AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 131:432–443 (2006)

Ontogeny of Facial Dimorphism and Patterns of Individual Development Within One Human Population

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KEY WORDS facial growth; longitudinal; geometric morphometrics; frontal bone; sexual dimorphism; Denver Growth Study

ABSTRACT Based on a longitudinal study of radiographs of the Denver Growth Study, we investigated the morphological development of individual and gender differences in the anterior neurocranium, face, and basicranium. In total, 500 X-rays of 14 males and 14 females, each with 18 landmarks and semilandmarks, were digitized and analyzed using geometric morphometric methods. Sexual dimorphism in shape and form is already present at the earliest age stage included in the analysis. However, the nature of dimorphism changes with age. Four factors apper to contribute to cranial sexual dimorphism in human postnatal development: 1) initial, possibly prenatal, differences in shape; 2) differences in the association of size and shape; 3) male hypermorphosis; and 4) some degree of difference in the direction of male and female growth trajectories. Studying changes in individuals, we find a low correlation between newborn and adult morphology, while 3-year-olds already show a high correlation with their adult form. We conclude that the adult pattern of interindividual difference in facial form in a single human population is established within the first few years of life. Am J Phys Anthropol 131:432–443, 2006.

In humans and other primates, sexual dimorphism has been studied from two different points of view: as sexual dimorphism in adult individuals, and as sexual dimorphism in ontogenetic processes that bring about adult sexual dimorphism. The presence of sexual dimorphism in adult craniofacial features of modern humans is not disputed, even though there might be a need for some clarification of its particular features (Rosas and Bastir, 2002). However, the developmental aspects of facial dimorphism in humans are not so clear.

A widely accepted view was expressed by Enlow (1990), who suggested that girls and boys do not differ in facial characteristics until about 13 years of age. At this time, pubertal facial growth slows down in females but continues in males.

Indeed, most studies carried out on measurements of the face, cranial base, and neurocranium seem to confirm that sexual dimorphism in the human face is mainly the result of a differential growth rate after puberty and during adolescence (Broadbent et al., 1975; Rosas and Bastir, 2002; Ursi et al., 1993).

However, some aspects of absolute growth do not agree with this general view. For example, Ursi et al. (1993) found that a number of craniofacial dimensions, such as anterior cranial base length (sella-nasion), are significantly larger in males from age 6 years. Some features are less dimorphic than others. For example, the cranial base angle and the sagittal position of the maxilla and mandible were found not to be dimorphic at any age. The maxillary and mandibular effective lengths, however, are dimorphic from age 9 years.

Ewing and Harris (2000) reported a modest level of sexual dimorphism in facial features in children between 5–18 years of age. Dimorphism in facial dimensions increases from childhood (ages 6–11 years, 2.7% dimorphism) to adolescence (ages 12–17 years, 3.5% dimorphism). Similar results were reported by Gaži-Čoklica et al. (1997) in a noninvasive longitudinal study of changes in craniofacial characteristics during the transition from the deciduous to permanent dentition in boys and girls between 4.7–11.8 years of age.

These studies concur with Humphrey (1998). She demonstrated that most of the dimorphism is indeed accumulated by features that attain their adult size during or shortly after adolescence in humans. However, a minor degree of sexual dimorphism in features that reach 90% of their adult size early in ontogeny is generally associated with neural structures. Those cranial features that exhibit a significant amount of sexual dimorphism are generally associated with the masticatory system, and reach 90% of their adult size between ages 12–18 years.

A considerable amount of data supports the presence of sexual dimorphism in the absolute and relative brain size of adults (Andreasean et al., 1993; Ankney, 1992; Blatter et al., 1995; Filipek et al., 1994; Harvey et al., 1994; Pfefferbaum et al., 1994; Willerman et al., 1991). Falk et al. (1999) showed that relative brain size in adult

E. Bulygina and P. Mitteroecker contributed equally.

Grant sponsor: Austrian Council for Science and Technology; Grant number: GZ 200.093/I–VI/2004; Grant sponsor: Austrian Science Foundation; Grant number: FWF-P13738.

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Received 29 October 2004; accepted 16 March 2005.

DOI 10.1002/ajpa.20317
Published online 4 April 2006 in Wiley InterScience (www.interscience.wiley.com).

TABLE 1. Landmarks and semilandmarks used in analysis

Name	Abbreviation	Description
Facial and basicranial landmarks		
Nasion	N	Meeting point for sutures between nasal and frontal bones.
Nasospinale	Nsp	Point on midline at inferior root of nasal spine.
Prosthion	Pr	Point on surface of alveolar process of maxilla between two central incisors.
Posterior nasal spine[1]	Pns	Average of most posterior and superior points on the maxillary tuberoisities projected on midsagittal plane. It is seen as an intersection of tip of the pterigomaxillary fissure and hard palate.
Basion	Ba	External midline tip of anterior rim of foramen magnum.
Clival point	CP	Midline point on basioccipital clivus inferior to point at which dorsum sella curves posteriorly.
Sella	S	Central point of sella turcica.
Sphenoidale	Sph	Most posterior, superior midline point of planum sphenoideum.
Greater wings of the sphenoid	Pmp	Average of projected midline points of most anterior point on lamina of greater wings of the sphenoid.
Planum Sphenoideum point	PS	Most superior midline point on sloping surface in which cribriform plate is set, taken in vicinity of superior angle of sphenoidal sinus.
Foramen Ceacum	FC	Pit on cribriform plate between crista galli and endocranial wall of frontal bone.
Frontal bone landmark		
Bregma	Br	Meeting point of coronal and sagittal sutures.
Semilandmarks on external surface of frontal bone outline		
Glabella	Gl	Most anterior midline point on frontal bone between two browridges.
Additional points		Comprise intersections of 30°, 45°, 60°, 75°, and 90° angles to Na-Sella chord with frontal bone outline. Sella serves as apex.

[1] Corresponds to pterigomaxillare (Ptm) (Lieberman and McCarthy, 1999).

males is on average 10% larger than in females. Sexual dimorphism in brain size, where males exhibit larger brains, was also detected in infants, based on autopsy material (Dekaban and Sadowsky, 1978; Pakkenberg and Voigt, 1964). Based on ultrascan data, Joffe et al. (2004) reported on the presence of a small but statistically significant sexual dimorphism in head circumference between fetal males and females. Dimorphism becomes more pronounced during the first 12 months of life, when boys have an approximately 2.4% larger cranial circumference. However, there is no significant difference in neonates. This apparent anomaly probably arises as a result of deformation of the infant head during the birth process.

Dimorphic craniofacial features, therefore, begin to develop at a very early stage of ontogeny in modern humans. However, most of the research to date has been based on traditional metric analyses. In contrast, Strand-Vidarsdottir (1999) partitioned size and shape of craniofacial features with the help of three-dimensional geometric morphometric methods (generalized Procrustes analysis). She carried out a cross-sectional study of an African-American population of known age and sex between age 9 months and adulthood. She found that sexual dimorphism in facial shape is present at all stages of growth. Moreover, shape dimorphism stays constant during development, resulting in parallel ontogenetic trajectories in shape space. Additionally, she found that sexual dimorphism in the final facial shape is achieved by the extension of the male size and shape growth vector.

Dean et al. (2000) studied size and shape of craniofacial features in boys and girls in a set of radiographs from the longitudinal Bolton Craniofacial Study. They demonstrated that between 8–18 years of age, the pattern of ontogenetic shape change in a group of the same sex and same ethnicity is grossly uniform. Unlike in females, male shape change peaks at 15 years of age, which correlates with the male growth spurt.

The purpose of the present study was to investigate when and how sexual dimorphism of the human cranial form emerges in postnatal ontogeny. We focused on questions of whether sexual dimorphism is already present at birth, and whether early dimorphism stays constant during postnatal development or differs from adult dimorphism. We further investigated when the adult pattern of interindividual differences in form appears in development. We addressed the above questions by applying geometric morphometrics to a longitudinal sample of a single population of European descent. The sample is represented by a sequence of X-rays starting as early as 1 month of age.

SUBJECTS, MATERIALS, AND METHODS

X-rays were collected during the Denver Growth Study, carried out between 1931–1966 (Maresh, 1948; Maresh and Washburn, 1938; McCammon, 1970, as cited by Lieberman and McCarthy, 1999). Individuals were radiographed at a distance of 7.5 feet in lateral and frontal view. The long distance between the X-ray source and the subjects renders enlargement factors insignificant and minimizes parallax (Merow and Broadbent, 1990). Lateral radiographs of 14 males and 14 females were taken at 1, 3, 9, and 12 months, and then approximately every year up to age 21 years or later (a total of

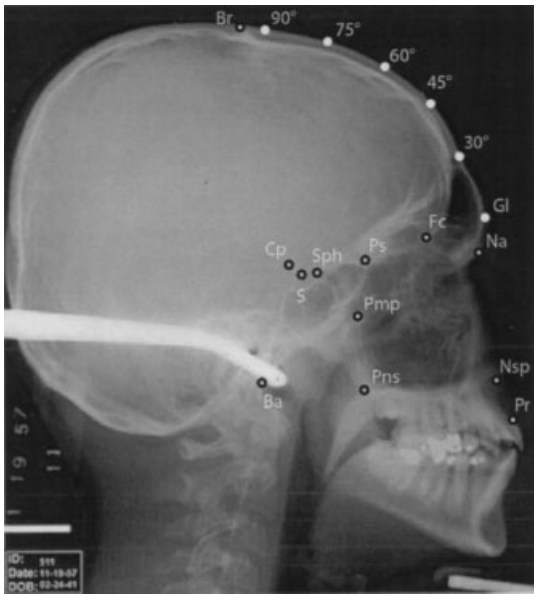

Fig. 1. Location of landmarks on sagittal X-ray. Abbreviations of landmarks and semilandmarks are spelled out in Table 1. White points are semilandmarks; others are traditional landmarks.

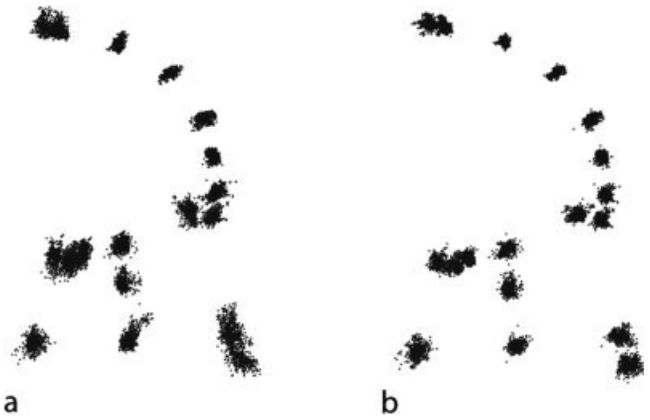

Fig. 2. **a:** Scatterplot of landmarks for all 500 X-rays after Procrustes registration. When both sex and age are regressed out, residual scatter is circular for every landmark except for semilandmarks. **b:** This regression (with a quadratic function for age) explains ca. 45% of complete shape variation in data.

500 radiographs). Participants were selected from the complete original Denver Growth Study data set on the basis of image quality and number of serial radiographs. The radiographs were transferred into digital format at full size, and then reduced by 20%.

The great majority of landmarks used in this study were used by other authors on cranial radiographs (Merow and Broadbent, 1990), and correspond to those employed by Lieberman and McCarthy (1999), whose analysis was also done on Denver Growth Study material. Other landmarks, such as glabella and prosthion, are anatomical and are frequently used for description of the facial profile (Aiello and Dean, 1990; Ravosa, 1991). The landmarks are described in Table 1 and Figure 1. They were chosen to reflect the shape of the frontal bone, outline of the middle-face, spatial position of the middle face, and outline of the basicranium (Fig. 1, Table 1). All landmarks were digitized in two dimensions (2D) by one person (E.B.) with the help of TPSdig software developed by F. James Rohlf, Department of Ecology and Evolution, State University of New York at Stony Brook (© 2001, F. James Rohlf).

The positions of landmarks on the frontal bone outline between bregma and nasion are very uncertain in the direction along the curve, but well-defined perpendicular to it. These "semilandmarks," including glabella, were allowed to slide along the frontal bone outline so as to minimize the net bending energy of the data set as a whole around its own Procrustes average. Their positions along the outline are thereby interpolated by the thin-plate spline function, and only the information on the landmark position perpendicular to the curve derives from the data themselves. For statistical analysis, these relaxed "sliding landmarks" can be treated as homologous within the sample and analyzed together with the other traditional landmarks (Bookstein et al., 1999; Bookstein, 1997; Gunz et al., 2005).

The 500 configurations of 18 landmarks and semilandmarks were superimposed by a Generalized Procrustes registration (Rohlf and Slice, 1990), resulting in a vector of 36 shape variables and the centroid size for each specimen. Centroid sizes were also computed for landmarks of the face and landmarks of the frontal bone separately. To compare sexual dimorphism in facial form at particular age stages, we computed sex-specific average forms at a number of age stages, using a moving average algorithm. This method models the average shape change for a given age period with a quadratic regression of all the shape variables on age. The regressions were then used to predict the sex-specific average shapes at 0.5, 2, 4, 6, 8, 10, 12, 14, 16, and 18 years of age. These average forms were compared by thin-plate spline (TPS) deformation grids (Bookstein, 1991) in order to visualize shape changes during growth and sexual dimorphism for the different age groups. The shape differences are exaggerated by an appropriate factor to ease interpretation.

We compare the overall pattern of male and female development by a principal component analysis (PCA) in shape space (also called relative warp analysis). The average sex-specific trajectories were compared by examining several different projections of the first three principal components (PCs). These rotations of three-dimensional (3D) graphs help us to understand the high-dimensional geometry of trajectories that cannot be read from a single 2D projection alone (Johnson and Wichern, 1998; Mitteroecker et al., 2004a,b). Additionally, we apply a relatively new technique, principal components in size-shape space, which is a PCA of the shape variables augmented by the natural logarithm of centroid size (Mitteroecker et al., 2004a,b). The resulting low-dimensional eigenspace allows the comparison of size and shape at once (i.e., form), whereas the usual PCA of Procrustes coordinates permits the analysis of shape only. A comparison of both analyses allows the assessment of differences and dissociations of the size-shape relationship between the two sexes and during development.

To assess the development of individual form characteristics, we correlated PC scores in size-shape space of 19-year-old forms with the scores of 1-month-olds (hereafter referred to as "newborns") and several older age groups (1, 2, 3, 6, 10, 15, and 19 years). This gives a correlation between the scores of adults and newborns for PC1, a correlation for 1-year-olds and adults for PC1, and so on until the correlation between 18-year-olds and adults. The same was done for the second, third, and fourth PC scores. The aim of this approach is to assess

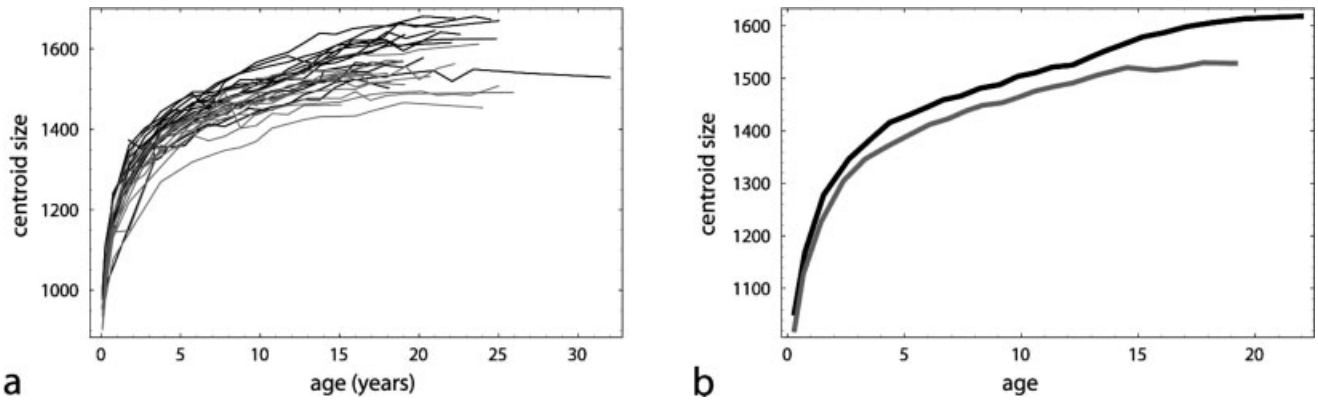

Fig. 3. Centroid size plotted against age. Males in black, females in grey (**a**) for each individual separately and (**b**) average sex-specific growth trajectory.

TABLE 2. Sexual dimorphism in centroid size for all landmarks, face, and frontal bone separately

	Average and SD, females	Average and SD, males	Difference (*t*-test)
All landmarks			
Newborns	976 ± 49.1	989 ± 41.5	n.s.
Adults	1,527 ± 42.8	1,608 ± 54.2	$P < 0.0001$
Neurocranial landmarks			
Newborns	530 ± 28.5	543.4 ± 24.1	n.s.
Adults	755 ± 30.2	782 ± 37.9	$P < 0.024$
Facial landmarks			
Newborns	295 ± 13.9	294 ± 21.0	n.s.
Adults	591 ± 21.0	643 ± 24.2	$P < 0.0001$

when and how interindividual form differences emerge during ontogeny. As individuals were not all X-rayed at the same age stages, we interpolated individual PC scores with a cubic interpolation function. Those individuals who had early or late radiographs missing were excluded from this part of the analysis, to avoid extrapolation of growth trajectories.

RESULTS

Procrustes superimposition

Figure 2a shows a scatterplot of all 500 superimposed landmark configurations. A regression of Procrustes coordinates on age and sex (with a quadratic function for age) explains approximately 45% of the complete shape variation in the data. The residual variation (Fig. 2b) is circular for each landmark, except for the semilandmarks (as a result of the sliding). Therefore, beyond the sex-specific average growth trends, everything else appears to be individual variation without additional major factors in the data (Dean et al., 2000).

Growth curves

Figure 3a shows centroid size plotted against age. A line representing an individual growth trajectory connects the data points belonging to a single individual. Both sexes overlap, but females show a tendency to be smaller than males at higher age stages. Figure 3b shows two smoothed sex-specific average growth trajectories that were computed by a moving average algorithm. While similar for newborns, the two trajectories are clearly separated thereafter, with males still increasing in size when females have stopped growing at about age 14 years (see Table 2).

Figure 4a shows sex-specific growth trajectories for the facial landmarks only (landmarks Na, Nsp, Pr, Pns, Pmp, PS, and FC; for all abbreviations, see Table 1). Although male facial size exceeds female facial size beginning a few years after birth, at approximately age 13 years the average male trajectory exhibits a growth spurt. Males still continue to grow when female growth has ceased. Most of the adult sexual dimorphism in facial size is reached during this prolonged growth of males. Figure 4b shows growth trajectories for neurocranial size (landmarks Br, 90°, 75°, 60°, 45°, 30°, Gl, Na, Sph, Ps, and FC). Nearly full adult size of the sagittal projection of the anterior neurocranium is attained around age 5 years. Sexual dimorphism in size is already established at the earliest age stage (0.5 years).

Figure 5 addresses the regional difference in sexual dimorphism during growth more directly by showing the size difference between the sexes for both the frontal bone and face. While Figure 5a shows the absolute size difference (as a subtraction of the female centroid size from the male one), Figure 5b expresses sexual dimorphism as a relative size difference (logarithm of the centroid size ratio). For both absolute and relative size difference, the sexual dimorphism of the anterior neurocranium is constant throughout postnatal development, indicating its prenatal origin. In contrast, dimorphism in the size of the face increases over time, and becomes especially pronounced during adolescence.

Change of shape and form

To study shape change during development, we compare the differences between age- and sex-specific average shapes. Figure 6 shows TPS deformation grids from each age stage to its next older stage for both males and females separately. During the first 4 years of age, there is a clear enlargement of the whole face relative to the neurocranium. The posterior cranial base flexes at the same time. As a result, the pharynx area appears compressed in Figure 6, indicating its relatively slower growth. In subsequent years, shape change is not as pronounced as during the first 4 years of development. There is still a relative enlargement of the face and especially of the maxilla, but the cranial base angle retroflexes (flattens) again. Males continue their facial devel-

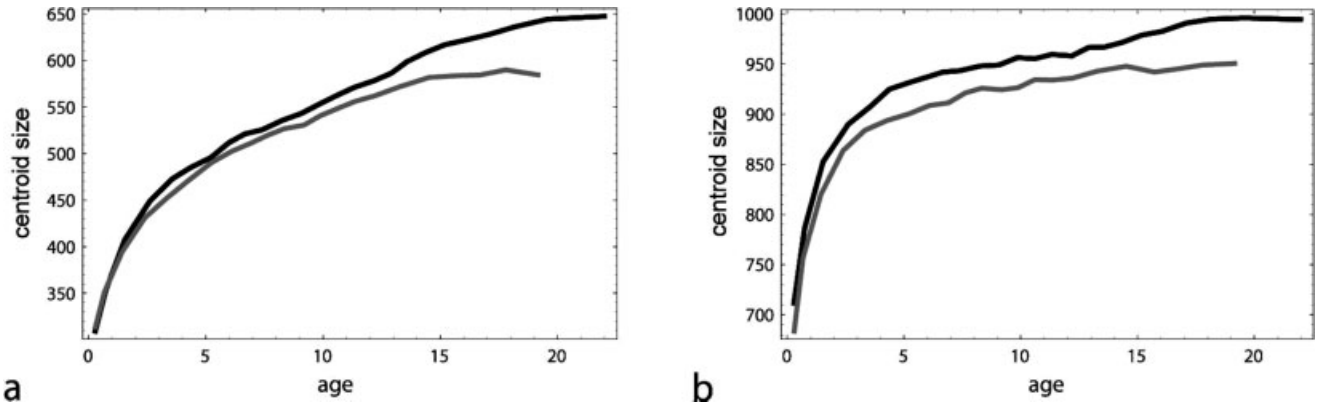

Fig. 4. Average growth curve of centroid size (**a**) for facial landmarks only (Na, Nsp, Pr, Pns, Pmp, PS, FC) and (**b**) for neurocranial landmarks (Br, 90°, 75°, 60°, 45°, 30°, Gl, Na, Sph, Ps, FC). Males are shown in black; females, in grey.

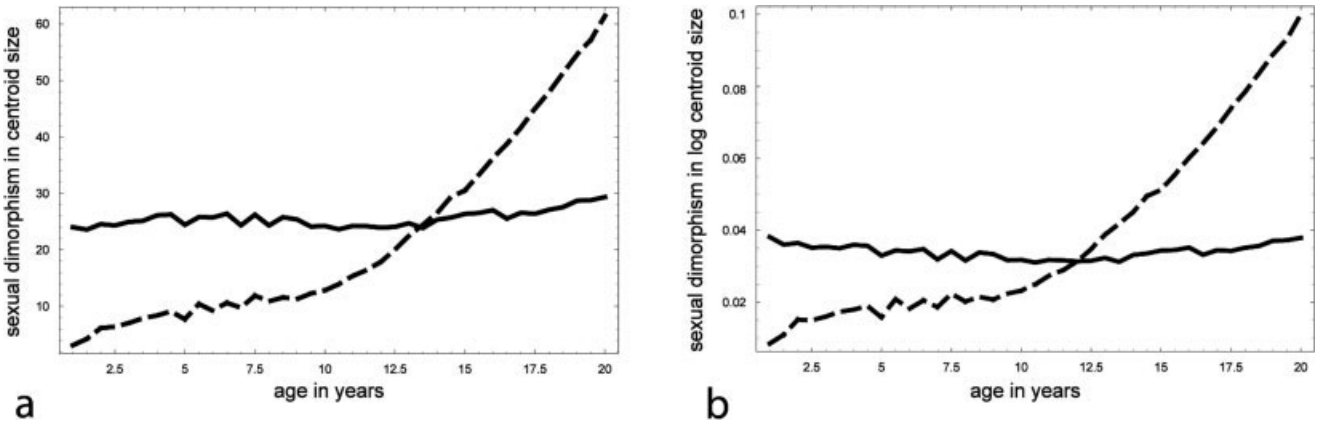

Fig. 5. **a:** Difference in centroid size between sexes for facial landmarks (dashed line) and neurocranial landmarks (solid line). **b:** Difference in natural logarithm of centroid size between sexes. This is equivalent to logarithm of fraction between male and female size values, and hence represents *relative* sexual dimorphism. Also, logarithm of centroid size is used to construct size-shape space of Figure 10, and thus corresponds to this particular metric.

opment, which mainly involves the enlargement of the supraorbital relief, after female average growth has ceased between 12–14 years of age.

Figure 7 shows the sexual dimorphism in facial shape for each age stage. A series of 10 TPS deformation grids (from 0.5–18 years of age) allows the visualization of average sexual dimorphism as a deformation of the female average shape into the male shape. In the early stages, males have more flexed cranial bases, relatively larger frontal bones, and smaller faces than females. This reverses in subsequent stages. During puberty, males begin to develop more pronounced supraorbital tori than do females. The smoothest deformation grids can be observed between ages 6–12 years, indicating that boys and girls are most similar in midsagittal shape during this particular age period.

Figure 8 shows three different projections of the first three PCs of shape space. Lines connect 10 male and 10 female average forms to represent male and female growth trajectories. The first three PCs explain approximately 99% of shape variation among the 20 average forms and ca. 62% of variation among all 500 original shapes. The particular shape changes along these trajectories are visualized in the TPS grids of Figures 6 and 7.

Figure 8a demonstrates that the two trajectories are separate from the earliest stage. While this projection yields two similarly shaped trajectories, Figures 8b and 8c show that the average trend of shape change begins to differ among males and females in puberty. The female growth trajectory stops earlier than the male one. Both male and female trajectories are curvilinear; they seem to change direction at about 4–6 years of age, perhaps due to cessation of brain growth.

We evaluated the statistical significance of sexual dimorphism in shape for both the youngest and oldest age groups with a Monte Carlo permutation test (Good, 2000). On account of the low sample size and substantial overlap of trajectories (Fig. 10), these tests are not significant. When carrying out the tests with the first four pairs of partial warps (Bookstein, 1991; Rohlf, 1995), sexual dimorphism for newborns is significant at $P \approx 0.018$, and for adults at $P \approx 0.025$. This test uses the eight variables containing the largest-scale shape features, and thus omits small-scale shape variation. Additionally, we performed a permutation test for sexual dimorphism in shape within the *two* youngest age stages and within the *two* oldest age stages to double the sample size. The individuals are permuted within their age group only, yielding significance levels of $P < 0.001$ and $P \approx 0.0012$ for infants and adults, respectively.

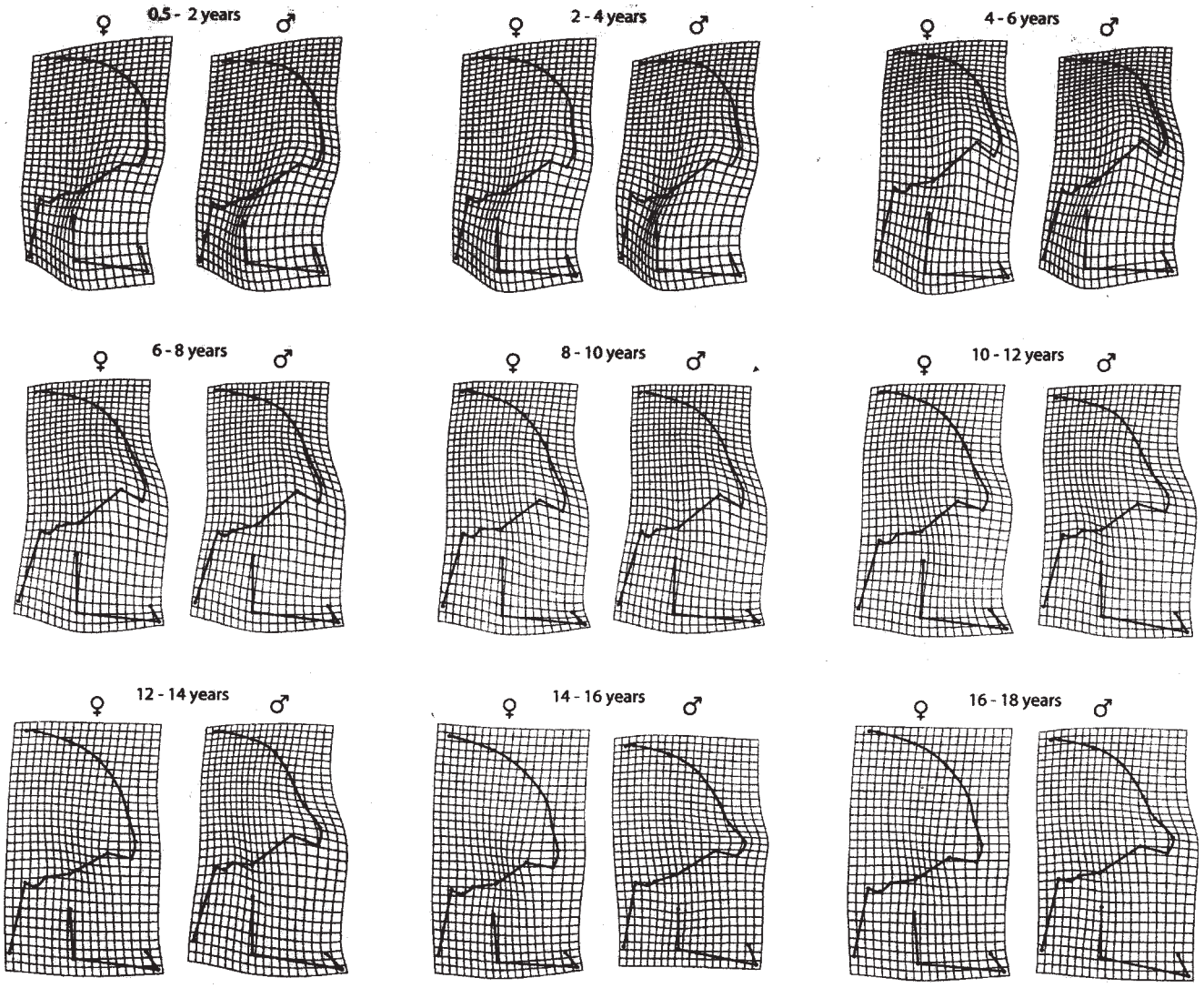

Fig. 6. Thin-plate spline deformation grids from each age stage to its next older stage for males and females separately. TPS grids visualize developmental shape change (exaggerated by factor of 6) for different age periods. Shape change is most pronounced in first 4 years of age. Later deformation grids mainly show relative enlargement of face and reorientation of cranial base. In puberty, male and female development differs most clearly.

In Figure 9, the average forms are projected onto the first three principal components of size-shape space. The plots contain information about both *shape and size* differences between individuals. These three PCs explain more than 99% of size *and* shape variation among the 20 average forms, and approximately 90% of variation among all 500 original *forms*.

The trajectories in this space look very similar to the ones in shape space, but are "stretched" along PC1, due to the high loading of centroid size on this PC. This overall similarity between the trajectories in shape space and size-shape space indicates that the size-shape relationship (the amount of shape change per size change) is similar between both sexes, even though their actual shape change differs. However, the relative positions of the age groups *along* the trajectories differ between the two analyses. When comparing average males and females of the same age in size-shape space (Fig. 9), males exhibit a more progressed form along the common direction of development. In shape space, on the contrary, females appear slightly more progressed in shape development before male hypermorphosis begins in puberty (Fig. 8). This means that, before puberty, males have larger faces than females of the same age, but are slightly delayed in the development of their facial shape.

Individual development

In Figure 10, growth trajectories in size-shape space are drawn for each individual separately. The newborns (i.e., the earliest available data for each individual, which is 1 month of age) already vary markedly among themselves, and the variance in shape during development stays approximately the same. The variances are 0.002476 and 0.002472 for the youngest and oldest group, respectively; they do not differ significantly. The postnatal development of *individual* adult form is therefore not a matter of divergence from a common early

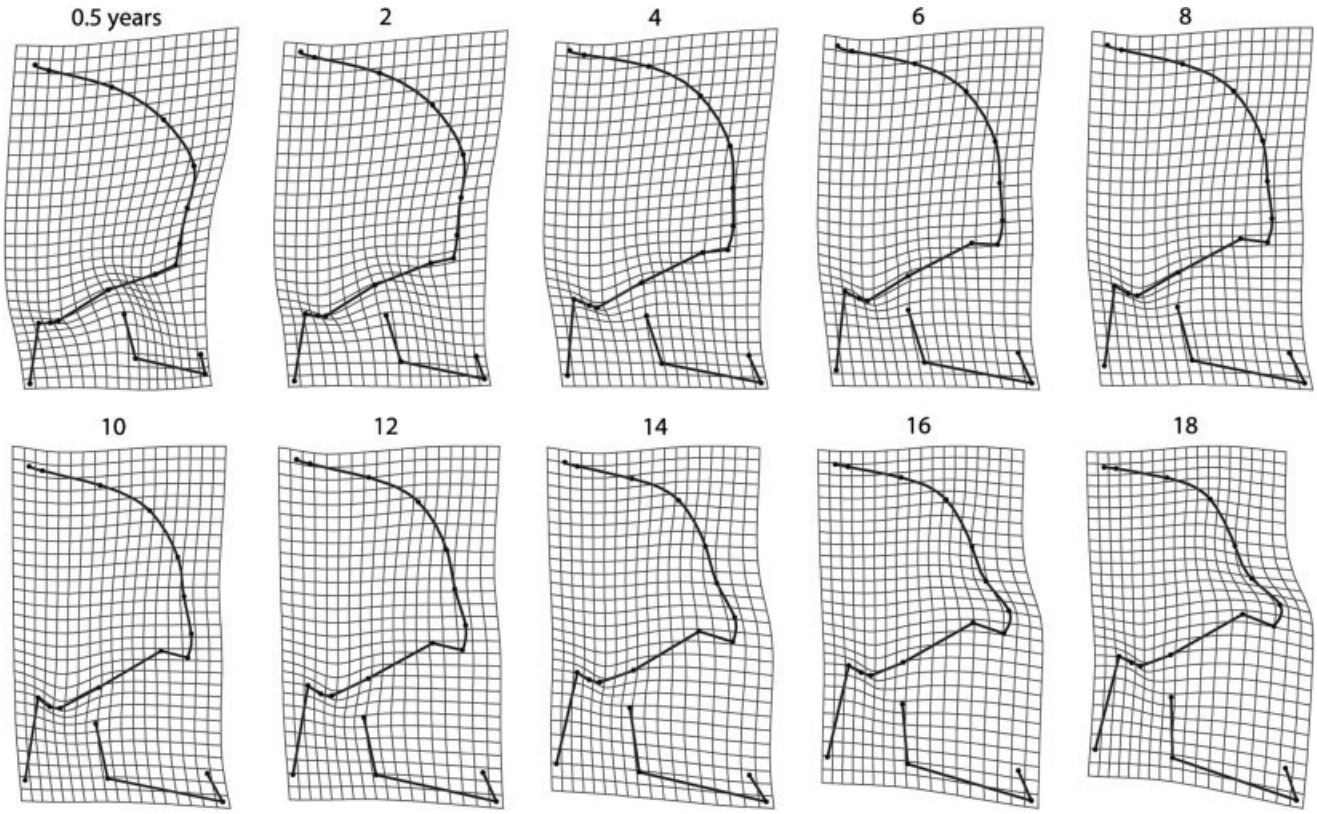

Fig. 7. Sexual dimorphism in shape for each age stage: female average shape is deformed toward male shape for each age group. There is continuous increase in relative size of posterior cranial base and face in males compared to females. Sexual dimorphism in face and supraorbital region becomes especially pronounced during puberty. Note how sexual dimorphism in angulation of cranial base reverses during ontogeny.

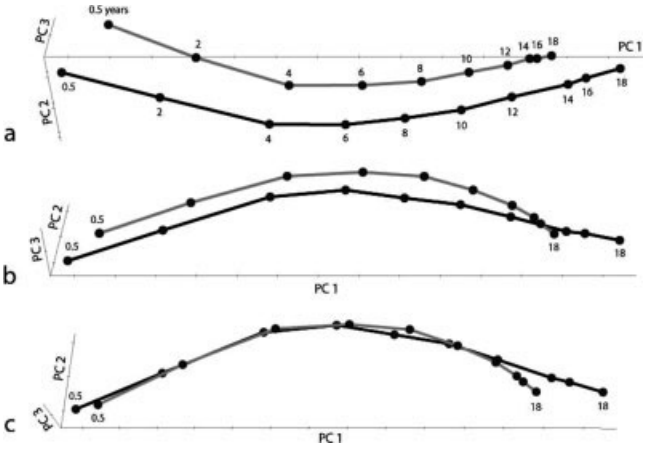

Fig. 8. Projection of 10 average forms for each gender onto first three principal components of *shape space*. Ten age-labeled male forms are connected by black line, females by grey line, to visualize two sex-specific growth trajectories. Three different rotations (**a–c**) of these PCs show their geometry that could not be read from a single projection. Trajectories are separated from earliest age on, and do not intersect. They are somewhat parallel until beginning of puberty, but differ in direction thereafter.

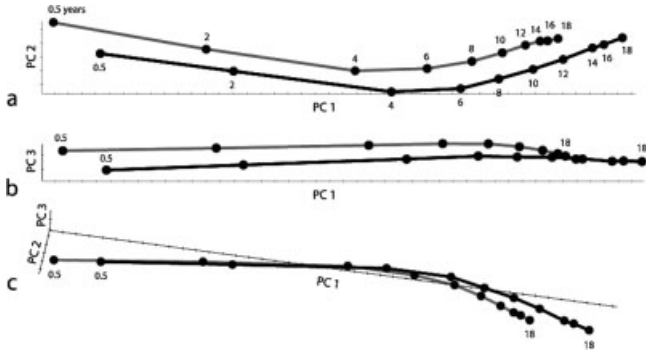

Fig. 9. Three different rotations (**a–c**) of first three principal components of *size-shape space*. Males, in black; females, in grey. Trajectories possess a similar geometry to those in shape space shown in Figure 8.

form. In order to assess when the adult pattern of interindividual shape differences becomes established during postnatal ontogeny, we compared Pearson correlation coefficients between PC scores of 19-year-olds (the adult pattern) and several younger age groups. Figure 11, first row, plots these correlation coefficients for the first four PCs in size-shape space. A similar comparison showing correlations of newborn scores with older age groups is shown in Figure 11, second row. Within the first 3 years of age, the correlation of PC scores with adult scores reaches a value of approximately 0.8, and the correlation with newborn scores decreases markedly. This does not mean that the PC scores of children are identical to those of adults at age 3. It only shows that the pattern of differences between individuals (the interindividual

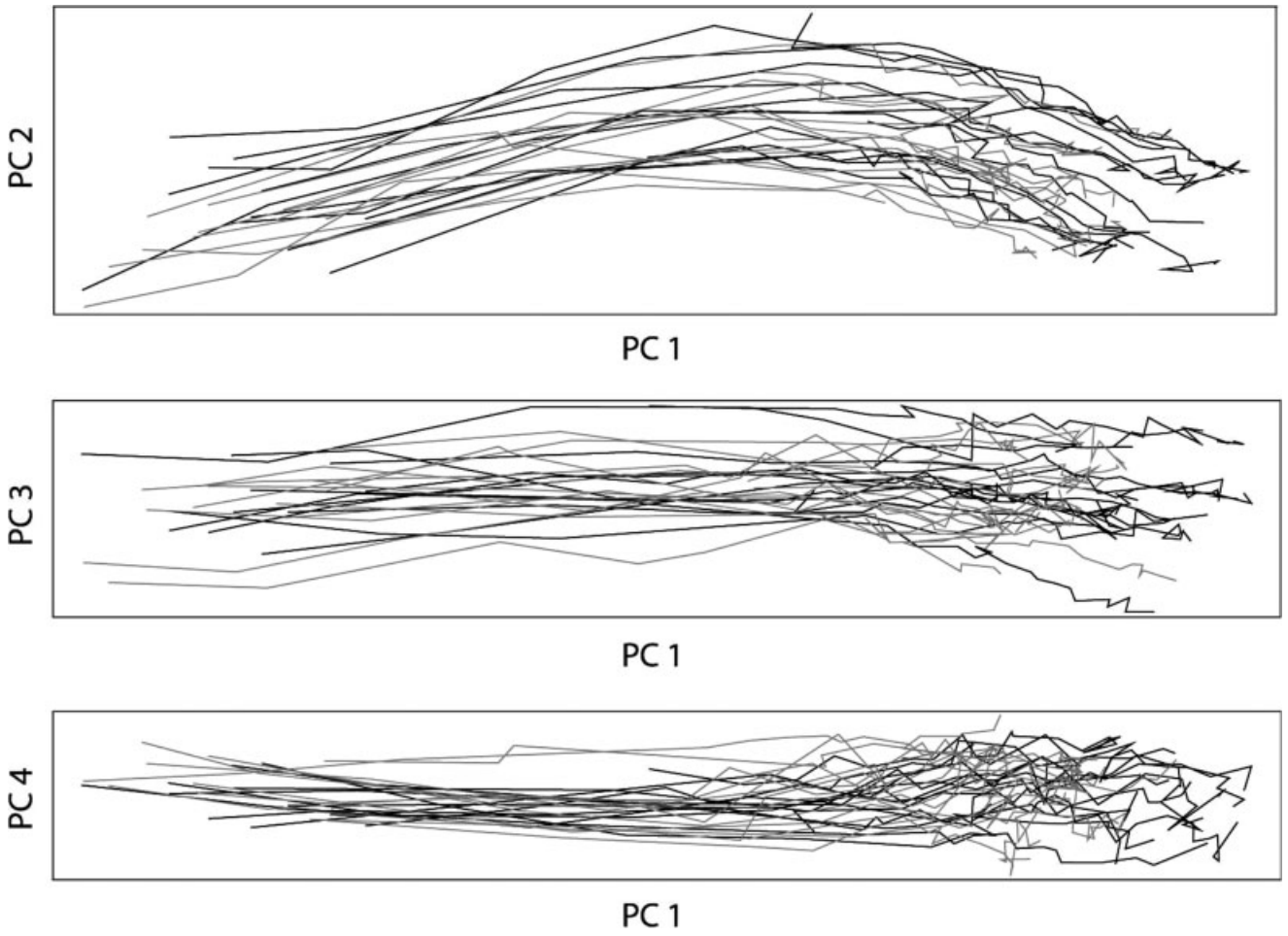

Fig. 10. Individual growth trajectories projected onto first two principal components of size-shape space. Each line connects data points of single individual. Males are shown in black, females in grey.

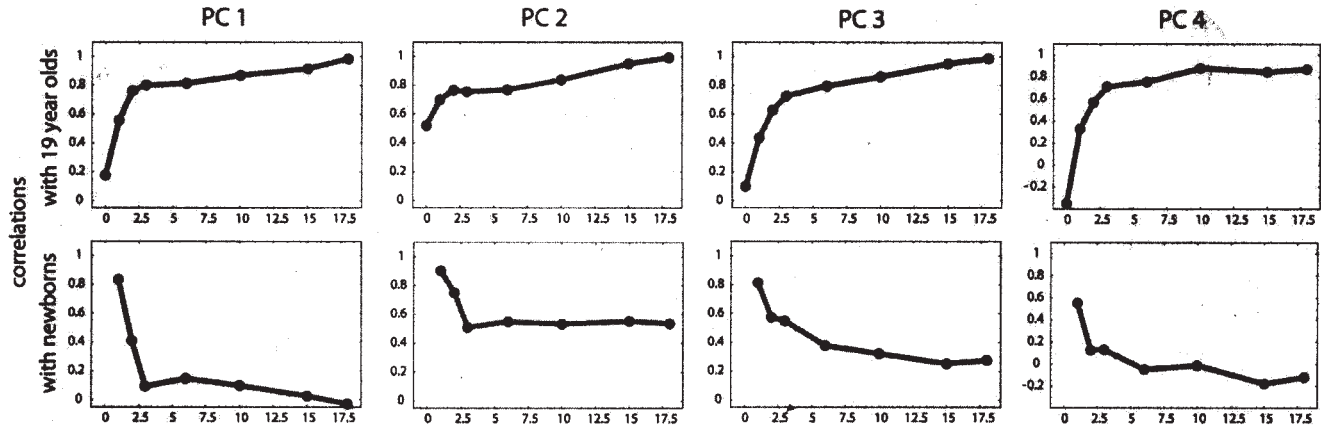

Fig. 11. Age vs. correlation coefficients of PC scores between different age groups and 19-year-olds (upper row) and newborns (lower row), respectively. Age-dependent pattern of correlations is shown for PCs 1–4.

differences) is very similar. Three-year-olds differ among each other in a way that is already similar to the way they will differ from each other as adults. This implies that all individuals follow a shared growth trend after about 3 years of age and later in puberty, whereas early shape changes are different by individual.

DISCUSSION

The radiographs of the longitudinal Denver Growth Study provide for a number of advantages over cross-sectional data. First of all, longitudinal data by nature have a lesser variance along ages due to sampling the same

individuals. This enables a reasonable inference even from a smaller sample. It also allows the study of correlations between infant, child, and adult forms that would be impossible in cross-sectional data.

In order to investigate sexual dimorphism in ontogeny, we study both the size increase of the neuro- and viscerocranium as well as developmental shape change. Sexual dimorphism in size of the anterior part of the neurocranium can be detected at the earliest ages available for this study, and stays practically constant over the whole period of investigation. This result corresponds with data on sexual dimorphism in the brain size of infants (Dekaban and Sadowsky, 1978; Pakkenberg and Voigt, 1964; Voigt and Pakkenberg, 1983) and in pre- and early postnatal head circumference (Joffe et al., 2004). The constant degree of size difference, however, is a new finding. It suggests that the full amount of sexual dimorphism in neurocranial size is established prenatally.

Unlike the neurocranium, facial size dimorphism develops postnatally and increases with age up to the latest stages of development available for this study, mostly due to male hypermorphosis. Female faces experience a significant decline in the rate of growth at approximately 13 years of age, and stop growing at about 15 years of age. These results are in agreement with Humphrey (1998), who demonstrated that most facial features attain their adult size later than neurocranial features.

We were able to detect sexual dimorphism in the shape of the face and the frontal bone as well as in the basicranium at the earliest stages of development included in the analysis. This result confirms the geometric morphometric study of Strand-Vidarsdottir (1999) on cross-sectional populations, where the youngest individuals were 9 months of age. However, in addition to the above work, we find that the pattern of shape differences between sexes changes with age. In infants, males have a relatively larger and more globular frontal bone, a smaller face, and a more flexed cranial base than do females of the same age. In adults, this pattern reverses: males tend to have a larger and more prognathic face, a less flexed cranial base, and a relatively smaller and flatter frontal bone. It was also found that male and female growth trajectories are not always parallel, but undergo some degree of divergence after about age 12 years. This divergence is mainly in shape change; the amount of shape change per size change seems to be similar in both sexes. However, before puberty, males possess a larger facial size than females of the same age, whereas females are slightly more advanced in the development of facial shape.

Our findings on sexual dimorphism of the cranial base contribute to the discussion of the relationship between relative brain size and the flexion of the cranial base. In the present study, cranial base flexion is not reported in terms of basicranial angles. Such angles can be misleading because of different approaches to their measurement that do not take into account the ways in which the anterior and posterior parts of the cranial base affect the angles (Bookstein et al., 2003; McCarthy, 2001). Rather, we visualize shape changes by thin-plate spline deformation grids. Differences in basicranial shape, including the cranial base angle, can then be identified as a displacement of the appropriate landmarks and a deformation of the corresponding grid cells.

The flexion of the cranial base has long been connected with relative brain growth in human ontogeny and phylogeny (Lieberman et al., 2000; Lieberman and McCarthy, 1999; Ross and Henneberg, 1995; Ross and Ravosa, 1993). This explanation concurs with our results. In infancy, the TPS grids of Figure 6 indicate a relatively larger anterior neurocranium, a smaller face, and a shortened cranial base for boys relative to girls. This morphology is associated with a more flexed cranial base in boys. In adulthood, the relative sizes of the face and anterior neurocranium are reversed in males and females. The cranial base angle also becomes more obtuse in men. In our analysis, the shape of the cranial base thus seems to be associated with the relative sizes of the face and anterior neurocranium.

A certain amount of difference was detected in the structure of the anterior cranial base between infant males and females. Infant females have a relatively longer cribriform plate than males, whereas males have a relatively longer diameter of the sphenoid plane. This result needs further investigation. It may be indicative of either different patterns of anterior cranial base growth in infant males and females at the earliest stages of postnatal development, or a sampling error due to the practical difficulties of placing sphenoid plane landmark in infants whose cranial base has not undergone complete ossification.

We show that individuals differ among themselves in size and shape at the earliest ages available for study. One-month-old individuals do not start development from a single point in size-shape space: each individual is unique. This result concurs with the intuitive perception of infant individuality. An unexpected result of this study is the absence of a correlation between newborn and adult forms and the establishment of a high correlation with adult form at age 3 years. One possible explanation might be connected with the high influence of epigenetic factors on the phenotype at early stages of life, and differential gene activity during ontogeny. For example, maternal investment (such as nursing ability and maternal care) in rodents (mice and rats) is an important factor in phenotypic expression at early stages of life (El Oksh et al., 1967). Moreover, phenotypic variance and heritability of size and shape measures increase during ontogeny, while the variance due to maternal effects decreases (Atchley and Rutledge, 1980; Herbert et al., 1979; Rutledge et al., 1972).

CONCLUSIONS

In conclusion, four factors contribute to cranial sexual dimorphism in human postnatal development: 1) initial, possibly prenatal differences; 2) differences in the association of size and shape; 3) male hypermorphosis at later stages of development; and 4) some degree of difference in the direction of male and female pubertal growth trajectories. The early appearance of sex-specific differences in overall size and shape concurs with the early establishment of sex-specific, population-specific, and also species-specific shape differences among primates (O'Higgins et al., 1990, 2001; O'Higgins and Dryden, 1993; O'Higgins and Jones, 1998; Richtsmeier et al., 1993; Richtsmeier and Cheverud, 1989; Strand-Vidarsdottir, 1999; Vidarsdottir et al., 2002). While some of these studies found the trajectories to be different but parallel during postnatal ontogeny (i.e., not diverging), Cobb and O'Higgins (2004) and Mitteroecker et al. (2004a) showed that these results are likely to be methodological artifacts, and that postnatal divergence of trajectories is an important aspect in developing adult shape differences.

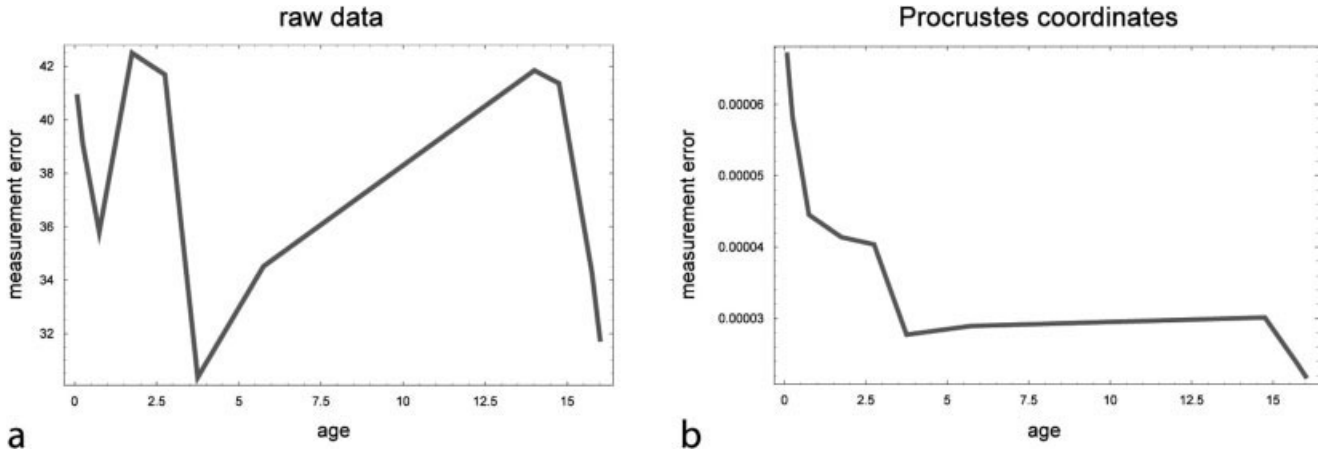

Fig. 12. **a:** Variance due to measurement error of raw coordinates. Error does not systematically change with age; highest and lowest values differ by about 30%. **b:** Measurement error after Procrustes superimposition. Measurement error for infants is more than 100% higher than for adults.

The extension or truncation of similar growth trajectories to produce sex-specific and species-specific differences is a debated topic. While older and usually univariate studies (e.g., Shea, 1981, 1983) view the major reason for differences in hominoid cranial form in the extension or truncation of *identical* trajectories, the studies cited above show that this assumption is too simplistic. Ontogenetic trajectories are usually not the same between species or between sexes of the same species. This notion is supported also by a number of studies on other mammals and vertebrates (e.g., Hingst-Zaher et al., 2000; Montiero et al., 1987; Zelditch and Bookstein, 1992). Zelditch et al. (2003) concluded that the ontogeny of the mammalian skull shape cannot be represented by a single strait line; nor are these trajectories of identical shape.

Our findings on sexual dimorphism in human cranial growth fit into a general pattern of primate and maybe even mammalian cranial ontogeny: ontogenetic trajectories are different very early, in fact prenatally, and continue to differ in direction and length to various degrees. This pattern was found by several authors between species, between different populations of a single species, and between sexes. The present study extends these observations to the interindividual differences in one homogeneous population of *Homo sapiens*. The individuals are distinguishable in their cranial form shortly after birth, and possess individually different trajectories until about age 3 years. Then the direction of development becomes common to all individuals, although the trajectories are of different lengths. We do not assume that these later trajectories are exactly parallel, yet 3-year-olds already possess a high correlation with their adult morphology, and this correlation remains constant during later development. The results of this study may be considerably enriched by investigation of individual growth patterns and the development of sexual dimorphism in different human populations, given an indication (Vidarsdottir and O'Higgins, 2001) that human groups may vary on how exactly they develop sexual dimorphism.

ACKNOWLEDGMENTS

This study was made possible through the kindness of Dan Lieberman and Robert C. McCarthy, who provided the authors with digital copies of the Denver Growth Study radiographs. We are also grateful to Ellie Simpson, who carried out the digitizing of the original radiographs. We thank Fred Bookstein, Philipp Gunz, Gerhard Weber, and F. James Rohlf for their support and advice during the analysis stage of the present work, and Christopher Dean and Charles Lockwood for their constructive criticism of the work. The manuscript was greatly improved through the comments of Dan Lieberman, Fred Bookstein, and Dennis Slice. Samuel Cobb and Nick Jones kindly provided help with technical issues related to this study. We also thank two anonymous reviewers for helpful comments, and the associate editor for pointing out the potential problem with measurement error. P.M. was supported by the Austrian Council for Science and Technology (GZ 200.093/I-VI/2004) and by the Austrian Science Foundation (FWF-P13738).

APPENDIX

Our results on individual growth patterns, as presented in Figure 11, could potentially be an artifact due to measurement error. The identification of landmarks from radiographs is to some degree imprecise. Even though most of the studied structures are either fully or partially endochondrially ossified by age 1 month (Scheuer and Black, 2000), there is still some risk of imprecise identification of landmarks in very young individuals. Also, if absolute measurement error is constant over age, its relative impact is higher in small individuals than in large ones. Thus, when correlating shape scores of young individuals with adults scores, the correlation might be lower than expected due to the relatively higher measurement error in young individuals. In contrast, when correlating adults with adolescents, this effect might not be present.

We estimated the measurement error for our data by measuring eight age stages for four individuals four times each. This gives four measurements for each of 32 X-rays. For all these X-rays, we calculated the variance of the raw data and of Procrustes coordinates, pooled

over all 12 traditional landmarks. Figure 12 shows the variances of the measurements against age. In the raw data, there is no association between measurement error and age, while the error clearly decreases with age for the Procrustes coordinates. The average Procrustes variance due to measurement error is 0.000067 for the 1-month-olds and 0.000026 for the 14–16-year-olds. Both parameters are pooled variances of $4 * 4 * 12 = 192$ values each. The ratio of these values, $2.58 \approx 1.6^2$, is the one expected for a relative size increase of about 1.6.

In the current study, we correlate principal components of size and shape variables among different age classes. The covariance between two variables does not change when additional error terms are added to the variables, as long as they are uncorrelated with the variables. The covariance stays constant as well if one error term increases. However, the standard error of the covariance increases. The situation is different with correlations, as the covariance is divided by the product of the standard deviations of the two variables. An increase in variance leads to a decrease of the correlation coefficient, reflecting the reduced amount of explained variance. Let us assume that $\mathrm{Var}(Y)$, the variance of the young individuals, is actually too high and should instead be $\mathrm{Var}(Y) - \mathrm{Var}(E_Y) + \mathrm{Var}(E_A)$, where $\mathrm{Var}(E_Y)$ and $\mathrm{Var}(E_A)$ are the amounts of shape variance due to measurement error for the young individuals and the adults, respectively. To have both variables with the same (adult) measurement error, $\mathrm{Cor}(Y,A)$ has to be multiplied with

$$\sqrt{\frac{\mathrm{Var}(Y)}{\mathrm{Var}(Y) - \mathrm{Var}(E_Y) + \mathrm{Var}(E_A)}}.$$

For our analysis, this means that the correlation between infants and adults should be multiplied by 1.171 to be comparable with the correlations of older age groups with adults. This number is also supported by simulation studies that we have done.

However, the correlations in Figure 11 are based on principal components in size-shape space, and it is known that centroid size is quite unaffected by measurement error (Dryden and Mardia, 1998). The influence of different (relative) amounts of measurement error on the correlation of size-shape scores is thus expected to be even below the value given above. The actual relative increase of correlation over age, as shown in the first row of Figure 11, ranges from 2–10, and is thus much higher than the maximum increase due to measurement error. Therefore, our empirical results stay valid, even when taking measurement error into account.

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