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Ontogeny and phylogeny of the cercopithecine cranium: A geometric morphometric approach to comparing shape change trajectories

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ABSTRACT

While the analysis of ontogenetic trajectories is common in geometric morphometrics (GM), the simultaneous comparison of several trajectories can be unwieldy and is, in some cases, unable to make use of one of the main advantages of GM, visualization. Furthermore, due to the paucity of the paleontological record, analyses of trajectories are often limited to extant taxa. We address these issues by presenting a method for visualizing the similarities and differences of cranial ontogenetic trajectories among taxa and a method for reconstructing ancestral ontogenetic trajectories, so that these differences can be investigated in a phylogenetic context. We also tested for the presence of phylogenetic signal in the ontogenetic trajectories themselves. Using an ontogenetic series of 522 crania, representing 17 cercopithecine species from 8 genera, we first calculated ontogenetic trajectories of cranial shape change for each species, and then entered these trajectories into a principal components analysis to produce a developmental shape-change trajectory PCA (δ PCA). Then, through an augmentation of the phylomorphospace approach, we projected a molecular phylogeny onto the major axes of trajectory shape variation from the δ PCA to produce an ‘ontophylomorphospace,’ using squared-change parsimony to reconstruct interior nodes. Through these procedures, we were able to determine that the δ PCAs illustrate patterns of variation in these developmental trajectories in a visually intuitive manner that allows for easier comparisons among taxa. Through examination of the ontophylomorphospace, we found that African papionins exhibit extensive homoplasy in the evolution of cranial ontogenetic trajectories, and that Asian species of *Macaca* show highly derived ontogenetic trajectories relative to other cercopithecines. Additionally, we found no support for the presence of a phylogenetic signal in cranial ontogenetic trajectories. The δ PCA and the ontophylomorphospace are ways in which to visualize and compare complex, multivariate shape transformations, both among extant taxa and over evolutionary time, respectively.

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1. Introduction

Investigations of the morphological aspects of growth and development have increased in number and in sophistication in recent decades. In part, this increase is due to the appreciation that evolutionary changes in adult form are the consequence of changes to the ontogenetic routes that lead to that form (Gould, 1977; Hall, 2003; Zelditch et al., 2004; McNulty, 2012). The availability of advanced methodologies for data collection (e.g., 3D digitizers and scanners) and analysis (typified by the ‘geometric morphometric

revolution’; Rohlf and Marcus, 1993; Adams et al., 2004) have also provided researchers with improved means to quantify and evaluate relationships between ontogeny and biological form. Investigations of ontogeny incorporating these methods have proven to be useful in a broad array of analyses, including: prediction of adult morphologies from juvenile specimens (Ackermann and Krovitz, 2002; McNulty et al., 2006; Singleton et al., 2010, 2016), estimation of the morphology of adult specimens were they to continue further along their ontogenetic trajectory (Singleton, 2012), and investigations of the evolutionary changes along extinct lineages (Simons and Frost, 2014). Additionally, ontogenetic investigations further aid in identifying the influence of allometry on shape, and can reduce the inclination to produce adaptive scenarios to explain particular cranial shapes that are in fact the

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byproduct of selection for body size (Ravosa and Profant, 2000; Marroig and Cheverud, 2005; Gilbert, 2011; Singleton, 2013). Thus, an ontogenetic perspective contributes to investigations of morphology, especially when coupled with advanced methods of shape analysis, as in geometric morphometrics.

Landmark-based geometric morphometrics is a type of statistical analysis that investigates the shape variation of landmark coordinates after factors of non-shape variation have been held constant, while also preserving the geometry of these coordinates (Bookstein, 1991; Rohlf and Marcus, 1993; Dryden and Mardia, 1998; O'Higgins, 2000; Frost et al., 2003; Slice, 2007; Mitteroecker and Gunz, 2009; Baab et al., 2012). A major benefit of geometric morphometric analysis is the ability to visually represent statistical results as actual shapes, allowing for visual comparison of analytical results with actual specimens (Rohlf and Marcus, 1993; Baab et al., 2012; Adams et al., 2013). Additionally, it allows for a determination of the magnitude and pattern of shape differences between data sets. For these reasons, the geometric morphometrics toolkit is especially suited to address hypotheses regarding shape changes that occur during ontogeny (Collard and O'Higgins, 2001; Ponce de León and Zollikofer, 2001; Penin et al., 2002; Mitteroecker et al., 2004; O'Higgins and Pan, 2004; McNulty et al., 2006; Cobb and O'Higgins, 2007; Singleton, 2012).

Comparisons of ontogenetic shape trajectories (i.e., the pattern and magnitude of shape changes associated with ontogeny) are a standard approach in geometric morphometrics (Cheverud and Richtsmeier, 1986; Leigh and Cheverud, 1991; O'Higgins and Jones, 1998; O'Higgins, 2000; Collard and O'Higgins, 2001; O'Higgins and Collard, 2002; Ackermann and Krovitz, 2002; Leigh et al., 2003; Cobb and O'Higgins, 2004; Leigh, 2006, 2007; McNulty et al., 2006; Singleton et al., 2010; McNulty, 2012; Simons and Frost, 2016). Previous investigations of primate cranial ontogenetic trajectories involving multiple taxa have compared either the first principal component axis of cranial shape change associated with development, as in Collard and O'Higgins (2001), O'Higgins and Collard (2002), and Mitteroecker et al. (2004), or the beta coefficients from a multivariate regression of Procrustes aligned shape coordinates against the covariate of developmental stage, as in McNulty et al. (2006) and Singleton et al. (2010). However, comparing the trajectories of many taxa simultaneously can be cumbersome and time-consuming, as the number of pairwise comparisons increases as a factorial function ($n-1!$) relative to the number of trajectories being evaluated.

This investigation presents two new approaches to compare the cranial developmental shape trajectories of cercopithecines, and visually assess the similarities and differences among them. Specifically, we wished to compare the relative magnitudes of development in various aspects of the cranium, and compare these magnitudes across taxa. We also investigated the importance of ontogenetic allometry in the production of adult phenotypes, and evaluated if any taxa exhibit aspects of their trajectories that are not correlated with size. Finally, we investigated how developmental trajectories have changed over evolutionary time, in order to determine if there are identifiable evolutionary trends, such as parallel evolution or lineage diversification among clades.

2. Materials and methods

2.1. Materials

Sample The dataset is composed of 17 cercopithecine species partitioned by dental eruption stage (Table 1), and is further described in Singleton et al. (2010) and Singleton (2012). The majority of specimens were wild-shot, however, a small number of zoo specimens (16 of 522 specimens) were used for genera that were poorly represented in collections (i.e., *Allenopithecus* [2], *Macaca sylvanus* [9], *Mandrillus* [2] and *Theropithecus* [3]). A breakdown of the sex composition of the sample is provided in Supplementary Online Material (SOM) Table S1.

Data collection Three-dimensional landmark data were collected using a Microscribe 3DX digitizer (Immersion Corp., San Jose, CA), using the 45 landmark protocol of Frost et al. (2003). However, because two landmarks (the left and right alveolar margin at distal M³, landmarks 36 and 42 of the protocol) were not able to be collected for the youngest specimens in our sample, these landmarks were subsequently dropped from all specimens, leaving a total of 43 landmarks (Fig. 1).

2.2. Analytical methods

Generalized Procrustes analysis Landmark coordinates were subjected to a generalized Procrustes analysis (GPA; Bookstein, 1991; Marcus and Corti, 1996; Rohlf, 1999). The GPA was performed in Morphue (Slice, 1998), as this program allows for superimposition even when some specimens are missing landmarks (which was the case in our sample). All specimens

Table 1
Study sample by dental stage, as defined by full eruption of nominal tooth.^a

	Abbreviation	pre-dP ⁴	dP ⁴	M ¹	M ²	C ^{1b}	M ³	Total
<i>Allenopithecus nigroviridis</i>	Ani	0	1	4	8	1	13	27
<i>Chlorocebus aethiops</i>	Cae	0	1	7	5	2	16	31
<i>Cercocebus agilis</i>	Cag	0	0	6	9	0	17	32
<i>Cercocebus atys</i>	Cat	0	1	6	6	0	20	33
<i>Cercocebus torquatus</i>	Cto	1	1	4	4	4	21	35
<i>Lophocebus albigena</i>	Lal	0	4	4	6	1	30	45
<i>Lophocebus aterrimus</i>	Lat	0	4	5	7	0	21	37
<i>Macaca assamensis</i>	Mas	0	2	2	0	4	11	19
<i>Macaca fascicularis</i>	Mfa	2	7	19	7	9	42	86
<i>Macaca leonina</i>	Mnl	0	1	3	3	1	5	13
<i>Macaca mulatta</i>	Mmu	0	4	5	5	0	8	22
<i>Macaca nemestrina</i>	Mne	0	1	2	1	0	8	12
<i>Macaca sylvanus</i>	Msy	0	3	2	3	0	25	33
<i>Mandrillus leucophaeus</i>	Mle	0	1	1	1	1	9	13
<i>Mandrillus sphinx</i>	Msp	2	0	2	5	0	12	21
<i>Papio hamadryas anubis</i>	Pha	0	5	9	6	1	28	49
<i>Theropithecus gelada</i>	Tge	0	0	0	4	2	8	14

^a Both sexes are included in the calculation of trajectories.

^b C¹ = Male with M¹–M³, but canine not erupted.

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