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ARTICLE

Common Patterns of Facial Ontogeny in the Hominid Lineage

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Recent evaluation of Neanderthal and modern human ontogeny suggests that taxon-specific features arose very early in development in both lineages, with early, possibly prenatal, morphological divergence followed by parallel postnatal developmental patterns. Here we use morphometric techniques to compare hominoid facial growth patterns, and show that this developmental phenomenon is, in fact, not unique to comparisons between Neanderthals and modern humans but extends to *Australopithecus africanus* and to the hominoid lineage more broadly. This finding suggests that a common pattern of juvenile facial development may be more widespread and that the roots of ontogenetically early developmental differentiation are deep—perhaps predating the ape/human split of 6+ million years ago. *Anat Rec (New Anat) 269:142–147, 2002.* © 2002 Wiley-Liss, Inc.

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It is well accepted that small changes in the rate or timing of developmental events can provide a mechanism for evolutionary change by generating morphological differences between species (Gould, 1977; Shea, 1983, 1989; Hall, 1984; Godfrey and Sutherland, 1996). Analyses of several juvenile fossil hominid crania and dentition indicate that their development is fast relative to that of modern humans; this is true for australopithecines and early *Homo* (Smith, 1986, 1991; Beynon and Wood, 1987; Bromage, 1987; Conroy and Vannier, 1987), as well as the more temporally recent Neanderthals (Dean et al., 1986; Stringer et al., 1990). Ponce de León and Zollikofer (2001) support the phylogenetic separation of Neanderthals and modern humans, based on developmental evidence indicating early ontogenetic divergence (see also Krovitz, 2000) followed by parallel postnatal developmental patterns, and comment on the dearth of information about earlier stages in hominid evolution.

In this study, we test whether developmental patterns showing early morphological divergence and later parallel development are more universal among hominoids, by examining the ontogeny of facial shape in *Australopithecus africanus*, modern humans, chimpanzees, bonobos and gorillas. We tested two possible explanations for divergent craniofacial morphology: (1) species-specific adult facial form is the result of developmental divergence during later ontogeny, or (2) species-specific facial morphology is present at an early developmental stage, suggesting early developmental divergence and similar later facial growth processes.

MORPHOMETRIC ANALYSIS OF SHAPE AND GROWTH SIMILARITY

Our analyses are applied to mean forms of juvenile and adult samples of modern humans, chimpanzees, bonobos, and gorillas, and to individual juvenile and adult specimens of *A. africanus*—Taung and Sts 5—from South Africa. The fossil specimens of Taung and Sts 5 represent juvenile and adult *Australopithecus africanus*, respectively. Sts 5 is generally considered an "average" individual, representing either a large female or a small male (Lockwood, 1999). Other adult *A. africanus* material (such as Stw 505) was not included in this analysis, because fragmentation and distortion reduced the number of landmarks shared with Taung and Sts 5. An ape-like tooth maturation pattern places Taung's age at death around 3–4 years (Smith, 1986; Beynon and Wood, 1987; Bromage, 1987; Conroy and Vannier, 1987). Extant cranial material consists of cross-sectional samples of juvenile and adult *Homo sapiens* ($n_{adult} = 141$, $n_{juv} = 21$), *Gorilla gorilla* ($n_{adult} = 115$, $n_{juv} = 11$), *Pan troglodytes* ($n_{adult} = 65$, $n_{juv} = 13$), and *Pan paniscus* ($n_{adult} = 23$, $n_{juv} = 27$). Juvenile specimens share the same dental pattern seen in Taung (erupted permanent M_1); therefore, the juvenile samples and Taung are all at roughly the same developmental stage, even though their chronological ages may differ. The sex of the juvenile individuals is unknown; adult

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TABLE 1. Facial landmarks and their abbreviations

Landmark abbreviation	Description
NAS	Nasion
ANS	Anterior nasal spine
IDS	Intradentale superior
ZYI	Zygomaxillare inferior
FZJ	Frontal-zygomatic junction
SZA	Zygo-temporal superior
MXT	Maxillary tuberosity
PNS	Posterior nasal spine

species samples consist of roughly equal numbers of male and female individuals.

The data set is composed of 36 Euclidean distances, derived from three-dimensional coordinates of eight unilateral and midline facial landmarks that were reliably locatable on both fossil specimens (Ackermann, 1998; Krovitz, 2000) (see Table 1). All landmarks are based on sutural morphology or defined craniofacial features, representing homologous, developmentally based, structures across species. This analysis was restricted to the face, and the number of landmarks was limited because of the incompleteness of the Taung child. The number and distribution of landmarks are sufficient for identifying significant differences among and between the juvenile and adult extant individuals (unpublished results).

We used Euclidean distance matrix analysis (EDMA, a three-dimensional morphometric method) (Richtsmeier and Lele, 1993; Lele and Richtsmeier, 1995; Lele and Cole, 1996; Richtsmeier et al., 1998; Lele and Richtsmeier, 2001) to test for differences in facial shape and growth patterns among the five species. EDMA is a coordinate-system invariant method (Lele and Richtsmeier, 2001) for comparing form, shape, or growth difference between two samples, which uses landmark coordinates as raw data and describes a three-dimensional object by the matrix of Euclidean distances between all possible unique landmark pairs. This matrix of distances is called the form matrix (FM). The form matrix [or FM(A) for object A] is an equivalent representation of the landmark coordinate data that is invariant to the nuisance parameters of translation, rotation, and reflection (Lele and Richtsmeier, 2001).

To evaluate differences in growth, growth matrices (GM) are calculated as the proportional change involved in transforming a juvenile form into an adult form. In other words, growth is the process that acts to change a form through time from configuration A_1 (at time T_1) to configuration A_2 (at time T_2) (Richtsmeier and Lele, 1993). The facial growth pattern between forms A_1 (juvenile) and A_2 (adult) within species A is quantified by calculating a growth matrix for species A, where $GM(A_2,A_1) = FM(A_2)/FM(A_1)$]. A growth matrix is also calculated for species B [$GM(B_2,B_1) = FM(B_2)/FM(B_1)$].

To compare growth patterns between the two species A and B, the like ratios of the growth matrices $GM(A_2,A_1)$ and $GM(B_2,B_1)$ are individually compared as ratios. This strategy results in a growth difference matrix, which is written $GDM(A_2,A_1:B_2,B_1)$ [i.e., $GM(A_2,A_1)/GM(B_2,B_1)$]. To compare shape changes associated with development across differently sized species, samples are size-corrected by the geometric mean (Darroch and Mosimann, 1985; Jungers et al., 1995; Lele and Cole, 1996) of all inter-landmark distances in the mean form matrix.

Nonparametric bootstrapping procedures are used to test the null hypothesis of similarity in shape or growth patterns in paired samples, and confidence intervals are used to localize individual linear distances that differ significantly between samples (Richtsmeier and Lele, 1993; Lele and Richtsmeier, 1995). As these are one-way tests for significance, one of the samples must be chosen as a bootstrap referent; we present our results using both samples as the reference population, except for *A. africanus*, which cannot be used as a reference population because of small sample size. We feel confident interpreting the statistics used in this analysis, despite the absence of information on the statistical power (see Lele and Cole, 1996), because the sample sizes are large and no trouble was encountered detecting significant static juvenile and adult morphological difference (unpublished results). Moreover, the confidence intervals (which factor in sample variability) agree with the null hypothesis tests and allow localization of significant differences in morphology and growth patterns.

To visualize variation in facial shape among these species, we use principal coordinates (PCOORD) analysis, which separates shape variability into independent components (Figure 1) (Richtsmeier et al., 1998). PCOORD analysis is carried out on the mean forms for the extant samples and the *A. africanus* individuals after they have been scaled by the geometric mean of all inter-landmark distances to adjust for potential size differences between samples. First, a dissimilarity metric (Richtsmeier et al., 1998) is calculated for every possible pair of adult and juvenile samples. The dissimilarity metrics are presented in a dissimilarity matrix, which is then subject to eigenanalysis. Each mean form or *A. africanus* individual receives coefficients for the eigenvectors, allowing them to be placed within the shape space on the basis of their original morphology (as re-

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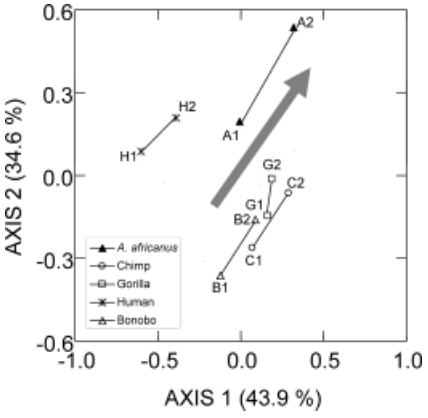

Figure 1. Shape variability for four living and one fossil species. The axes represent variation in the first two principal coordinates (representing 78% of variation) calculated from landmark data for adult and juvenile extant sample means and *A. africanus* individuals. Juvenile and adult samples are labeled as follows: *A. africanus* (A_1, A_2), Bonobo (B_1, B_2), Chimp (C_1, C_2), Gorilla (G_1, G_2), Human (H_1, H_2), and are connected by a line that indicates a "growth trajectory" in shape space. Shape variation is shown by the distance between the trajectories, and differs for each species. The direction of shape change, as indicated by the gray arrow, is generally similar for all species, with the exception of the gorilla. In other words, although the morphology of juveniles and adults in each species is different, the growth patterns (i.e., shape change during later ontogeny) necessary to get from juvenile to adult forms for each species is similar.

flected in the mean form matrix). The first principal axis through the shape space accounts for the greatest amount of variation between samples. The second principal axis explains the next largest amount of variation within the shape space, and so on, to the last principal axis. The number of potential axes equals the number of samples minus one, although most variation within the sample is usually explained by the first few axes, as is the case here. Correlations between the original inter-landmark distances and the eigenvector coefficients allow interpretation of the principal coordinate axes in terms of original morphology. Shape differences that are important in separating individuals along a given principal axis are indicated by high positive or negative correlations for those particular linear distances. A more detailed description of this particular application of PCOORD for EDMA can be found in Richtsmeier et al. (1998).

Inter-species comparisons of juvenile facial shape among all five species indicate that significant differences in facial shape are established by the eruption of the first permanent molar and that these differences persist into adulthood. Additionally, the results of growth difference comparisons between the five species show, with one exception, similar postnatal growth patterns in all species (see Supplementary Table S1, which is available online at *The New Anatomist* Web site through *Wiley InterScience*: www.interscience.wiley.com/jpages/0003-276X+/suppmat/index.html). The exception is that growth difference comparisons between gorillas and other extant species are significant at either $P = 0.10$ or $P = 0.05$ level when the other extant species are used as the bootstrap referent. This finding indicates either unique qualities in the gorilla facial growth patterns, or increased variability in the gorilla sample. To test whether this finding is simply reflecting differences in patterns of sexual dimorphism between the gorillas and the other extant species, separate principal coordinate analyses are performed for juveniles and male adults, and for juveniles and female adults. Both of these analyses produced similar results, suggesting that the facial growth pattern observed in gorillas is not simply due to increased sexual dimorphism in the gorilla sample (see Supplementary Figure S1, which is available online at *The New Anatomist* Web site through *Wiley InterScience*: www.interscience.wiley.com/jpages/0003-276X+/suppmat/index.html).

Importantly, this may demonstrate a unique pattern of facial growth for gorillas, possibly lending morphological support for the molecular data indicating a chimp/human clade to the exclusion of gorillas (Ruvolo, 1997). There is no significant difference between facial growth in *A. africanus* and any of the four extant species.

Although statistical comparisons of growth for each linear distance (Figure 2) confirm similar patterns of growth in these five species, there are specific regions where growth patterns differ. Nonparametric confidence intervals (Lele and Richtsmeier, 1995) calculated for each pair-wise growth difference matrix comparison indicate individual linear distances that differed significantly between samples. Deviations from the overall pattern of growth similarity are illustrated in Figure 3. Humans and *A. africanus* have relatively more anteroposterior growth in the maxilla, whereas *A. africanus* shows decreased

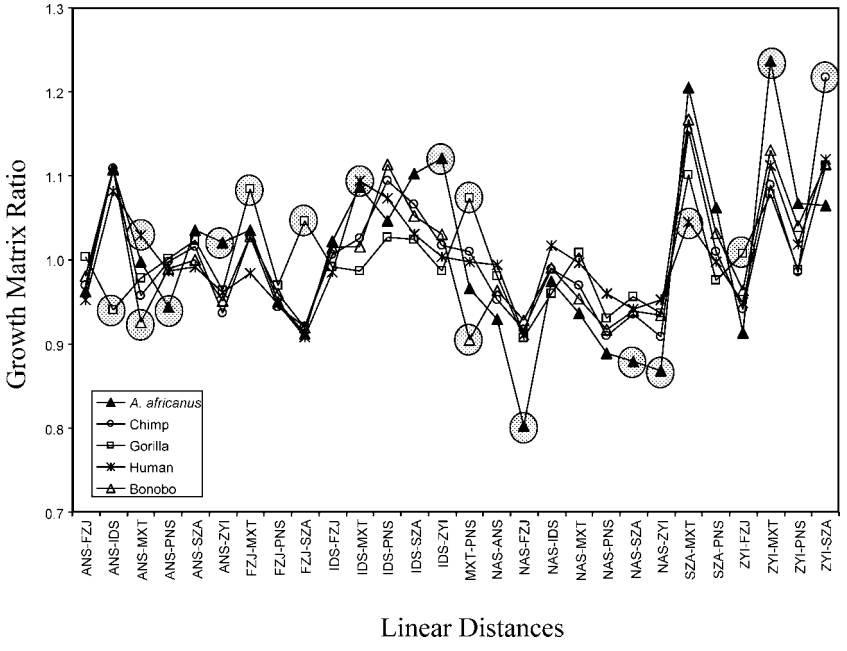

Figure 2. Growth ratios (y-axis; the ratio of the adult inter-landmark distance to juvenile inter-landmark distance) are presented for each linear distance (x-axis) for the five species. Linear distances that are significantly different in at least three of four pair-wise growth difference matrix comparisons for each species are indicated with a shaded circle. This method details the similarity among species growth patterns.

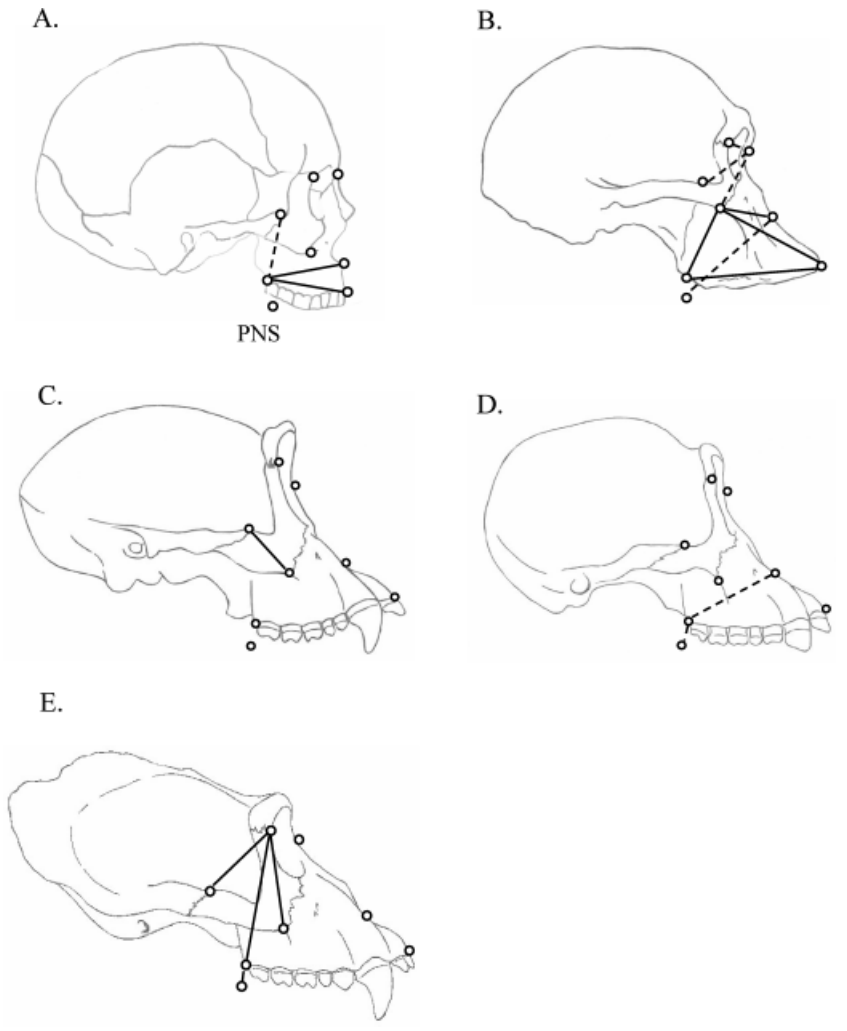

Figure 3. Euclidean distance matrix analysis growth difference comparisons between species. Linear distances that are significantly different in at least three of four pair-wise growth difference matrix comparisons are shown for (**A**) human, (**B**) *A. africanus,* (**C**) chimp, (**D**) bonobo, and (**E**) gorilla. Solid lines indicate relatively more growth, whereas dashed lines indicate relatively less growth compared with the other species. Because landmark PNS is not visible in this lateral view, it is shown below the third molar, as indicated.

growth in upper facial breadth. Conversely, gorilla growth is relatively increased in the zygomatic region, perhaps due to the association between this region and bulky chewing muscles. Chimpanzees show increased growth through the zygomatic, whereas bonobos grow relatively little in the anterior-posterior dimensions of the midface. The increased similarity among humans and australopithecines relative to the great apes may indicate that as early as three million years ago (Vrba, 1982; Delson, 1988), human ancestors were already demonstrating some human-like aspects of facial growth.

To summarize, these results indicate that, although there are some differences in growth among these species, the growth patterns after the emergence of the first molar are remarkably similar (with the possible exception of the gorilla) and contribute less than might be expected to the final adult form. Instead, the differences in form seem to be largely in place before this juvenile stage.

HYPOTHETICAL MORPHOLOGY AS AN INDICATOR OF GROWTH SIMILARITY

Because these results were surprising, we further explored the relative influence of juvenile morphology and growth patterns on adult facial shape by creating simulated "hypothetical" adult forms. This approach is accomplished by "growing" the juvenile sample of one species (the juvenile form species) by the facial growth patterns of another species (the growth matrix species) to create adult forms (Richtsmeier and Lele, 1993). Normal growth in a species A is defined by the growth matrix $GM(A_2,A_1)$, which is created by dividing each element in the adult mean form matrix $FM(A_2)$ by the corresponding elements in the juvenile mean form matrix $FM(A_1)$. To simulate what an adult of species B would look like if it grew with the growth pattern of species A, the elements of the juvenile mean form matrix of species B, $FM(B_1)$, are multiplied with the corresponding elements in the growth matrix of species A, $GM(A_2,A_1)$. The resulting simulated adult form $SFM(B_2)$ was scaled by the geometric mean of all inter-landmark distances, and then compared with observed adult samples of species A (the growth matrix species) and species B (the juvenile form species). Further detail on the creation and validation of simulated forms is found in Richtsmeier and Lele (1993). If the simulated (hypothetical) adult is most similar to observed adults of the juvenile form species then species-specific juvenile facial shape is having a substantial influence on adult facial shape. However, if the simulated adult is more similar to the growth matrix species, then species-specific facial growth patterns largely influence adult facial shape.

Simulated forms were produced by using all possible combinations of growth patterns and juvenile facial morphologies of the five species, resulting in 20 different simulated adult forms. By using EDMA, facial shape was then compared between the simulated adults and the observed adult samples of the juvenile form species and the growth matrix species and significance was assessed (Lele and Richtsmeier, 1995) (see above). None of the simulated adults differ significantly in facial shape from the observed adult samples of the juvenile form species, whereas many simulated forms are significantly different from the observed adult samples of the growth matrix species (see Supplementary Figure S2 and Supplementary Table S2, which are available

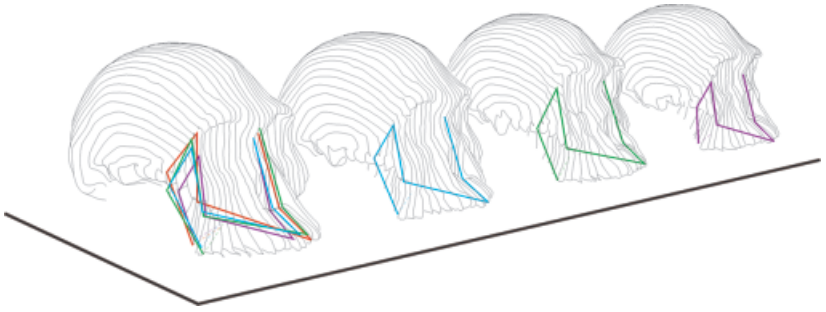

Figure 4. Three-dimensional representations of (left to right) actual *A. africanus* adult (Sts 5), and simulated adult forms of *A. africanus* grown with chimpanzee, gorilla, and human growth matrices. Colored lines pass through facial landmarks unilaterally and represent simplifications of form differences in *A. africanus* (red), chimp-grown *A. africanus* (blue), gorilla-grown *A. africanus* (green), and human-grown *A. africanus* (purple). The first cranium (left) shows all four form lines superimposed on Sts 5; the next three illustrate the necessary modifications of the face of Sts 5 in three-dimensions to "fit" the colored line for the differing simulated forms. (No alterations were made to the neurocranium, as it was not part of the analysis.) Note that, although the facial form varies among these individuals, the differences are moderate, and not unlike those seen within the species *A. africanus*, illustrating how little applying different patterns of growth affects the final morphology of the adult hominid. Note: These representations are for illustrative purposes only—they were created by using NURBS modeling software (Rhino 1.1), where a point or region can be "pulled" in three dimensions, creating virtual distortion or sculpting of a three-dimensional form.

online at *The New Anatomist* Web site through *Wiley InterScience*: www.interscience.wiley.com/jpages/0003-276X+/suppmat/index.html). This indicates that no matter which hominoid growth matrix is applied, the simulated form still most closely resembles the observed adult sample of the starting species (see Figure 4).

DEVELOPMENTALLY EARLY DETERMINANTS OF FACIAL SHAPE

Two important conclusions can be drawn from the results of these analyses. First, overall adult facial shape is already largely determined by time of the eruption of the first permanent molar tooth. Eruption of the first permanent molar is an important developmental event, as this usually defines the end of the infancy period, and is highly correlated with measures of life history (Smith, 1991). Certainly there are taxon-specific patterns of change that occur during later developmental processes, but those changes do not alter the basic species-specific facial shape. This finding suggests that morphological differences between species result from early (infant or possibly prenatal) ontogenetic processes. Changes in the developmental timing, spatial locations, or sizes of intramembranous or cartilaginous craniofacial growth centers could create species-specific facial morphology quite early. Because the cranial base also influences facial form (Lieberman et al., 2000), it is possible that many facial differences seen in adult apes and humans are the result of processes driving basicranial growth and flexion in prenatal or early postnatal ontogeny. Identification of differences in prenatal or early postnatal patterns of growth could provide important clues regarding the kinds of genetic changes responsible for morphological diversification. Additionally, the results suggest that maternal factors could play a bigger role in evolutionary diversification than previously thought. Overall, these results lend support to arguments that ontogenetically early differences in timing or rate of growth drive evolutionary diversification in the hominid lineage (Richtsmeier and Walker, 1993; Krovitz, 2000; Ponce de León and Zollikofer, 2001).

Second, although there are minor developmental differences among humans, chimps, gorillas, bonobos, and *A. africanus* after the eruption of the first permanent molar, the level of overall growth similarity is striking. In fact, these later growth patterns are so similar that applying differing species growth patterns does not alter the unique aspects of the starting species' overall form. One possible exception is the gorillas, whose growth patterns differ somewhat; this divergence may provide much-needed morphological corroboration of the emerging molecular evidence which links humans and chimps to the exclusion of gorillas (Ruvolo, 1997). But for *H. sapiens*, *Pan*, and *A. africanus*, it appears that juvenile growth plays a relatively minor role in determining final adult facial morphology. Richtsmeier and Walker (1993) arrived at similar conclusions in their study of adolescent facial growth in *H. ergaster*, *H. sapiens*, and *Pan troglodytes*, and concluded that such patterns might indicate the establishment of recognizable species traits early in ontogeny and a more generalized pattern of primate facial growth (see also Cheverud and Richtsmeier, 1986; Corner and Richtsmeier, 1992). Our results support those findings and suggest that common facial developmental patterns extend further back in evolutionary time (to include the type species of *Australopithecus*), ontogenetic time (to include younger juveniles), and more broadly among living primates (to include *Pan paniscus*). It is not surprising that similar juvenile developmental patterns exist among great apes (Shea, 1983) or among later members of the genus *Homo* (Krovitz, 2000; Ponce de León and Zollikofer, 2001), given each groups' close morphological resemblance and phylogenetic relationship. What is surprising is that a shared pattern of juvenile facial development is more widespread among the hominoids, possibly representing either the primitive condition for the African great ape/human clade, from which gorillas diverged, or the derived condition of the *Pan*/human clade. The remarkable similarity in ontogenetic pattern across the human and *Pan* lineage seems to point toward ancient unifying principles of facial growth and development in this clade, and makes research into species-specific differences that occur in early ontogeny a priority for understanding human evolution.

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