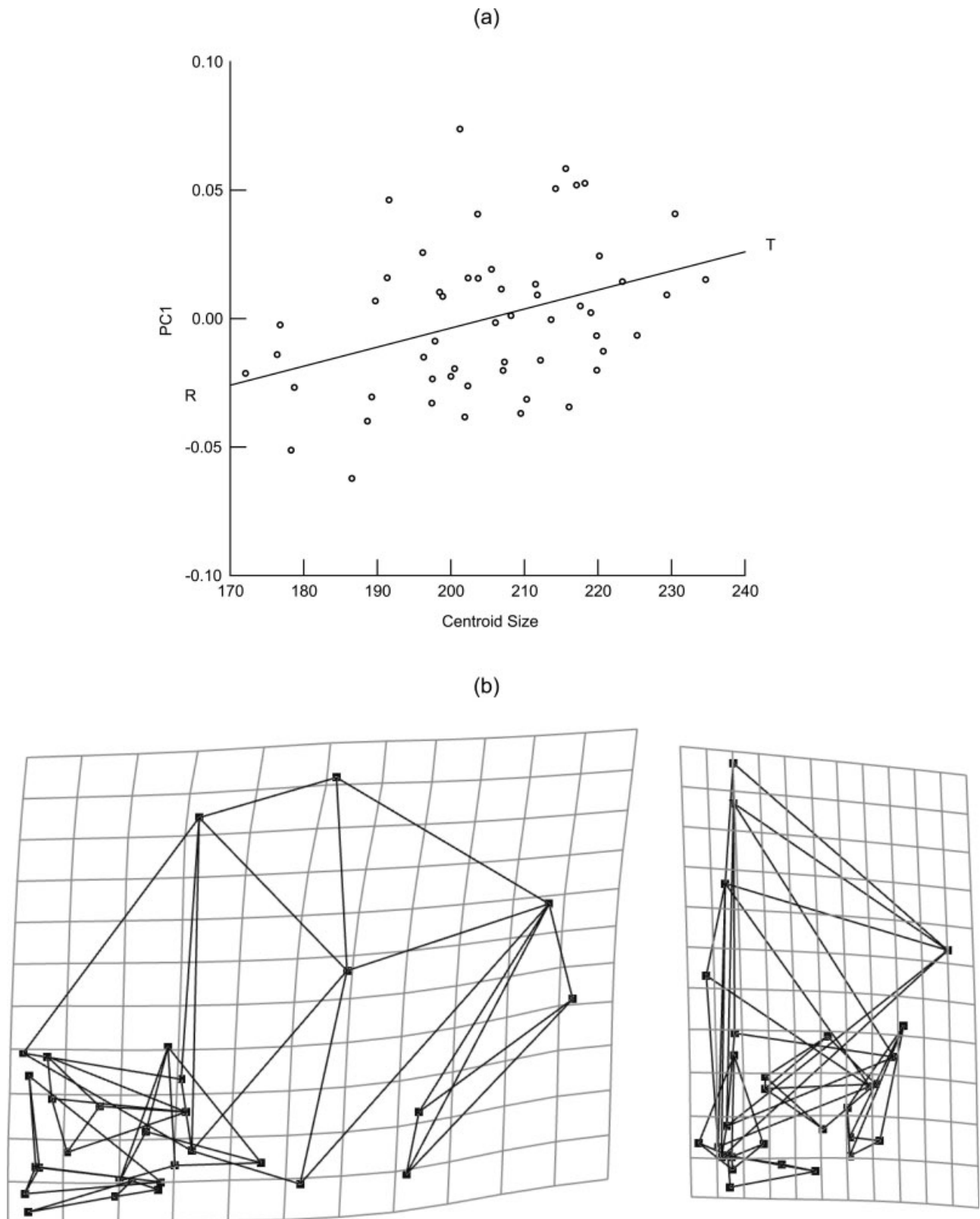


Fig. 2. Principal Components Analyses of the tangent space coordinates. **a:** Centroid size vs. PC 1. **b:** Transformation grids in lateral (left) and frontal (right) view. Points where the reference (R) and the target (T) were placed are indicated.

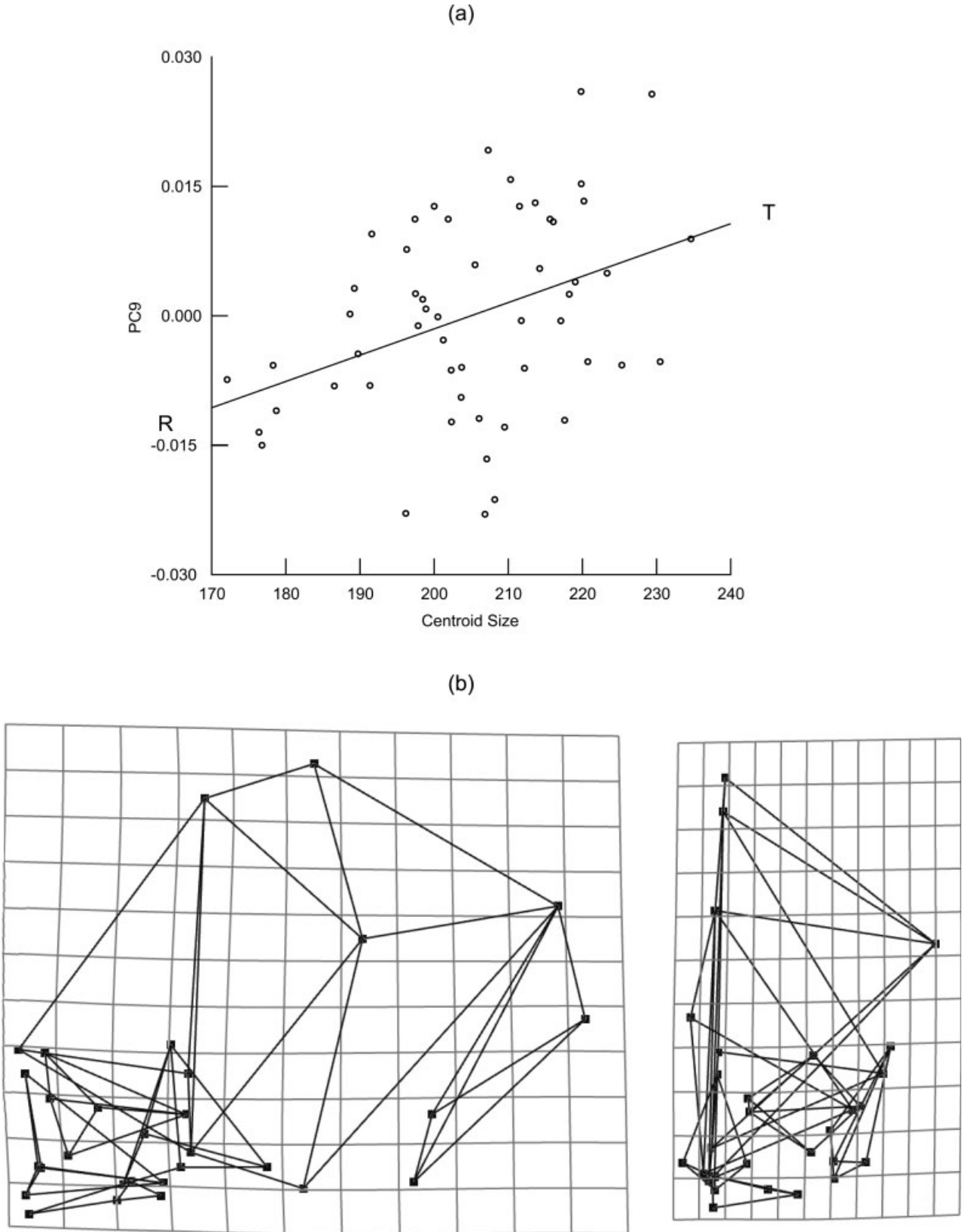


Fig. 3. Principal components analyses of the tangent space coordinates. **a:** Centroid size vs. PC 9. **b:** Transformation grids in lateral (left) and frontal (right) view. Points where the reference (R) and the target (T) were placed are indicated.

pression of the vault. The PC 9 accounts for 2.9% of the variation and it exhibited a subtle deformation (Fig. 3) involving part of the neurocranium and the face. Both, the anteroneural component and the face are placed forwardly, but facial components did not show deformation (Figs. 2, 3).

According to the transformation grids, the most important axis in which changes were found to occur was the anteroposterior axis followed by the vertical axis. Variation in mediolateral axis could only be observed in the PC 1, which involves the shape of the vault. This finding is coincident with analyses made on macaques and humans (Zumpano, 1997, 2002).

## DISCUSSION

The present findings indicate that there are small but highly significant size-related shape changes in the craniofacial skeleton between 32 and 47 weeks of gestational age; thus, the hypothesis proposed is not rejected. Our model of 3D cranial components enabled the isolation of units, while the transformation grids enabled the detection of interactions among units. Thus, processes by which units interact across ontogeny are better understood (Lieberman et al., 2000b). Different patterns of size-related shape variations were observed for the neurocranium and the face. The main shape changes were located in the neurocranial module. The axis of maximal shape variation (PC1) represents variation in the vault, thus, as cranial size increases, the vault becomes more anteroposteriorly elongated and posteriorly elevated (Fig. 2). In the remaining axes, PC 9 was the most correlated with centroid size and it represents variation in the anterior portion of the skull (Fig. 3). The face, on the other hand, seems to be quite isometric. These findings indicate that, in the short ontogenetic period considered in this study, major modules of the craniofacial skeleton show independent shape changes produced by different functional and developmental constraints intervening on both the neurocranium and face.

Shape variation in the cranial vault (Fig. 2) can be associated with brain morphology, because both the brain and vault are highly integrated in their development (Moss and Young, 1960; Richtsmeier et al., 2006). Important changes in the brain hemispheres begin around 33 weeks of gestational age by infolding of the cerebral cortex (Feess-Higgins and Larroche, 1987; Lan et al., 2000). This in turn exerts pressures on the calvarial bones of the midneural and posteroneural components, resulting in changes in sutural growth and displacement (Opperman et al., 2005; Sperber, 2001).

Ontogenetic allometries reported in Figure 3 indicate a forward displacement of the anteroneural and facial components. This finding may be explained by either extrinsic (i.e., brain growth) or intrinsic factors acting only on the anterior cranial base, because the cranial base is located in the interface between the cranial vault and face and affects positional changes of both the frontal bone and the face.

Associations between basicranial shape and brain have been suggested in several studies (Ross and Henneberg, 1995; Lieberman and McCarthy, 1999; Lieberman et al., 2000a,b; Ross et al., 2004). Ontogenetically, Lieberman and McCarthy (1999) observed that the cranial base flexes across postnatal ontogeny and attains

adult values at around 2 years of age, which coincides with the period in which the brain (Guihard-Costa and Ramírez Rozzi, 2004) and neural cranial components (Sardi and Ramírez Rozzi, 2007) exhibit their highest growth rates. However, other ontogenetic studies indicate that the cranial base is quite independent from brain expansion, because throughout mid-term gestation the basicranial angle retroflexes, even if brain expands significantly (Jeffery, 2002, 2005; Jeffery and Spoor, 2002); in contrast, basicranial retroflexion has been associated with enlargement of the upper airway (Jeffery, 2005).

The anterior displacement of the anteroneural component and face can be connected with the differential growth of the cranial base. The anterior basicranial portion elongates prenatally relatively more than the posterior portion (Sperber, 2001; Jeffery, 2002; Zumpano and Richtsmeier, 2003; Jeffery and Spoor, 2004), because the anterior portion contains three ossification centers, whereas the posterior portion has only two. Additionally, the posterior portion ossifies earlier than the anterior portion (Sperber, 2001; Jeffery and Spoor, 2002). Thus, it seems more probable that the anterior cranial base is elongated by intrinsic growth potential of the cartilaginous synchondroses (Opperman et al., 2005) rather than by external forces associated with brain growth or with any other functional matrix. As a mechanistic consequence of this elongation, the frontal bone and the face, both attached to the cranial base, are placed forwardly.

Data from the transformation grids (Figs. 2, 3) did not indicate facial shape variation, in contrast with the study of Plavcan and German (1995). This finding is noteworthy because the growing teeth, tongue, and other muscles of deglutition may exert loads on the mid-face (Moyers and Carlson, 1996), mainly in the alveolar component.

This overall pattern of shape change between 32 and 47 weeks of gestational age was different compared with changes reported to occur in an earlier ontogenetic stage. Zumpano and Richtsmeier (2003) described human cranial growth by means of Euclidean Distance Matrix Analysis (EDMA), between middle (mean age = 24 weeks of gestational age) and late prenatal stages (mean age = 34 weeks of gestational age). They observed significant changes between both stages, mainly in the midface and along the mediolateral axis of the cranial base, and nonsignificant changes were reported for the neurocranium (Zumpano and Richtsmeier, 2003).

One important outcome of our results is that changes in both the cranial base and face are quite independent from changes in the vault and, thus, not affected by changes in brain size. This pattern of shape variation differs with respect to patterns observed in comparisons among hominid species.

The cranial base has been proposed to be the structure that produces the overall integration of the craniofacial skeleton (Lieberman et al., 2000a,b). Phylogenetically, the human basicranial shape has been associated with encephalization and facial orthognatism (Ross and Henneberg, 1995; Lieberman et al., 2000b; Ross et al., 2004). One of the most important variables of basicranial shape is flexion in the midsagittal plane. An acute basicranial angle has been correlated with encephalization in trans-specific comparisons (Ross and Henneberg, 1995). Some

studies have corroborated that basicranial flexion is correlated with brain morphology among adult humans (Lieberman et al., 2000a,b) and among adult specimens of “archaic” *Homo sp.* (Bookstein et al., 2003). Associations between basicranial morphology and face have also been proposed (Lieberman et al., 2000b; Bastir and Rosas, 2005). Bastir and Rosas (2005) reported a strong integration of the posterior face (i.e., the mandibular ramus) with lateral basicranial structures in adult humans.

Because of interactions of the cranial base with the face and the cranial vault, Enlow and Hans (1996) stated that, in adult humans, different neurocranial “shapes” are associated with specific facial “shapes.” For example, individuals with narrow and longer braincases tend to present less flexed cranial bases and longer and protrusive faces. Even when allometries observed at the ontogenetic level cannot be directly extrapolated to comparisons at a single ontogenetic stage (normally adult; Cheverud, 1982b), results of this study suggest that different neural shapes cannot be associated with any given facial shape. This is supported by observations from postnatal ontogeny studies in humans and chimpanzees (Bastir and Rosas, 2004).

Our ontogenetic results also indicated (Figs. 2, 3) that basicranial flexion does not change throughout the late prenatal and early postnatal ontogeny. The only shape change in the cranial base was an anterior elongation, and it does not seem likely that the growing brain drives these changes. Thus, basicranial shape was not so dependent from the main shape changes in the vault, although it is possible that connections between the vault and basicranium were obscured because we only analyzed external basicranial landmarks. On the other hand, the cranial base does influence facial position as was observed across mid-term gestation (Jeffery, 2005).

The isometry of the face relative to overall craniofacial growth may be relevant in evolutionary terms because facial shape is differentiated at early ontogenetic stages in comparisons of higher taxonomic levels. Specifically, between hominoids (Ackermann and Krovitz, 2002; McBratney-Owen and Lieberman, 2003; Bastir and Rosas, 2004), between hominids (Ponce de Leon and Zollikofer, 2001), and between human populations (Strand Vidarsdottir et al., 2002). Our findings suggest that part of human facial differentiation present at early postnatal ontogeny has been already established before the third trimester of prenatal life. Another important part of facial differentiation in trans-specific comparisons may be partially associated with dental development, thus accentuated in later ontogenetic stages, because dental development is delayed in humans and strongly associated with primate life-histories (Smith et al., 1994; Zuppano and Richtsmeier, 2003).

## CONCLUSIONS

This study used cross-sectional samples of human skulls between 32 and 47 weeks of gestational age and assessed ontogenetic allometries throughout the prenatal and the postnatal growth period. Results indicated that the skull grows allometrically; however, changes in this transitional ontogenetic stage were somewhat different with respect to changes observed in other ontogenetic stages. Thus, the hypothesis proposed was not

rejected. Main shape variation takes place in the vault, which behaves quite independently with respect to the cranial base and face. Morphologic changes in the brain were the main factor that produces size-related shape variation. The small basicranial variation was due to the elongation of the anterior portion of the cranial base. This induces positional changes in the face, which resulted in forward displacement. Shape changes in the facial components were not observed, suggesting that early postnatal facial shape was established before the third trimester of prenatal life.

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