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Ontogenetic Patterns of Morphological Variation in the Ectocranial Human Vault

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ABSTRACT

The skull is considered a modular structure in which different parts are influenced by different factors and, as a result, achieve adult shape at different ages. Previous studies have suggested that the basicranium presents a modular pattern that distinguishes sagittal and lateral parts, probably affected by the brain and masticatory structures, respectively. The vault of modern humans, in contrast, has been considered as a highly integrated system mainly influenced by brain growth. Here, we explored developmental shape variation in sagittal and lateral ectocranial vault in humans in order to assess if both regions are ontogenetically dissociated. We used a sample of 135 cranial computed tomography images from 0 to 31 ages. Landmarks and semilandmarks were collected on sagittal and lateral regions and geometric morphometric techniques were applied separately for each region. On the shape coordinates, we used Goodall's *F*-test in order to assess the age when the adult configuration is attained. Principal component analysis enabled us to evaluate shape variation during ontogeny. Results indicated that both sagittal and lateral structures attain adult shape at early adolescence. Both regions express coordinated shape modifications probably due to shared developmental factors. It is concluded that masticatory muscles may not exert a strong enough influence to produce independent variation in the lateral traits. Thus, it is likely that the brain integrates sagittal and lateral parts of the vault across human ontogeny. Anat Rec, 296:1008–1015, 2013. © 2013 Wiley Periodicals, Inc.

Key words: ectocranium; ontogeny; modularity; geometric morphometrics; computed tomography images

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Anatomical systems are influenced by several developmental, functional, and evolutionary factors that affect the morphology and association of their parts or traits. It is expected that those traits that are under the effect of the same developmental processes or are functionally linked are associated and vary in a coordinated fashion (Olson and Miller, 1958). In contrast, when traits are affected by local factors, it is expected that they vary more independently. In this case, the resulting phenotype is a hierarchical network where traits belong to modules of different levels. A module is considered a unit, whose parts have stronger interactions among them than with parts of other modules, being therefore, more integrated (Klingenberg, 2009). The detection of patterns of morphological integration and modularity is essential to understand morphological evolution because integrated traits tend to evolve as a whole while unrelated traits may evolve independently (Cheverud, 1996).

Studies on human evolution have traditionally focused on the skull because of its preservational characteristics but, especially, due to the wide range of developmental and phylogenetic information that can be obtained from it. Although the skull is an integrated structure, it is widely accepted that the neurocranium is a cranial module with some level of independence from the face (Cheverud, 1982, 1995). As well, the vault and the base are recognized as neurocranial modules of less hierarchy because they differ in their mode of ossification, the functions in which they are involved and their interactions with the face. They also differ in the timing of growth and development (Bastir et al., 2006).

The differential timing in which structures develop was described by Enlow and Hans (1996) in terms of "craniofacial levels" with the neurobasicranial complex being the first to attain final morphology, followed by the facial complex and, later, the mandible. This stratigraphic model implies that different components display some degree of independence among them.

Other studies have also observed that lateral basicranial structures are, in humans, decoupled from the sagittal ones, probably due to differences in the timing of maturation (Bastir and Rosas, 2005, 2006). This basicranial modularization has been discussed in relation to the sequential brain regionalization, especially the differential development of temporal and frontal lobes, as well as facial structural association with lateral traits (Bastir and Rosas, 2006; Bastir et al., 2008, 2011). Similar results were obtained by Hallgrímsson et al. (2007) analyzing mutant and control mice. These authors also observed that lateral parts of the basicranium are strongly integrated with lateral parts of the vault and the face.

The vault has been considered in humans as a linear system where morphological changes are mainly associated with brain and meningeal membranes (Moss and Young, 1960), being thus characterized as a highly integrated module. Although this conclusion has support for the endocranial surface that is in contact with the brain through the meninges (Neubauer et al., 2009), it should not be extrapolated to the ectocranial vault. Vault bones have a particular structure consisting of an outer and an inner table of compact bone separated by a layer of trabecular bone, known as dipole (Sperber, 2001). Even if the outer table is modified by brain development, it also responds to forces generated by masticatory and postural muscles, which would not affect to the same extent the morphology of the inner table (Herring, 1993). In nonhuman primates, well-developed masticatory and nuchal muscles exert large forces upon the ectocranial surface, promoting the development of crests and superstructures. In many mammalian species, the remarkable muscular development is likely the cause of the low integration of the vault (Goswami and Polly, 2010).

However, because masticatory muscles are relatively thinner in humans (Aiello and Dean, 2002; Stedman et al., 2004), it has been hypothesized that the overall morphology and integration of the vault is mainly affected by the brain and sense organs (Moss and Young, 1960; Cheverud, 1996), with minor influence of remodeling on the external surface (Enlow and Hans, 1996). Furthermore, Stedman et al. (2004) suggested that the reduction in masticatory muscles across the hominid lineage might remove an evolutionary constraint on encephalization. Encephalization has been proposed to underlie vault globularity (Lieberman et al., 2002, 2004), one of the diagnostic features of anatomically modern *Homo sapiens* (Aiello and Dean, 2002; Lieberman et al., 2002, 2004), which has been evaluated in sagittal view.

In order to know how evolutionary novelties might evolve one need to address how transformations occur across ontogeny. Lieberman (2011) stated that the comparison of ontogeny of different modules or anatomical parts contains information about integration among those parts. This would enable us to assess how important is the integration of the vault in humans and to infer the potential influence of evolutionary novelties in the pattern of integration.

Consequently, the aim of this study was to explore developmental patterns of shape variation in sagittal and lateral traits of the ectocranial surface of the human vault in order to assess if both regions are ontogenetically dissociated and, thus, to infer if the vault is a modular structure. The timing of growth and maturation of the sagittal vault has been already explored and it seems associated with brain development (Bastir et al., 2006). However, it remains unknown if lateral traits of the vault are developmentally dissociated with respect to the sagittal ones. It is feasible that lateral traits are structurally tightened to lateral basicranial traits, which in addition are associated with facial traits due to similar functional demands, such as the maturation of mastication. Our hypothesis states that sagittal and lateral regions behave as separate developmental modules showing spatiotemporal dissociation. It would be expected therefore that the age in which adult shape is attained differs. In particular, it is anticipated that lateral structures attain adult shape later than the sagittal ones. It would also be expected that sagittal and lateral regions display variation in diverse spatial directions, that is, the pattern of shape change is not coordinated due to the potential influence of different factors.

MATERIALS AND METHODS

This study uses a sample of 135 computed tomography (CT) cranial images from a data set constructed at FLENI (Fundación para la Lucha contra las Enfermedades Neurológicas de la Infancia, Buenos Aires, Argentina), which belong to nonpathological humans from 0 to

31 years old of both sexes. Based on the human pattern of dental eruption (Smith, 1994), individuals were divided into the following age groups: infant–child (0–5 years), juvenile (6–11 years), adolescent (12–17 years), and adults (18–31 years). Sample size and sexes distribution are displayed in Table 1. A trial version of Avizo 6.0 software (Visualization Science Group) was used to examine CT images. From CT slices, a three-dimensional (3D) superficial reconstruction was created using a chosen density threshold that corresponds to the Hounsfield unit scale (Spoor et al., 2000). Surface extraction thresholds, which need to be stipulated to produce a reconstruction, were determined empirically. A threshold of 1,150 Hounsfield units was chosen to show the maximum amount of bony tissue with the least amount of distortion.

The 3D reconstructions were used to localize 12 landmarks and 9 semilandmarks that describe sagittal and lateral regions of cranial vault (Table 2, Fig. 1). While landmarks are defined as anatomical loci that can be recognized as the same loci in all the studied individuals (Zelditch et al., 2004), semilandmarks are often used to study regions where discrete anatomical points are rare, for example in curves and contours. Semilandmarks were placed as evenly spaced points and they were replaced along the outline curve using a linear interpolation between the original curve points in order to be treated as landmarks in posterior analyses (Reddy et al., 2004).

To eliminate variation due to measurement error, an intra-observer analysis was carried out and only one of the authors (J.B.-A.) digitized the morphometric points. On a sample of 15 skulls ranging from 0 to 31 years landmarks were placed three times and measurement error was estimated with different and complementary methods (Barbeito-Andrés et al., 2012).

Geometric morphometric techniques were applied on these raw coordinate configurations in order to eliminate variation due to position, rotation and scale. In this context, shape was defined as the geometric information that remains once scale, position, and rotational effects were removed (Kendall, 1977). Generalized Procrustes superimpositions were performed in sagittal and lateral points separately and, after that, form was studied from one variable of size (centroid size) and a set of shape variables (shape coordinates).

In order to obtain more precision for establishing the age of attainment of adult shape, juvenile and adolescent stages were subdivided into age classes with

TABLE 1. Sample composition

Age group	Females	Males	Total
Infant–child (0–5 years)	7	12	19
Juvenile (6–11 years)	11	14	25
Adolescent (12–17 years)	15	12	27
Adult (18–31 years)	49	15	64
Total	82	53	135

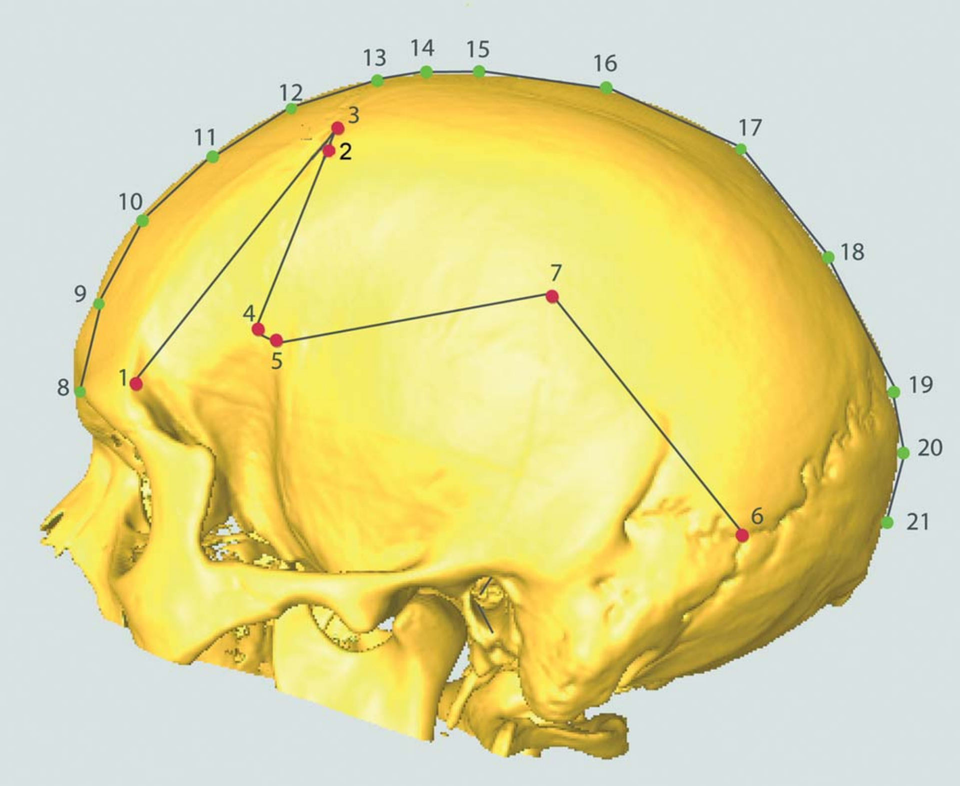

Fig. 1. Landmarks and semilandmarks distribution. Sagittal points are green and lateral points are red, respectively. Wireframes used to display shape change are shown.

TABLE 2. Landmarks and semilandmarks

Number	Name	Description	Lateral/sagittal
1	Fronto-temporal	The point where the temporal line reaches the most anterior and medial position	Lateral
2	Stephanion inferior	The point where the coronal suture and the inferior temporal line meet	Lateral
3	Stephanion superior	The point where the coronal suture and the superior temporal line meet	Lateral
4	Sphenion	Frontal-zygomatic-parietal intersection	Lateral
5	Pterion	The middle point on the zygomatic-parietal suture	Lateral
6	Asterion	The point where the lamboidal, parietal, and occipital suture meet	Lateral
7	Euryon	The most lateral point of the brain case	Lateral
8	Glabella	Most anterior midline point on the frontal bone. Usually above the frontonasal juncture	Sagittal
9	Semilandmark 1		Sagittal
10	Semilandmark 2		Sagittal
11	Semilandmark 3		Sagittal
12	Semilandmark 4		Sagittal
13	Bregma	The midline point where the sagittal and coronal sutures intersect	Sagittal
14	Semilandmark 5		Sagittal
15	Vertex	The most superior point of the skull in the sagittal line	Sagittal
16	Semilandmark 6		Sagittal
17	Semilandmark 7		Sagittal
18	Semilandmark 8		Sagittal
19	Lambda	The midline point where the sagittal and lamboidal sutures intersect	Sagittal
20	Opisthocranion	The most posterior point of the skull in the sagittal plane	Sagittal
21	Semilandmark 9		Sagittal

TABLE 3. Shape mean differences from adults measured through Goodall's *F*-test for detailed juvenile and adolescent stages

Age group	*n*	Sagittal	Lateral
Infant–child (0–5 years)	19	8.21 ($P < 0.0001$)	8.84 ($P < 0.0001$)
Juvenile 1 (6–7 years)	8	2.71 ($P < 0.0001$)	3.38 ($P < 0.0001$)
Juvenile 2 (8–9 years)	8	4.30 ($P < 0.0001$)	2.90 ($P = 0.0002$)
Juvenile 3 (10–11 years)	9	1.69 ($P = 0.0072$)	2.18 ($P = 0.0071$)
Adolescent 1 (12–13 years)	9	1.10 ($P = 0.3137$)	1.45 ($P = 0.1249$)
Adolescent 2 (14–15 years)	11	1.25 ($P = 0.2658$)	0.37 ($P = 0.9833$)
Adolescent 3 (16–17 years)	7	0.68 ($P = 0.9268$)	0.28 ($P = 0.9960$)

Significance is expressed as probability between parentheses.

adequate sample size. Differences between adults and subadult groups of different ages were compared by means of Goodall's *F*-test, which highlights differences in groups' mean shape (Bastir et al., 2006). Significance levels were obtained by permutation methods after 1,000 iterations. If a group differs from the adult mean shape, this structure is still having ontogenetic change. Contrary, if Goodall's *F*-value is not significant, then adult shape has been already achieved.

Shape variation was separately described in sagittal and lateral regions by principal components (PCs) analyses using the adjusted shape coordinates. This enabled us to obtain new tangent variables (PCs) based on covariance among shape coordinates, which capture main shape variation in a reduced number of these axes (Bookstein, 1991; Rohlf, 1993). In order to explore sagittal and lateral ontogenic trajectories, Pearson correlation was calculated between the individual scores across PCs with respect to age and centroid size—both transformed into natural logarithms. Individuals were plotted according to their position along the most relevant PCs and visualization of morphological variation was shown as changes in the relative positions of landmarks through wireframe deformation. Shape changes, represented by the main axes, provided a depiction of variation in each region to discuss potential sources of differentiation between them.

RESULTS

According to the Goodall's *F*-test, adult shape is achieved at the same stage in sagittal and lateral regions (Table 3), being adults similar to adolescents even with respect to the youngest ones.

For the sagittal region, our results indicated that the first three PCs accounted for more than 75% of total variation. PC1 (33.3% of variation) was neither statistically related to age (-0.106, $P = 0.22$) nor to centroid size (-0.11, $P = 0.18$). Shape changes explained by PC1 (Fig. 2a) expressed variation in the occipital and frontal projections. PC2 (26.7% of variation) was significantly related to age (0.30, $P < 0.0001$) and to centroid size (0.22, $P = 0.01$). PC2 explained changes in the occipital region, which became more curved in later stages (Fig.

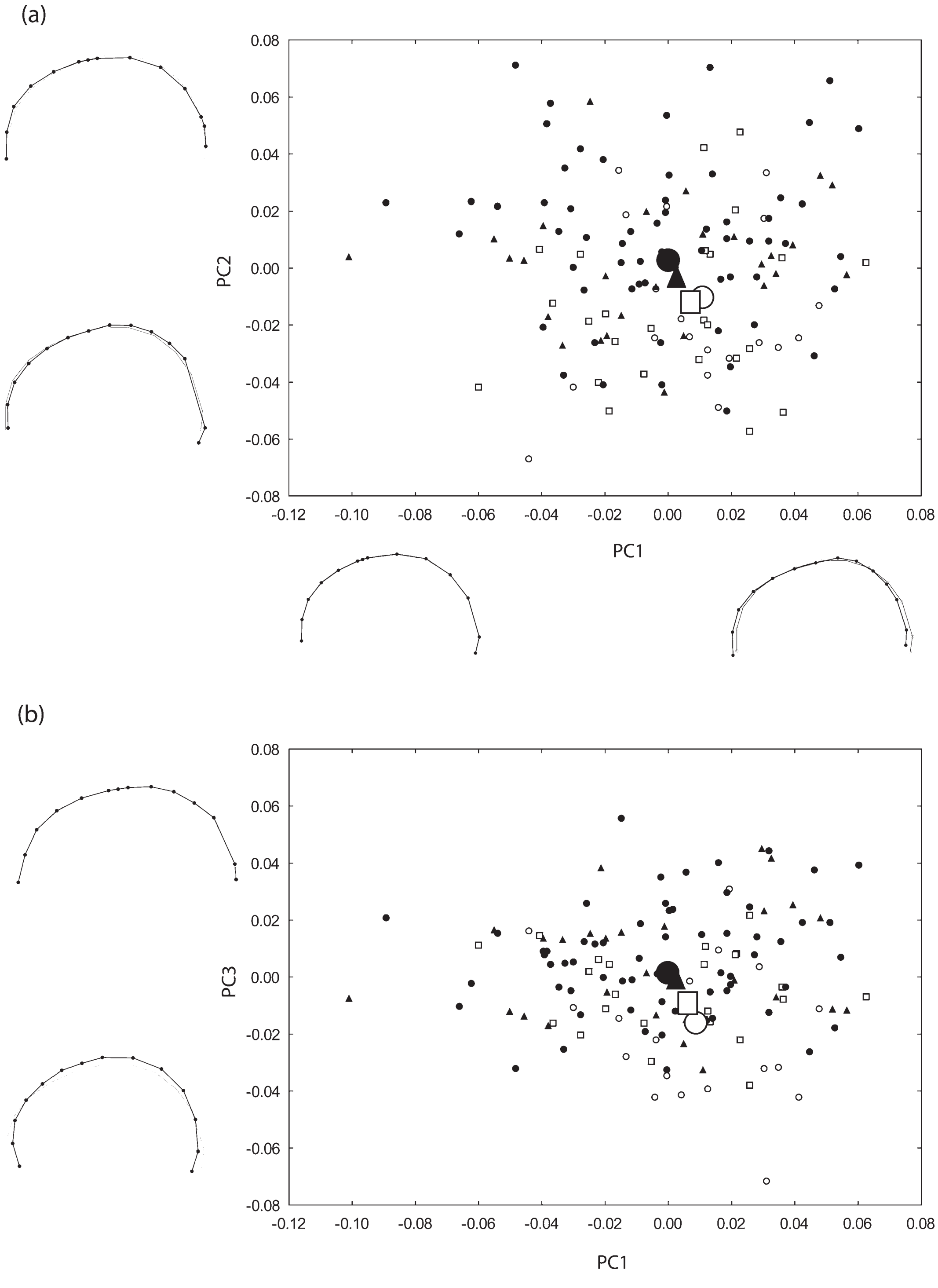

Fig. 2. PCA on sagittal region. Age groups: Infant–child: empty circles, Juvenile: squares, Adolescent: triangles, Adults: full circles. Mean values of each group are indicated with larger symbols. Black wireframes show shape changes associated with positive and negative extremes of distribution in comparison with mean shape displayed through gray wireframes.

2a) because the opistocranium was placed closer to lambda. Finally, PC3 (15.2% of variation) was related to age (0.45, $P < 0.0001$) and centroid size (0.33, $P < 0.0001$). This axis expressed a reduction of vault globularity with age with the respective anteroposterior elongation (Fig. 2b).

In the lateral traits, the first three PCs accounted for approximately the 64% of variation. PC1 (34.6% of variation) was significantly related to age (0.21, $P = 0.01$) and centroid size (0.19, $P = 0.02$). It resumed the relative displacement of the widest projection of the vault (euryon), being more backwardly located in adolescents and adults and decreasing its distance from the asterion (Fig. 3a). PC2 (17.5%) had a highly significant association with age (-0.44, $P < 0.0001$) and centroid size (-0.47, $P < 0.0001$). Along ontogeny, there is an increase in the distance between uppermost insertions of the temporal muscle (inferior and superior stephanions) and the pteric region (pterion and sphenion) (Fig. 3a). PC3 (12.0% of variation) showed a highly significant association with age (0.36, $P < 0.0001$) and with centroid size (0.28, $P = 0.001$). It represented changes in the relative position of the pteric region, which was more forwardly located with respect to the fronto-temporal in younger individuals (Fig. 3b).

DISCUSSION

The present findings indicate that there are some differences in the developmental variation of sagittal and lateral regions of human vault. Main PCs capture more variation in sagittal structures (75%) than in lateral ones (64%). Furthermore, for sagittal traits PC1 is associated neither to age nor to centroid size. The following axes (PC2 and 3) capture around 42% of variation and represent developmental change linked to the loss of globularity (Fig. 2). For lateral traits, all the analyzed axes represent developmental variation. However, the associations with age and centroid size were lower for the first axis than for the second and the third ones, representing also uncorrelated variation of the middle and anterior regions (Fig. 3).These results show that postnatal development accounts for less variation and covariation across the midline than in the lateral vault. This fact suggests that vault morphology is, in some proportion, already developed at birth, being thus less plastic than other cranial structures (Humphrey, 1998; Sperber, 2001; Opperman et al., 2005).

Because lateral structures of the vault are related to lateral basicranial parts and to temporal muscle, all involved in mastication, it was anticipated that they attain maturation later than sagittal traits. Despite differences observed in sagittal and lateral PCs, results of Goodall's *F*-test indicate that sagittal and lateral structures attain adult shape at the same developmental stage (Table 3), before 12 years old, expressing that both regions are somewhat integrated.

The patterns of variation also reflect that both regions display a coordinated change. For instance, the main vault changes during ontogeny involves variation in the occipital morphology (PC2, Fig. 2a) and vault flattening (PC3, Fig. 2b) in the sagittal region, together with backward displacement of the euryon (PC1, Fig. 3) in the lateral region. As well, the relative upward displacement of the inferior and superior stephanions (PC2, Fig. 3a) may be related to the relative flattening of the vault.

Considering overall results, the hypothesis that sagittal and lateral regions of the human vault behave as separate developmental modules has to be rejected. Aspects of developmental variation of the ectocranial surface analyzed in this study suggest that the vault is a quite integrated structure, as was observed for the endocranial surface (Neubauer et al., 2009). As suggested by many authors (Lieberman et al., 2000; Hallgrímsson et al., 2007; Porto et al., 2009), the brain is likely to be the factor that integrates vault morphology. The brain expands during ontogeny and vault bones are passively displaced outward producing deposition of new bone on the edge of sutures (Enlow and Hans, 1996; Opperman et al., 2005). Thus, the brain influences upon different vault dimensions, such as length and width (Lieberman et al., 2000). In a study based on models of craniosynostosis, it has been demonstrated that there is a general strong and positive interaction between the brain and the skull (Richtsmeier et al., 2006). In this study, two kinds of craniosynostosis were evaluated: premature closure of the sagittal suture and the coronal suture. Richtsmeier et al. (2006) failed to detect differences in the skull size as well as in the overall association between the skull and the brain despite of what suture was affected. In other words, the brain has a predominant effect on vault growth even when other factors affect lateral or sagittal structures (Richtsmeier et al., 2006). It is likely that the lateral parts of the vault in humans may develop more independently from the base, whose lateral parts are integrated to masticatory structures (Bastir and Rosas, 2005).

Brain growth may influence in part on the loss of globularity occurred during ontogeny, as well as on the developmental changes of the occipital squama because brain growth is mainly directed posteriorly rather than radially because of the expansion of frontal and the flattening of the parietal lobes (Trinkaus and LeMay, 1982; Ventrice, 2011). However, the influence of the brain over vault shape can only be supported until the juvenile period, when brain stops growing. Ventrice (2011) demonstrated that while the endocranial surface and the brain exhibit similar changes during infant–child and juvenile stages, both structures follow different trajectories during adolescence and adulthood. After adolescence, the brain still displays some amount of shape variation probably due to the loss of brain gray matter volume around puberty (Lenroot and Giedd, 2006; Ventrice, 2011) while the endocranium does not. The ectocranial surface, which was analyzed in this study, may also become less globular due to the development of frontal paranasal sinus and occipital crests for muscle attachment (Enlow and Hans, 1996; Sperber, 2001).

Muscular compressive forces exerted on vault bones and sutures promote osseous surface apposition that act upon the ectocranial surface (Beecher and Corruccini, 1981; Herring, 1993; Herring and Teng, 2000; Mavropoulos et al., 2004). However, in humans, the influence of muscles on external vault morphology is low compared with those found in the postcranial skeleton (Rawlinson et al., 1995). Consequently, masticatory muscles may not be a factor strong enough to modify lateral traits independently from those of the midline. The transition to food production and the consumption of soft diets among modern humans have reduced muscular forces leading to gracilization and different morphological changes, particularly in craniofacial structures related to masticatory function, such as the temporal fossa (Sardi et al., 2004, 2006; González-José et al., 2005; Paschetta et al., 2010; Lieberman, 2011).

In sum, our results indicate that in humans there are some minor differences between sagittal and lateral traits in the vault, but developmental changes are quite

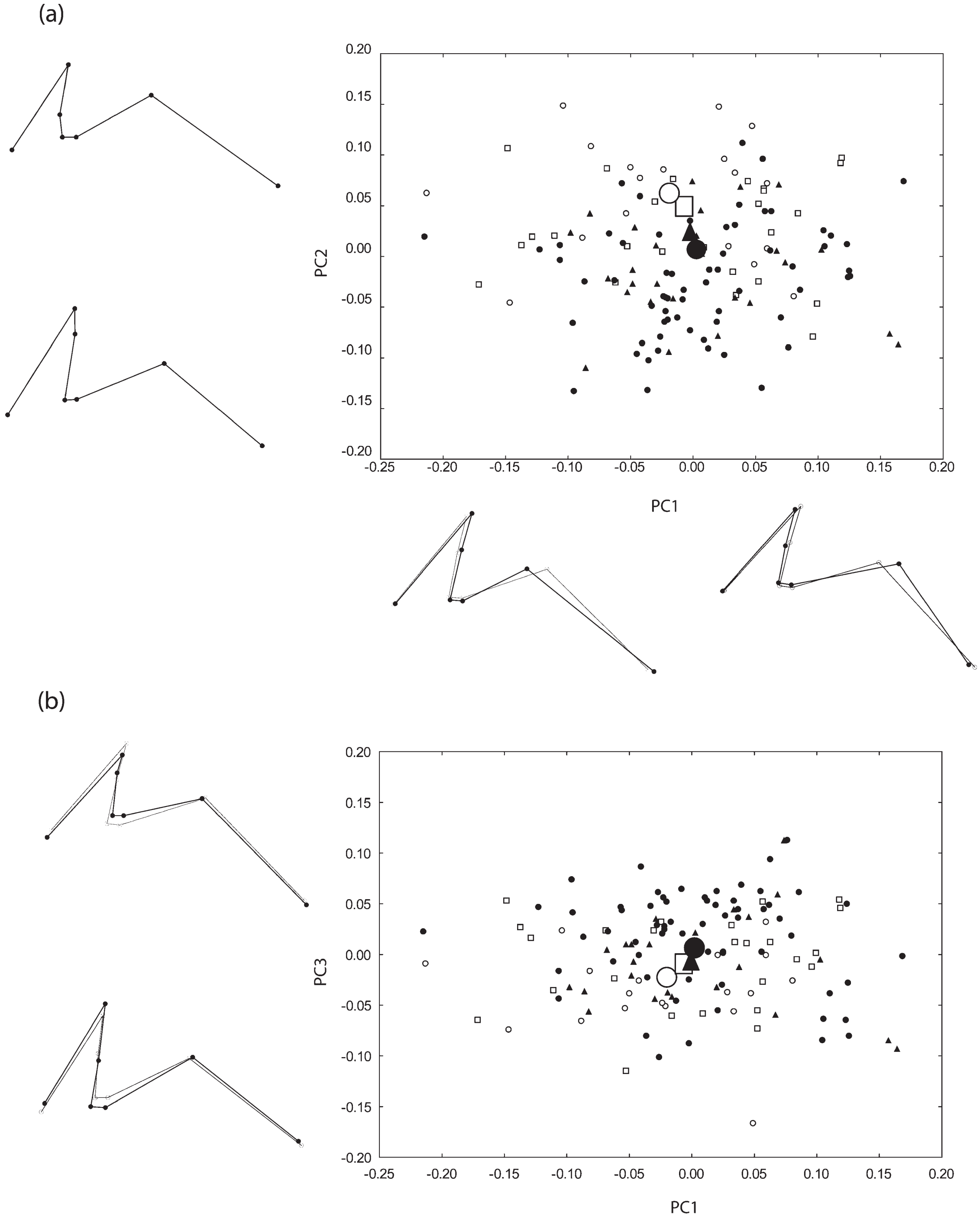

Fig. 3. PCA on lateral region. Age groups: Infant–child: empty circles, Juvenile: squares, Adolescent: triangles, Adults: full circles. Mean values of each group are indicated with larger symbols. Black wireframes show shape changes associated with positive and negative extremes of distribution in comparison with mean shape displayed through gray wireframes.

temporally and spatially integrated. This high ontogenetic integration, compared with that of other mammals (Goswami and Polly, 2010) may be the result of two evolutionary novelties occurred across the hominid lineage: muscular reduction and brain expansion (Lieberman et al., 2002; Stedman et al., 2004). In humans, it is probable that the brain affects primarily the midline skeletal traits. This integration between the brain and the vault would be established during prenatal life. Due to the low thickness of vault bones during all postnatal life, lateral traits would be also influenced by brain growth. In absence of other strong constraints (e.g., muscular forces), lateral traits would become secondarily integrated with those of the midline. In other words, the minor influence of muscles in the skull would explain why the vault is a quite integrated structure in humans.

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