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Comparative ontogeny in humans and chimpanzees: Similarities, differences and paradoxes in postnatal growth and development of the skull

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Summary. The hypothesis of retarded development is a classic and controversial issue in human evolution. It depends directly on the understanding of ontogenetic trajectories and their basic constituents: timing, rate and associated patterns of maturation. In the present study, we applied geometric morphometrics to investigate postnatal ontogeny in human and chimpanzee skulls (N = 302). We evaluated postnatal ontogenetic rates, based on comparisons of properties of size and shape in adults. At different dental ages the percentage of the adult mean size (growth) and adult mean shape (development) was used to quantify patterns of maturation. We found significantly higher levels of ontogenetic maturity in humans than chimpanzees during pre-M1 and M1 eruption. However, during this ontogenetic period the human increments were lower than those of chimpanzees suggesting lower rates. During and after M2-eruption species did not differ in their ontogenetic trajectories. The results indicate that higher prenatal and lower peri- and postnatal maturation rates characterize human ontogeny when compared with chimpanzees. If mandibular ontogeny is considered alone, a paradox was found. Whereas growth maturation proceeded in an expected trajectory continuously approximating 100% adult mean size, developmental maturity was different. After M1-eruption in both species the morphological distance, which had increased before, became reduced again, and reached adult mean shape in a second developmental peak. Such a tendency was found in humans and chimpanzees. This indicates that both size and shape maturation must be considered to understand the complexity of postnatal mandibular ontogeny.

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Introduction

One important component of phylogenetic changes in morphology is the evolutionary modification of ontogenies (Riedl 1975; Gould 1977; Raff 1996). It is an internal source for morphological variation upon which natural selection can act (Riedl 1975; Alberch 1990; Raff 1996). Heterochrony describes the evolution of ontogeny by modifications in the rate and timing of important constituents of ontogenetic trajectories, such as onset, offset and rates of growth and development (Zelditch and Fink 1996; Zelditch et al. 2003). Such parameters are intimately linked to patterns of maturation and the resulting morphologies (Gould 1977; Alberch et al. 1979; McKinney and McNamara 1991). Heterochrony is thus a key issue in research connecting ontogeny and phylogeny and led to the current prominent role of evolutionary development in evolutionary theory (Arthur 2002).

In human evolution, a specific case of heterochrony i. e., the retardation in development, or "neoteny" (Gould 1977), has been postulated. Similarly, its earlier version of "Fetalisation" *sensu* Bolk (Gould 1977) has attracted considerable, albeit polemic interest in primatology (Kummer 1952; Biegert 1957; Starck and Kummer 1962; Gould 1977; Shea 1989; Bastir 2004). While some authors found evidence that favored neoteny (Gould 1977) others have argued against it (Kummer 1952; Starck and Kummer 1962; Shea 1989).

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This hypothesis of neoteny grounds on the morphological similarity between newborn and juvenile chimpanzees and adult humans. The juvenile chimpanzee-adult human similarity was observed early in anthropology, but Gould (1977) elaborated a theoretical framework for quantitative tests. Based on this he concluded that the rate of human development is characterized by general retardation relative to chimpanzees (Gould 1977).

However, recent research has seriously challenged this hypothesis (Shea 1989; McKinney and McNamara 1991). The specific biphasic pattern of human ontogeny is characterized by an early acceleration during fetal growth and development and a prolongation of this period into the first two years of life, followed by a period of retardation and slower ontogeny in later postnatal life (McKinney and McNamara 1991; Godfrey and Sutherland 1996).

Klingenberg (1998) clarified factors of potential confusion in the debate of human heterochrony. His emphasis is on the word "retardation", which he considers "responsible for much of confusion" (Klingenberg 1998:94) and may relate either to the slowing of rate (as a continuous scalar process) or the delay of development (as a discrete event) along a given time scale. This definition is rarely made clear in literature but it is specifically important regarding the morphological changes attributed to a given developmental period.

In an ontogenetic sequence "A–B–C", in which "A" is related to brain growth and "B" to facial growth (see Biegert 1957; Enlow and Hans 1996), any effect yielding an increased morphogenetic net effect (higher rates, but also sequentially delayed – and thus prolonged – morphogenesis) in phase "A" will produce skull morphologies, basically characterized by brain growth. The result may be considered peramorphic, as the earlier effect becomes over-expressed, or paedomorphic as the important morphological influence simply occurs "early" with respect to later ontogeny ("B").

In the light of the human biphasic ontogeny the precise heterochronic diagnosis "Neoteny" versus "Hypermorphosis" becomes thus relative. Depending on the ontogenetic phase taken, humans are either 1) accelerated (higher rate) compared to chimpanzees during fetal ontogeny or 2) retarded (slower rate) relative to chimpanzees in postnatal ontogeny (Klingenberg 1998).

Both aspects of this hypothesis will be tested in Hypothesis 1 (H1) that predicts higher maturity rates in humans than chimpanzees in early postnatal ontogeny. There is, however, another aspect in Gould's (1977) hypothesis of neoteny, which is not relative. It postulates dissociation of size and shape, with retarded shape during sexual maturation. This hypothesis predicts that, during the time of sexual maturation (a precise ontogenetic stage), decreased values of maturity resulting from decreased rates should be expected for neotenic humans as a consequence of their retarded (*sensu* Gould 1977) rates. This is the second hypothesis (H2) tested in this study.

Both hypotheses will be tested on cranio-mandibular data. However, ontogenetic morphological relationships will be explored also for mandibles alone. This is of general interest because heterochrony is also relevant in another aspect of human evolution. It has been suggested that hypermorphosis (i. e., the extension of common ontogenetic trajectories beyond ancestral adults in either time or rate; Shea 1989) of Middle Pleistocene mandibles could be involved to some degree in the evolution of Neandertals (Rosas 2000; Rosas and Bastir in press).

Material and Methods

The major part of the human sample (adults and juveniles, $n_{total} = 215$) is housed at the Institute of Anthropology, University of Coimbra, Portugal (Rocha 1995) and in part (juveniles) at the Anthropological Department of the Natural History Museum, London (Spitalfields collection; Molleson et al. 1993). The age at death and sex is known for the complete human sample.

The chimpanzee sample ($n_{total} = 87$) is housed at the Department of Mammals, Natural History Museum, London. Sex of the adult specimens and age at death was evaluated by craniodental criteria by one of us (MB) and the juvenile chimpanzees were treated without sexual attribution. The human and chimpanzee data were divided into five age-classes based on the criteria of Shea (1989). The human sample consisted thus of eight individuals of the Pre-M1 group, thirteen of M1, nine of M2, and nine of M3 group and 177 adults and the chimpanzees comprised fourteen individuals of the Pre-M1 group, thirteen of M1, eight of M2, three of M3 group and 48 adults.

Three-dimensional coordinates of 29 common cranio-mandibular landmarks were digitized using a Microscribe 3DX© digitizer. Definitions of the landmarks and details about data acquisition, 3D-2D data conversion and missing data treatment for geometric morphometrics have been described elsewhere (Rosas and Bastir 2002).

Geometric morphometric methods. Procrustes based geometric morphometrics of landmark data are based on the separation of shape and size. These two essentially different kinds of variables are obtained by Procrustes superimposition, in which effects of specimen orientation are minimized and scale factors are sequestered (Rohlf and Slice 1990; Bookstein 1991). The 2D coordinate data of each species were converted into a partial warp and uniform component scores matrix (Bookstein 1991; Rohlf 1996). These shape descriptors are derived from thin plate spline (TPS) analysis and contain the full-coverage shape information, whereas size (centroid size) is documented as a common scaling factor (Bookstein 1991). Centroid size is the square root of the sum of squares of the distances between each landmark and the centroid of the form (Bookstein 1991).

Patterns of maturation rates. Recent geometric morphometric studies in primatology improved our morphological understanding of postnatal growth and development (O'Higgins et al. 2001; Ponce de Leon and Zollikofer 2001; Viðarsdóttir et al. 2002). Growth is defined by the ontogeny of size, whereas development is defined by the ontogeny of shape (Gould 1977; Hingst-Zaher et al. 2000; Zelditch et al. 2003).

As maturity is reached in the adult developmental stage, maturity degrees of size at a given dental age group can be calculated as a percentage of the mean centroid size of the adult subsample (which is set to 100% in the adults). Rates of growth are thus measured as the ontogenetic increment of the percentage of

Table 1. Non-parametric mean comparisons of maturation percentages (Mann Whitney U-test; Sokal and Rohlf 1998)

Category	*System*	*Dental ages*	*humans*	*chimpanzees*	*difference (p)*
Growth	Skull	Pre-M1	77.89	66.68	0.00006
		M1	88.8	78.89	0.0004
		M2	92.01	90.36	0.2
		M3	97.46	95.1	0.1
	Mandible	Pre-M1	91.14	87.29	0.00014
		M1	95.79	92.86	0.00043
		M2	97.17	97.27	0.9
		M3	99.6	97.98	0.3
Development	Skull	Pre-M1	40.14	27.94	0.1
		M1	66.49	53.86	0.019
		M2	72.95	70.53	0.6
		M3	95.72	90.4	0.5
	Mandible	Pre-M1	58.01	51.8	0.4
		M1	80.01	83.88	0.8
		M2	69.75	68.15	0.7
		M3	100.1	85.56	0.3

adult mean centroid size for each species. As both species will terminate their ontogenetic trajectories at 100% of adult size, species differences in the percentage of adult size at a given dental age group can be interpreted as the result of differences in their growth maturation rate.

The same principle is applied to the evaluation of the rates of maturity of shape, which is, however, more difficult to measure. In a recent paper, Zelditch and colleagues (2003) have proposed a method in which shape maturity was measured as the Procrustes distance from the mean of the youngest group to the mean of the adults. Procrustes distance is the metric that defines Kendall's shape space (i. e., the conventional distance measure in Procrustes geometric morphometrics; Bookstein 1996). Procrustes distance can be imagined as the geodesic (angular) distance in curved shape space between two Procrustes superimposed landmark configurations, which correspond to two points at the surface of the hyperhemispherical shape space of Kendall (Bookstein 1996; Slice 2001). In a given set of Procrustes superimposed data this distance is correspondingly smaller the closer the specimens are located to the reference configuration, where the distance is zero. All configurations that plot along a circumference whose center is the reference configuration will show identical Procrustes distances. These configurations have been termed "shape-manifolds" (Bookstein 1991:181). If the reference is the mean of the youngest specimens, Procrustes distance increases as shape differentiates away from the least developed age toward the adults, where this distance is largest (Zelditch et al. 2003). Thus, the mean value of Procrustes distance in the adult sample indicates maturity of shape, whereas its ontogenetic increase is the result of the rates of maturation in shape (developmental, skeletal maturation) (Zelditch et al. 2003).

In geometric morphometric theory there have been important comments regarding the choice of the reference configuration (Rohlf 1998). It is generally recommended to use the grand mean shape of a sample resulting from a generalized least square Procrustes superimposition (Rohlf and Slice 1990) in order to "minimize the errors in the approximation of shape space" (Rohlf 1998: 149) to tangent space. However, if the correlations between the distances in shape space and the corresponding distances in Euclidean tangent space (where multivariate statistics are carried out) are high, the use of an alternative reference is justified. This was tested by Regress 6 + Beta (Sheets 2001). The high correlations [in chimpanzees: r = 0.999989 (skull), r = 0.999998 (mandible); in humans r = 0.9999915 (skull), r = 0.999995 (mandible)] support our approach.

The maturation patterns in both size and shape are analyzed as the ontogenetic trajectory described by the percentage of group specific means of the adult mean values. Linear postnatal ontogenies are assumed (O'Higgins et al. 2001; Ponce de Leon and Zollikofer 2001; Viðarsdóttir et al. 2002) and thus least square regressions were used to calculate the Procrustes distances from the mean shape of the smallest five individuals of the youngest group. These distances were calculated separately for each species by Regress6 software (Sheets 2001). Then, the mean value of Procrustes distance of the adults was set to 100% and for each specimen its percentage of the adult mean was calculated. The ontogenetic modification of this percentage across the dental age groups reflects thus the patterns of maturation.

A Kolmogorov Smirnov test (Sokal and Rohlf 1998) indicated that a normal distribution could not be assumed. Therefore non-parametric statistical analyses were necessary that do not make any assumptions on a given (e. g., normal) distribution. We used Mann-Whitney U-tests (Sokal and Rohlf 1998) for mean comparisons to test the hypotheses of species differences in maturity levels in corresponding dental age groups, which is the non-parametric analogue to Student's t-test (Sokal and Rohlf 1998). Means shapes were compared by Two-Group6 (Sheets 2001).

Results

Skull maturation. The results indicated that H1 is supported. Table 1 shows that both ontogenetic parameters displayed increased values, growth maturity (size) during preM1- and M1-eruption, developmental maturation (shape) only during M1-eruption (see also Fig. 1 a, b). Absence of significant differences during and after M2 eruption suggests that H2 is not confirmed. The morphological changes are depicted in Figure 2.

Mandibular maturation. While mandibular growth maturation (Fig. 1 c) showed similarity to the skull (Fig. 1 a)

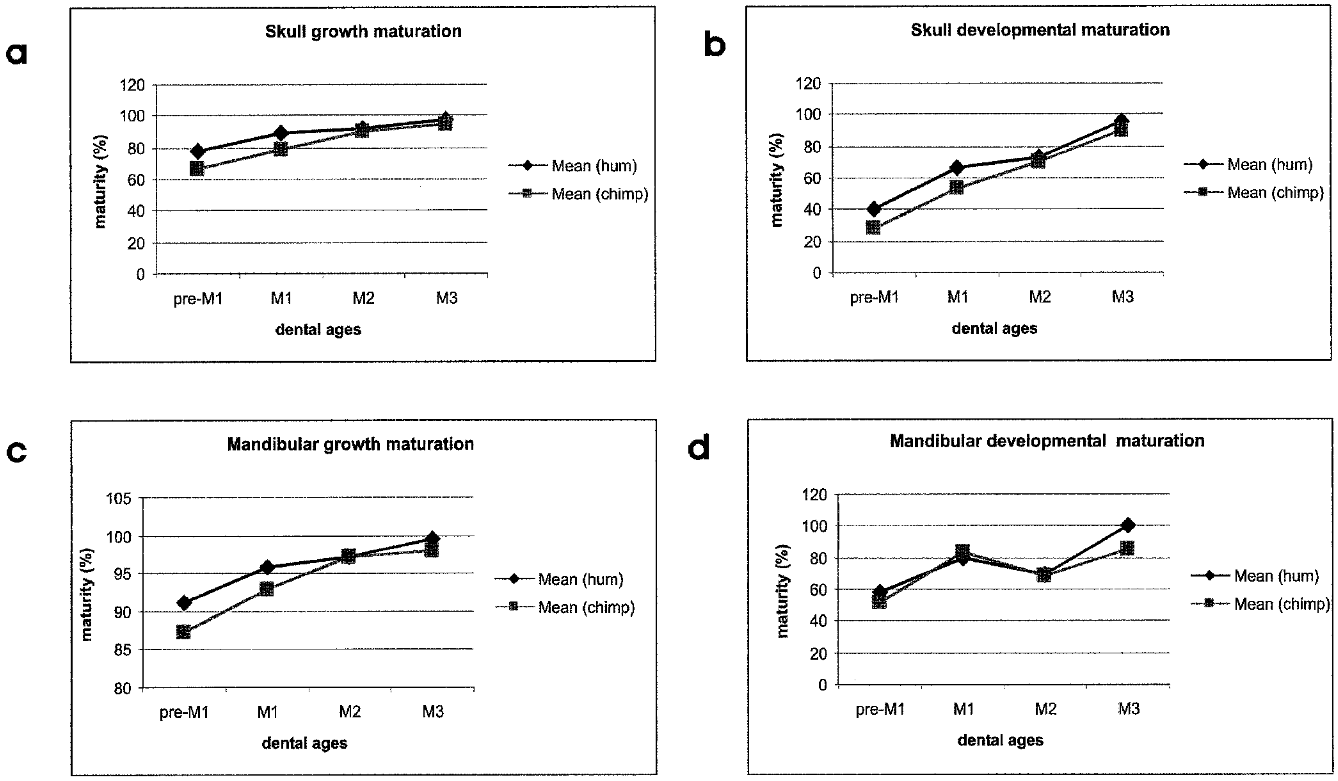

Fig. 1. Species-specific postnatal trajectories of maturation patterns. (a) skull growth, (b) skull development, (c) mandibular growth, (similar to skull growth) (d) mandibular development (paradox). Human skull maturation is characterized by increased levels of growth and development before M2-eruption. Afterwards no differences exist. Mandibular growth is similar to skull growth while mandibular development is peculiar. In both species shape shows decreased maturity levels during sexual maturation.

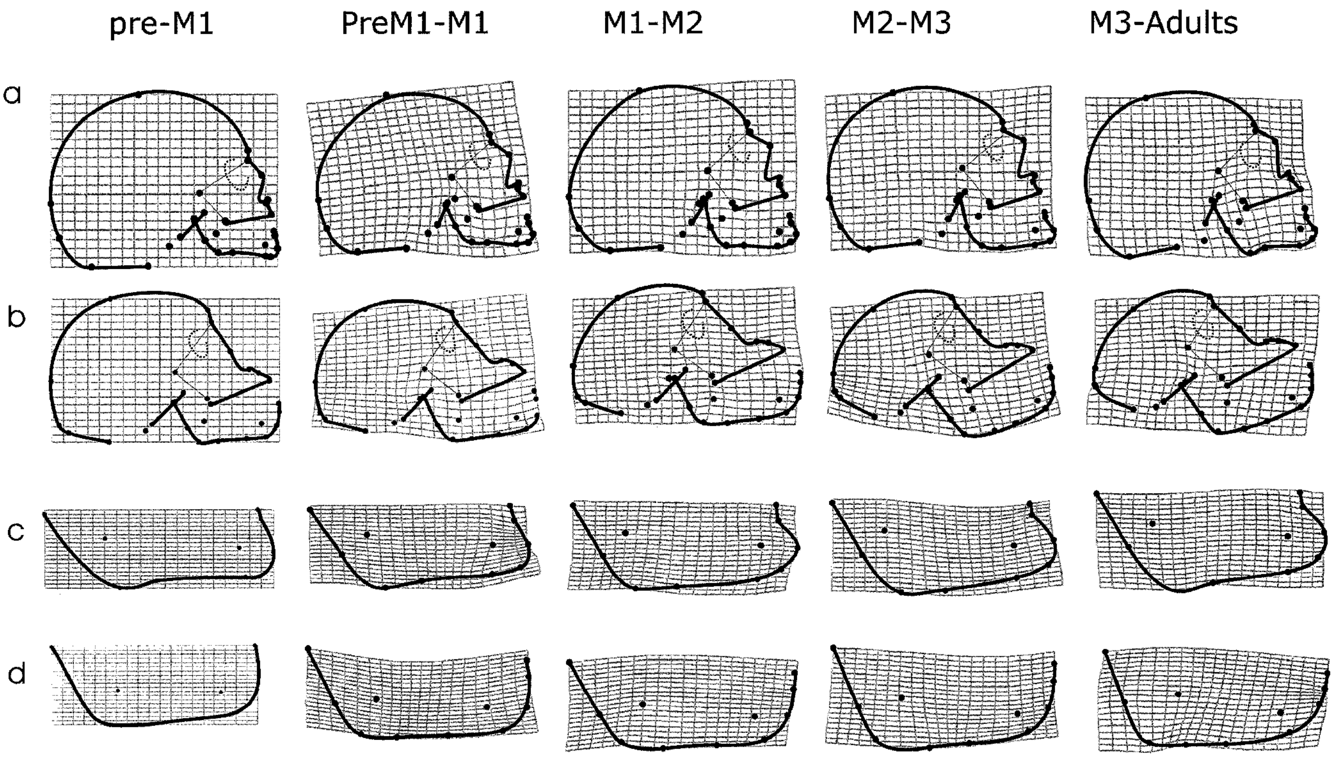

Fig. 2. Age-specific ontogenetic shape changes as TPS deformations of the younger into the next older developmental stage. (a) humans skulls, (b) chimpanzee skulls, (c) human mandibles, (d) chimpanzee mandibles. Each developmental stage is characterized by significant specific morphological changes, which in sum add to the adult morphological picture (additive morphogenesis). Note however, that stage-specific difference are also influenced by individual non-ontogenetic variation within each group.

the patterns of developmental maturation were different to skull development and remarkably similar between both species (Table 1, Fig. 1 d).

Discussion

The present study investigated patterns of maturation by comparing corresponding dental age stages of skull ontogenies of humans and chimpanzees. Specifically, we tested heterochronic hypotheses of the early (fetal) acceleration of humans with respect to chimpanzees (H1) (McKinney and McNamara 1991) and later postnatal (neotenic) retardation of human shape with respect to size, compared with chimpanzees (H2) (Gould 1977). Further, we explored specific geometric morphometric techniques for future application in skulls and mandibles of hominid fossils.

The increased maturity levels of both growth (pre-M1, M1) and development (M1) in humans are compatible with the hypothesized fetal and early postnatal ontogenetic acceleration as suggested by McKinney and McNamara (1991). However, when percentages of the adult value are measured (which, in humans, in the case of neoteny, were decreased) it would be still possible that the increased earlier maturity levels arose from retarded late postnatal growth. Nevertheless, Table 2 shows that this is not the case, because later developmental stages at M2 and M3 are indistinguishable between humans and chimpanzees. These findings lend thus support to the interpretation that the differences in skull maturation patterns prior and during M1 eruption, a period that is markedly influenced by brain maturation (Smith 1989), is a consequence of early acceleration related to brain growth (Biegert 1957; Shea 1989; McKinney and McNamara 1991, and references therein).

Figures 1 a and b indicate also that human growth and developmental rates decrease in early postnatal ontogeny compared to chimpanzees particularly between M1 and M2 dental age. While humans during M1-eruption were significantly more mature than chimpanzees, during M2-eruption no such difference existed anymore, which is a result of increased slopes in chimpanzees during these stages. From a biological view, such ontogenetic patterns reflect general mammal life history patterns that contrast altricial (humans) and precocial (chimpanzees) characteristics (Zelditch et al. 2003).

If the differential increment of relative maturity in growth and development from one dental age group to the subsequent one is taken as representative for the rates between those dental age groups, our data show that at least three different periods should be considered comparing humans and chimpanzees. During an early stage, (pre- and perinatal) humans display accelerated ontogenetic rates. That is an important aspect, because it was already mentioned that this life history period is most closely related to early and intensive cerebral maturation. Hypotheses of early epigenetic developmental cascades of craniofacial components and their interactions as outlined in the craniofacial levels of Enlow and colleagues (Enlow et al. 1971; Enlow and McNamara 1973; Enlow and Hans 1996) receive considerable support in a morphogenetic perspective. These authors suggested a spatiotemporal sequence of maturation of craniofacial components for humans. According to their principles of growth- counterparts the spatial conditions set by the mature brain and the basicranium determine the potential growth fields for nasomaxillary and mandibular structures, which mature much later. These "craniofacial levels" are defined by different timings of maturation (Enlow and Hans 1996: 14; Bastir 2004). However, endocranial data should be studied for an appropriate geometric morphometric evaluation of such hypotheses (Bastir et al. 2004). A second ontogenetic phase is the juvenile period prior to M2 eruption, the time of sexual maturation. During this period humans are characterized by lower rates compared to chimpanzees, which show maturation rates that appear to make up the difference resulting from human fetal acceleration (Figs. 1 a, b). During sexual maturity and somatic maturation (M2 and M3 eruption; Smith, 1989), no further differences are observed in maturation patterns, which implies that H2 does not receive support (Tab. 1). This period could be considered a third ontogenetic phase and it may be an interesting detail with some predictive connotations to note that when this phase starts both species have achieved approximately 90% of adult skull size and 70% of adult skull shape.

The fact that at least three different phases in ontogenetic trajectories of humans and chimpanzees can be distinguished is a strong argument against a "generalized" retardation and in line with other studies (Shea 1989; Raff 1996). This is relevant because it has been suggested that explaining morphological changes by "numerous local heterochronies is both to lose the elegance of a global heterochronic explanation and potentially to obfuscate the causes of the complex changes in pattern" (Raff 1996: 289). Raff (1996) also suggested that more important than to determine the specific heterochronic category might be to investigate whether temporal aspects of morphogenesis are the proximate causal mechanisms of modifications of the developmental process. This causality, however, is questionable because craniofacial ontogeny is a 4D process and necessarily occurs along a temporal axis. Thus, most evolutionary modifications of development may cause some kind of shifts of developmental events along this axis. But developmental processes others than heterochrony, namely spatial integration, dissociation and constraints occur during evolution (Kummer 1952; Raff 1996; Zelditch and Fink 1996; Bastir 2004; Bastir and Rosas 2004; Bastir et al. 2004; Rosas and Bastir in press). Viewed from the temporal perspective, they may appear as heterochronic modifications, but these need not necessarily be the causal origins of the observed morphological changes (Raff 1996).

Figure 2 shows that each ontogenetic stage is characterized by a typical pattern of morphological modification. By additive morphogenesis each ontogenetic stage becomes successively morphologically integrated into subsequent stages with different morphogenetic effects. This continues until finally maturity of size and shape is yielded as the sum of all particular morphogenetic events. If this hypothesis is correct, then representations of ontogenetic developmental trajectories as linear models may not reflect all the information. Specific ontogenetic stages are possibly characterized by specific processes, which have been reported recently in mammal skull development (Zelditch et al. 2003). This needs further investigation in primate skulls.

Particularly the mandibular ontogenies can be interpreted in this non-linear perspective as they show a paradox trajectory. In both species after an increase in developmental maturity from Pre-M1 to M1 a decrease from M1 to M2 is observed (Fig. 1 d). This may relate either to mandibular growth rotations and associated remodeling processes (Skieller et al. 1984; Björk 1991) producing similarities in shape between those stages or to some properties of Kendall's shape space (Slice 2001). Curvilinear mandibular ontogeny could produce mandibular "shape-manifolds" (Bookstein 1991: 181) with identical Procrustes distances to the reference (Pre-M1 and M2, Fig. 1 d) but with different morphologies (Figs. 2 d).

Although more investigation is necessary to shed light on these problems this study discovered triphasic skull ontogenies in humans and chimpanzees. While the present method can be used to investigate heterochrony in skulls, its application to hominid mandibles, particularly the maturation of shape, requires some caution.

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