



Morphological evolution through integration: A quantitative study of cranial integration in *Homo*, *Pan*, *Gorilla* and *Pongo*

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ABSTRACT

Morphological integration refers to coordinated variation among traits that are closely related in development and/or function. Patterns of integration can offer important insight into the structural relationship between phenotypic units, providing a framework to address questions about phenotypic evolvability and constraints. Integrative features of the primate cranium have recently become a popular subject of study. However, an important question that still remains under-investigated is: what is the pattern of cranial shape integration among closely related hominoids? To address this question, we conducted a Procrustes-based geometric morphometrics study to quantify and analyze shape covariation patterns between different cranial regions in *Homo*, *Pan*, *Gorilla* and *Pongo*. A total of fifty-six 3D landmarks were collected on 407 adult individuals. We then sub-divided the landmarks corresponding to cranial units as outlined in the ‘functional matrix hypothesis.’ Sub-dividing the cranium in this manner allowed us to explore patterns of covariation between the face, basicranium and cranial vault, using the two-block partial least squares approach. Our results suggest that integrated shape changes in the hominoid cranium are complex, but that the overall pattern of integration is similar among human and non-human apes. Thus, despite having very distinct morphologies the way in which the face, basicranium and cranial vault covary is shared among these taxa. These results imply that the pattern of cranial integration among hominoids is conserved.

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Introduction

Integration is reflected in structures varying with change in other structures and explicitly refers to coordinated variation among parts of an organism (Olson and Miller, 1958). The concept of morphological integration goes as far back as the *Origin of Species*. Darwin emphasized the importance of correlated variation and its impact on the direction and rate of evolutionary change by either facilitating adaptation or acting as a constraint on morphological evolution. This concept is similar to one of ‘correlation Pleiades’ furthered by Berg (Terentjev, 1931; Berg, 1960). Correlation Pleiades address the degree of correlation between quantitative traits, similar to examining the magnitude of integration among different parts of an organism. The main premise of most studies on integration is that traits, which are related developmentally and/or functionally will be correlated and covary more closely than any other traits (Olson and Miller, 1958). Morphological integration has

been extensively researched in evolutionary and developmental biology (Zelditch and Carmichael, 1989; Pigliucci et al., 1991; Klingenberg and Zaklan, 2000; Marroig and Cheverud, 2001; Hallgrímsson et al., 2002; Klingenberg et al., 2003; Young and Hallgrímsson, 2005; Goswami, 2006; Willmore et al., 2006; Klingenberg, 2008; Drake and Klingenberg, 2010; Roseman et al., 2011), but James Cheverud was the first to actively apply this concept to primate evolution, mainly the primate cranium (Cheverud et al., 1982, 1988, 1989, 1995; Ackermann and Cheverud, 2000). The general consensus among most studies on cranial integration in primates is that developmentally and/or functionally related traits are highly integrated across most primates (Cheverud et al., 1989; 1995; Ackermann and Cheverud, 2000, 2004; Ackermann and Krovitz, 2002; Ackermann, 2005; Martínez-Abadías et al., 2009). In particular, the role of the basicranium in generating overall integration in the primate cranium has been investigated in a number of studies (Lieberman et al., 2000a, b; González-Josè et al., 2004; Bastir and Rosas, 2005; Bastir et al., 2008). However, some studies have also shown that the face and neurocranium are de-coupled from each other, suggesting a certain

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degree of modularity in the primate, particularly human, and possibly the mammalian cranium in general (Polanski and Franciscus, 2006; Marroig et al., 2009; Porto et al., 2009).

While a number of studies have explored different aspects of integration in primates, the majority of them focused on the general covariation and correlation among cranial units (Polanski and Franciscus, 2006; Porto et al., 2009). The question of whether cranial integration in hominoids has a tendency to evolve or is constrained, specifically, what the patterns of shape covariation are, needs to be further addressed. The main aim of this study is to quantify and analyze patterns of integration between different cranial regions, and identify aspects of cranial integration that are possibly shared among living apes. We are primarily concerned with the evolution of cranial *shape* integration patterns, which is quantified as the covariation between structures rather than the strength of association between regions and the relative contribution of biological mechanisms that generate trait covariation. Moreover, if integration patterns are similar among hominoids, how can we understand morphological distinctions such as prominent supraorbital tori, orthognathism, and conditions such as airorynchy (to name a few), in the context of integration? Some authors (Hallgrímsson et al., 2007a; 2009) have made a distinction between integration and covariation, defining integration as a property of developmental systems, and rather as a process than a pattern. However, in this study we refer to integration and analyze it strictly in the context of the original definition by Olson and Miller (1958) – as the covariation within and between morphological structures or modules. In doing so, our study will reassess previous findings on cranial integration in hominoids to better understand factors that influence overall phenotypic variability. Our objectives are as follows: 1) to examine associated shape changes between functional regions of the extant hominoid cranium. The context of function here is that of the ‘functional matrix hypothesis’ (Moss 1962, 1968, 1969, 1997a); 2) to identify overall *patterns* of cranial shape covariation among all extant hominoids; 3) finally, to address whether covariation patterns evolve or whether they are conserved among extant hominoids.

Materials and methods

The total sample comprises dried crania of 407 adult individuals of *Homo*, *Pan*, *Gorilla* and *Pongo* (Table 1). The sex ratio was nearly equal in all groups. Only specimens with fully erupted dentition and fully fused sphenoccipital synchondrosis were considered as adults and included in the study. Fifty-six 3D landmarks, including bilateral points, were measured on the entire cranium (Fig. 1). Landmarks were chosen based on anatomical correspondence and repeatability across taxa. For individuals with prominent mid-sagittal and nuchal crests, landmarks such as bregma and lambda were taken on top of the crests and two additional points were taken on the neurocranium on either side of the landmarks. The latter two points and landmarks taken on top of the crests were later averaged and the averaged points were included in the analysis. All individuals with missing and/or mislabeled landmarks were excluded from the analysis. An assessment of intra-observer error is provided in Table 2. Landmarks are listed and illustrated in Fig. 1, respectively.

All measurements were taken by NS using a G2X MicroScribe (Immersion Corporation, San Jose, CA), which has a measurement accuracy of 0.23 mm. Digitizing was done in two orientations, dorsal and ventral, to register all of the landmarks as efficiently as possible. While measuring, the specimens were mounted on modeling clay to keep them stationary. In order to match the digitized landmarks from the two separate sessions, we took four ‘orientation points’ in the two views. To ensure matching the two

Table 1
Species included in this study.

Species	No. of individuals	Source
<i>Pan t. troglodytes</i>	42	Naturkundemuseum, Berlin
<i>Pan t. verus</i>	35	MPI-EVA, Leipzig & Peabody Museum, Boston
<i>Pan t. schweinfurthii</i>	45	Royal Museum of Central Africa, Tervuren
<i>Pan pansicus</i>	36	Royal Museum of Central Africa, Tervuren
<i>Gorilla beringei</i>	49	Royal Museum of Central Africa, Tervuren
<i>Pongo pygmaeus</i>	68	Zoologische Staatssammlung, Munich
<i>Homo sapiens</i>	132	
Luis Lopez	69	Natural History Museum, Lisbon
Point Hope	48	American Museum of Natural History, New York
Khoisan	15	University of Vienna, Vienna
Total	407	

sets of landmarks accurately, these points were taken in exactly the same place each time. DVLR (dorsal-ventral-left-right fitting) program was used to combine the two sets of landmarks to make one individual. More information about this software can be found on the NYCEP morphometrics group homepage.

Cranial modules

Regions of the mammalian cranium differ in their developmental origin and functional demands. Accordingly, we sub-divided the cranium into three functional components: (a) facial skeleton, including the zygomatic processes, nasal, lacrimal and maxillary bones, (b) cranial vault, consisting of the frontal and parietal bones, and (c) basicranium, comprising the non-squamous parts of the temporal and occipital bones. We choose to call these modules ‘functionally’ derived because they are loosely based on Moss’ functional matrix hypothesis (Moss and Young, 1960; Moss, 1968, 1997a, 1997b, 1997c), however, they are primarily distinguished based on differential growth patterns. According to the ‘functional matrix hypothesis’ the skull can be sub-divided into ‘functional components’ based on functional/mechanical demands, influencing bone growth through the function of soft tissues and cavities within which skeletal components develop. Moss (1968; Moss and Young, 1960) described two types of functional matrices: periosteal and capsular. Periosteal matrices are concerned with the effects of muscle interactions on growth and development of skeletal components. Capsular matrices are concerned with the indirect effects on growth and development caused by soft tissue organs, brain, orbits and pharyngeal cavities.

The facial skeleton follows a somatic growth pattern, whereas the neurocranium follows a neural growth pattern (Moore and Lvelle, 1974). Typically, the face grows well into adulthood making it more susceptible to environmental stimuli (Collard and Wood, 2001; Bastir and Rosas, 2004). Consequently, differential growth patterns and muscular/functional demands make the face semi-independent of the neurocranium. Neurocranial components can be largely divided into the basicranium and vault. Growth in the cranial vault is through intramembranous ossification and the basicranium grows from endochondral ossification. The basicranium is additionally influenced by somatic growth factors largely attributed to hormones affecting the corresponding cartilage growth (Bogin, 1988; Hall, 2005).

Geometric morphometrics

We used Procrustes-based geometric morphometric methods to analyze our data. Landmark configurations of each specimen were superimposed using the generalized Procrustes analysis (GPA)

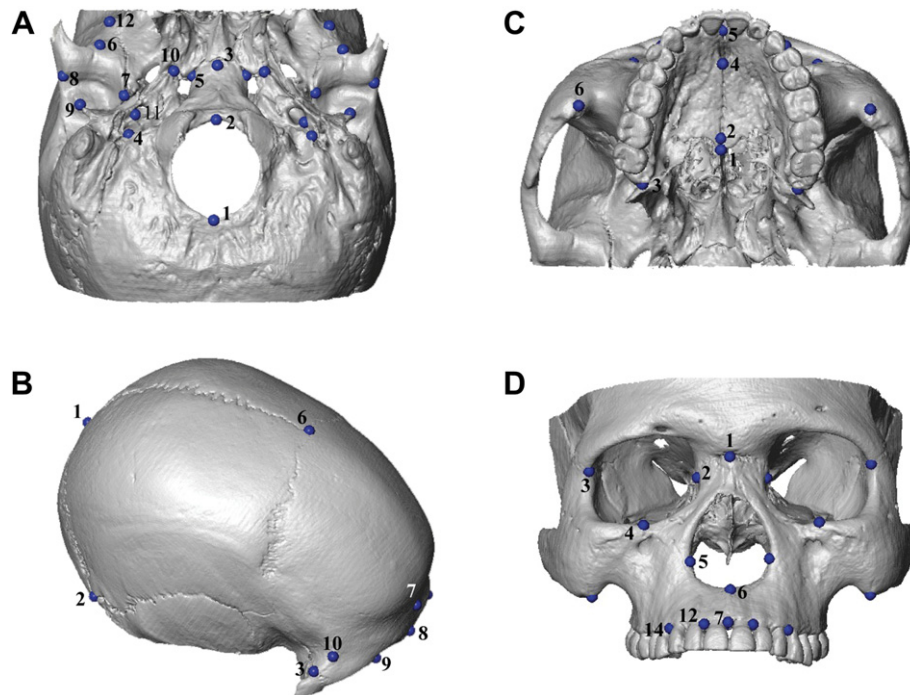


Figure 1. Cranial landmarks included in this study: A) Inferior view of the basicranium: 1. Opisthion; 2. Basion; 3. Mid-point on basio-spheno synchondrosis; 4 and 13. Jugular point; 5 and 14. Basilar bone; 6 and 15. Articular eminence point; 7 and 16. Entoglenoid process; 8 and 17. Articular tubercle; 9 and 18. Postglenoid process; 10 and 19. Apex of petrous bone; 11 and 20. Carotid canal; 12 and 21. Infratemporale, B) Supero-lateral view of cranial vault: 1. Lambda; 2 and 4. Asterion; 3 and 5. Frontomale; 6. Bregma; 7. Post-toral sulcus; 8. Glabella; 9 and 11. Mid-orbit torus inferior; 10 and 12. Frontotemporale, C) Inferior view of face: 1. Staphylion; 2. Midline anterior palatine suture; 3 and 8. Sphenopalatine suture; 4. Incisive foramen; 5. Orale; 6 and 7. Zygomaxillare, D) Anterior view of face: 1. Nasion; 2 and 8. Dacryon; 3 and 9. Frontomale; 4 and 10. Zygoorbitale; 5 and 11. Alare; 6. Nasiospinale; 7. Prosthion; 12 and 13. 1st -2nd Incisor alveolar septum; 14 and 15. Canine – Premolar alveolar septum.

method (Rohlf and Slice, 1990; Bookstein, 1996; Rohlf, 1999). GPA is used as a standard procedure in most recent geometric morphometric studies on shape analysis. The procedure involves extracting shape coordinates by translating, scaling and rotating the landmark configurations; hence, removing all information unrelated to shape. A size measure, commonly known as centroid size, and related to the dispersion of landmarks around their baricenter, is obtained for each specimen (Dryden and Mardia, 1998).

In the present study, as part of the Procrustes superimposition, object symmetry was calculated by reflecting and relabeling each set of paired landmarks. Object symmetry is a form of bilateral symmetry in which a structure is inherently symmetrical (Klingenberg et al., 2002). A biological form such as the mammalian cranium is a good example of object symmetry. The object symmetry analysis was conducted in MorphoJ (Klingenberg, 2011), which as part of the Procrustes fit yields separate components for symmetry and asymmetry. Subsequent multivariate statistical analyses were done on the symmetric shape components, which are calculated through reflected relabeling of the paired landmarks. Using the symmetric shape component is useful to reduce dimensionality in datasets where variables exceed sample size.

Measurement error Repeat measurements were taken for 200 specimens, out of which 48 were re-digitized two years apart (at the beginning and end of data collection) to further assess measurement accuracy. Measurement error was quantified using the Procrustes ANOVA method outlined in Klingenberg and McIntyre (1998). This method is analogous to the two-factor ANOVA model developed by Palmer and Strobeck (Palmer and Strobeck, 1986; Palmer, 1994) and is useful for estimating measurement error in datasets. The Procrustes ANOVA involves a four-step procedure: quantification of among individual shape variation in the dataset; calculating the effects of directional asymmetry; accounting for fluctuating asymmetry, which is done

by calculating each side*specimen interaction; and finally, quantifying variation among replicates, which is the residual and a value for measurement error in the dataset. Procrustes ANOVA yields large degrees of freedom, more so than in a regular ANOVA. For the purposes of this study, the Procrustes ANOVA was mainly employed to look at measurement errors in the dataset and was performed separately for each taxon in the sample. In addition, we calculated Procrustes distances between the original and repeat measurements to ensure there were no outliers in the data.

Analysis of covariation We use the two-block partial-least squares (2B-PLS) approach to examine integration or covariation between the different cranial modules (Rohlf and Corti, 2000). The partial least squares approach has been extensively used in social sciences (Bookstein, 1990) and is only recently being applied to anthropological datasets, to name a few (Bookstein et al., 2003; Gunz and Harvati, 2007; Mitteroecker and Bookstein, 2007, 2008; Bastir et al., 2008). Two-block partial least squares analysis emerges from a group of statistical techniques that is based on a singular value decomposition of the between-block covariance matrix (Mardia et al., 1979; Rohlf and Corti, 2000; Mitteroecker and Bookstein, 2007). Accordingly, it finds pairs of axes – one axis per block per dimension – which account for the maximum amount of covariation between the two sets of variables examined (Rohlf and Corti, 2000; Bookstein et al., 2003; Klingenberg et al., 2003; Mitteroecker and Bookstein, 2007).

In the present study, we first sub-divided the landmarks into the respective blocks as outlined in the ‘functional matrix hypothesis’ and performed separate Procrustes superimpositions for each block (face, basicranium and cranial vault) of landmarks. To explore patterns of integration between the blocks, we performed pooled within-species 2B-PLS analysis. The pooled within-species analysis subtracts the species’ mean differences and facilitates examining

Table 2

Measurement error tests: separate Procrustes ANOVA tests for the taxa included in this study. Individual effects represent overall variation in the dataset. Side is the measure for directional asymmetry. Individual*side is the measurement for fluctuating asymmetry. Error 1 is the measurement error calculated from the variation among repeat measurements. 'SS' is sum of squares, 'MS' is mean squares, 'df' is degrees of freedom, 'F' F statistic and 'p' P-value. Measurement error (Error 1) is relative to the Ind*side interaction.

Effect(param.)	SS	MS	df	F	p
<i>Gorillas: Shape, Procrustes ANOVA:</i>					
Individual	0.17612759	5.77846E-05	3048	8.95	<0.0001
Side	0.00181909	1.58182E-05	115	2.45	<0.0001
Ind*Side	0.01782854	6.4596E-06	2760	33.24	<0.0001
Error 1	0.0010818	1.944E-07	5566		
<i>Bonobos: Shape, Procrustes ANOVA:</i>					
Individual	0.15301585	0.000022733	6731	7.46	<0.0001
Side	0.00269028	2.33937E-05	115	7.68	<0.0001
Ind*Side	0.01857773	0.000003048	6095	9.18	<0.0001
Error 1	0.00016078	3.322E-07	484		
<i>Humans: Shape, Procrustes ANOVA:</i>					
Individual	0.08007854	2.74148E-05	2921	5.92	<0.0001
Side	0.00221287	1.92423E-05	115	4.16	<0.0001
Ind*Side	0.01224441	4.6293E-06	2645	24.56	<0.0001
Error 1	0.00018247	1.885E-07	968		
<i>Orangutans: Shape, Procrustes ANOVA:</i>					
Individual	0.329559	6.19006E-05	5324	11.58	<0.0001
Side	0.00381311	3.49826E-05	109	6.55	<0.0001
Ind*Side	0.02562663	5.3433E-06	4796	9.48	<0.0001
Error 1	0.00583472	5.637E-07	10350		
<i>Chimpanzees: Shape, Procrustes ANOVA:</i>					
Individual	0.10109703	2.48762E-05	4064	7.62	<0.0001
Side	0.00194026	1.68718E-05	115	5.17	<0.0001
Ind*Side	0.0120169	3.2655E-06	3680	14.1	<0.0001
Error 1	0.00005604	2.316E-07	242		

integration patterns for the same shape features across taxa (Mitteroecker and Bookstein, 2008) by computing the 2B-PLS scores collectively for all species in the sample, as in a principal component analysis. Subsequently, the integration patterns can be identified by looking at the species' distributions along the same components of shape. Because investigating sexual dimorphism is not one of the objectives of this study, we chose to pool the sexes to account for mean differences between males and females, particularly in gorillas and orangutans. We also pooled different human populations and chimpanzee sub-species to minimize possible group mean differences within taxon.

Shape changes were visualized on surfaces generated in AMIRA (Mercury Computer Systems Inc.). This was done by warping the PLS vectors of the three pair-wise analyses onto the grand mean shape of the face, basicranium and cranial vault. Rather than using the species mean shapes, we used the grand mean to avoid undue influence of mean differences between species when visually interpreting shape covariation patterns. The original surface used was that of a modern human cranium. The modern human surface was first warped to the grand mean shape of all the taxa and then warped along the PLS vectors to visualize the shape changes. All analyses were conducted in MorphoJ (Klingenberg, 2011) and programming software R version 2.6.2 (R development core team, 2008).

Results

Measurement error

We calculated measurement error for each group separately using the Procrustes ANOVA method. The degree of measurement error is assessed relative to the degree of specimen*side (Ind*side interaction) variation or fluctuating asymmetry in the dataset (Table 2). Fluctuating asymmetry comprises a very small portion of the phenotypic variation and is greatly influenced by measurement

error. Results show that the level of measurement error relative to the level of fluctuating asymmetry (Ind*side interaction) is negligible, as indicated by the mean square (MS) values (Table 2). The Procrustes distances (not reported here) between the repeat and original specimens showed that the largest Procrustes distance between the repeated specimens and their corresponding original was 4–5 times smaller than the smallest distance between individuals in the total sample.

Functional components

We conducted a pooled within-species 2B-PLS analysis for the face, basicranium and cranial vault. Here, we focus on the first two dimensions and illustrate shape changes only along PLS 1 because it accounts for the maximum covariance in the dataset for all three analyses and captures the main shape changes. Fig. 2 shows PLS plots of pair-wise comparisons between different cranial regions. The species' scatters cluster together and overlap in all three 2B-PLS analyses. This is because in a pooled within-species analysis, the PLS scores for the different taxa have an average score of 0.0.

Associated shape changes in the face and basicranium PLS 1 accounts for 34% of the total covariance in the dataset. The PLS plot (Fig. 2) of the face vs. basicranium analysis shows *Homo*, *Pan*, *Gorilla* and *Pongo* to cluster close together. The general orientation of the species' scatters in Fig. 2 suggests that the species have a similar pattern of integration in the face and basicranium; that is, one unit change in the face, leads to one unit change in the basicranium in all taxa (Mitteroecker and Bookstein, 2008). Shape changes from lower to higher scores along PLS 1 correspond to an elongated face and projecting pre-maxillary region associated with an anteriorly narrow cranial base with a posteriorly placed foramen magnum, and a relatively short and slightly wide face associated with an overall wide and short cranial base with an anteriorly placed foramen magnum (Fig. 3). Species' scatters along PLS 2, which accounts for 19% of the total variance in the sample, are similar to PLS 1. Lower scores along PLS 2 relate to an elongated face and downwardly projecting premaxilla region associated with an expanded mandibular fossa and posteriorly placed foramen magnum. Higher scores relate to a short and wide face, with a retracted premaxilla covarying with a laterally placed mandibular fossa and anteriorly placed foramen magnum. The main shape changes along PLS 2 were in aspects of the mandibular fossa and position of the foramen magnum.

Associated shape changes in the cranial vault vs. basicranium PLS 1 accounts for 48.2% of the total covariance in the dataset. All four species show similar integration pattern between the basicranium and cranial vault (Fig. 2). This is indicated by the general orientation of the species' scatters as seen in the face vs. basicranium analysis. However, orangutans and chimpanzees show more within-species variation than the other taxa. Shape changes along the lower scores are associated with an anteriorly robust and posteriorly expanded cranial vault, covarying with an expanded mandibular fossa and posteriorly placed foramen magnum in the basicranium. Higher scores on PLS 1 show an anteriorly rounded and expanded cranial vault, covarying with a relatively wide and slightly short cranial base, with a contracted mandibular fossa and a slightly anteriorly placed foramen magnum (Fig. 4). The main shape changes are in aspects of the anterior vault, which vary from a robust ape-like to a more rounded human-like shape, i.e., from prominent supraorbital torus and post-orbital constriction to a slightly rounded and relatively gracile overall shape. PLS 2 accounts for 18% of the total variance in the dataset and shows overlap among the taxa. Low scores on PLS 2 relate to an elongated cranial vault, with a contracted anterior and expanded posterior vault, relative to a slightly narrow basicranium, and high scores relate to an

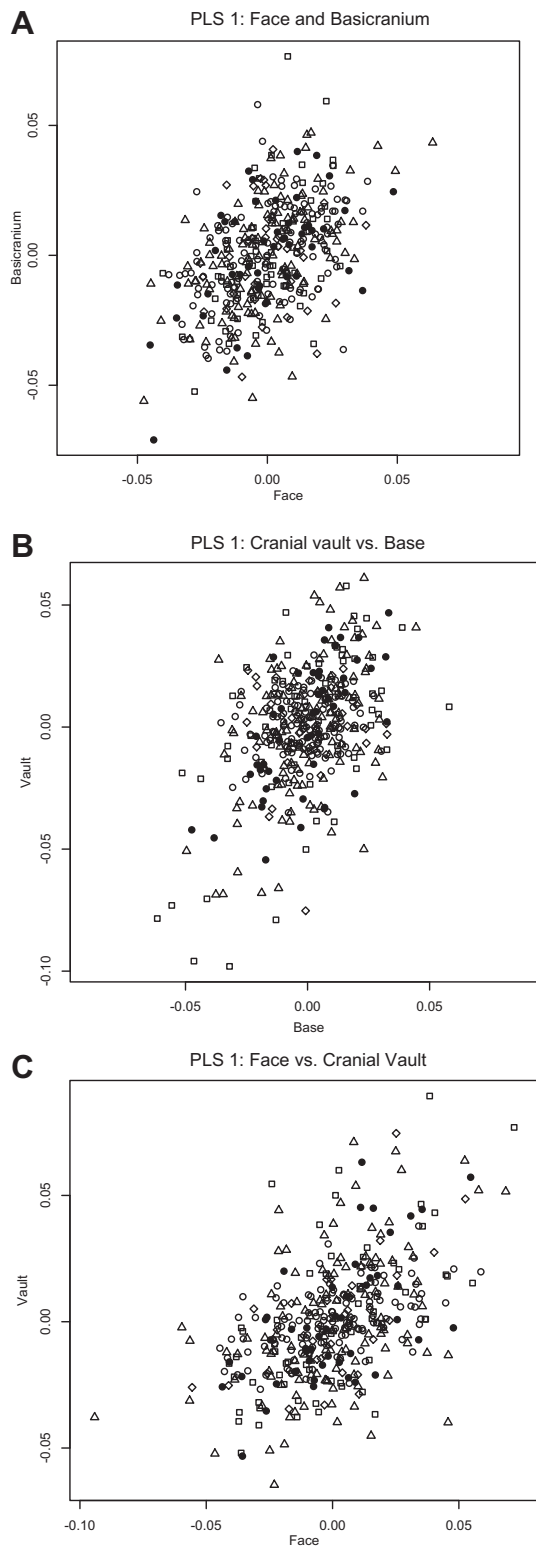


Figure 2. Pooled within-species 2B-PLS plots of the: (A) Face vs. basicranium; (B) Cranial vault vs. Base; (C) Face vs. Cranial vault. These plots illustrate the maximum covariation between the different cranial regions. • *Gorilla* △ *Pan troglodytes* ◇ *Pan paniscus* ○ *Homo* □ *Pongo*.

anteriorly expanded and short cranial vault associated with a slightly wide basicranium.

Associated shape changes in the face vs. cranial vault PLS 1 accounts for 65% of the total covariance in the data. As seen in the

first two 2B-PLS analyses, the PLS 1 plot (Fig. 2) of the face and cranial vault also shows complete overlap among the taxa. Lower scores show a wide and relatively short face and broad inter-orbital distance, covarying with a slightly short and rounded cranial vault. The higher scores along PLS 1 relate to a markedly elongated face and narrow inter-orbital distance, covarying with a robust and elongated cranial vault (Fig. 5). Compared to the integrated shape changes in the face and basicranium and cranial vault and basicranium, this pair-wise comparison shows the most pronounced and ‘uniform’ changes among the taxa. PLS 2 plot, which accounts for 10% of the covariance in the dataset, shows a similar pattern of species’ scatters as in PLS 1. Shape changes are mainly associated with a retracted premaxilla and laterally flared zygomatics associated with an expanded posterior cranial vault, and the high scores correspond to a narrow face with an anteriorly projected premaxilla associated with a narrow cranial vault.

Discussion

The mammalian cranium is a complex integrated structure, but within this structure there are semi-independent units or modules. In this study, we used the traditional sub-division of the cranium into the face, basicranium and cranial vault (Moss and Young, 1960; Cheverud, 1982). The facial component is responsible for the sensory organs, whereas the cranial vault and basicranium encase the superior and inferior aspects of the brain. Our primary aim here was to identify and compare patterns of integration between different cranial regions rather than the strength of association between them. We used pooled within-species 2B-PLS analysis to identify overall patterns of cranial integration. All three pair-wise comparisons show similarities in patterns of integration across species. A pooled within-species approach was particularly important for this study to distinguish morphological differences due to integration from differences due to species’ mean shapes. If two or more species have different average shapes, then it can misleadingly suggest differences in covariation. Therefore, to minimize the effects of species’ means, we conducted a pooled within-species analysis (Mitteroecker and Bookstein, 2008).

Overall shape changes between the cranial regions show a ‘uniform’ pattern of integration, particularly between the face and basicranium and the face and cranial vault (Figs. 3 and 5). Here, a ‘uniform’ pattern of integration refers to a narrow face covarying with a narrow basicranium and cranial vault, in contrast to a short and broad face covarying with similarly dimensioned basicranium and vault, i.e., brachycephaly vs. dolichocephaly. While this ‘uniform’ pattern of cranial shape change has been a more consistent finding among humans (Enlow, 1968; Enlow and Hans, 1996; Lieberman et al., 2000a; Bastir and Rosas, 2004), our results indicate that non-human apes too follow a similar trend. This pattern is further supported by ontogenetic data (Mitteroecker and Bookstein, 2008), which despite showing deviations in human cranial growth trajectories and mean shape, suggest that the neurocranium and face are developmentally integrated in a similar, but not identical, way among gorillas, chimpanzees and humans.

The question then arises is, how can we understand distinct phenotypic traits, particularly features such as airorynchy in orangutans, in the context of morphological integration? Airorynchy is a structural condition that refers to an upward deflection of the palate relative to the basicranium, and is one of the dominant features that distinguishes Asian apes from the African apes and humans. Other cranial features in orangutans such as narrow inter-orbital breadth, ovate orbits, vertical forehead and reduced supraorbital tori (relative to African apes), have been associated to airorynchy (Shea, 1985). Compared with orangutans, chimpanzees, gorillas and humans have

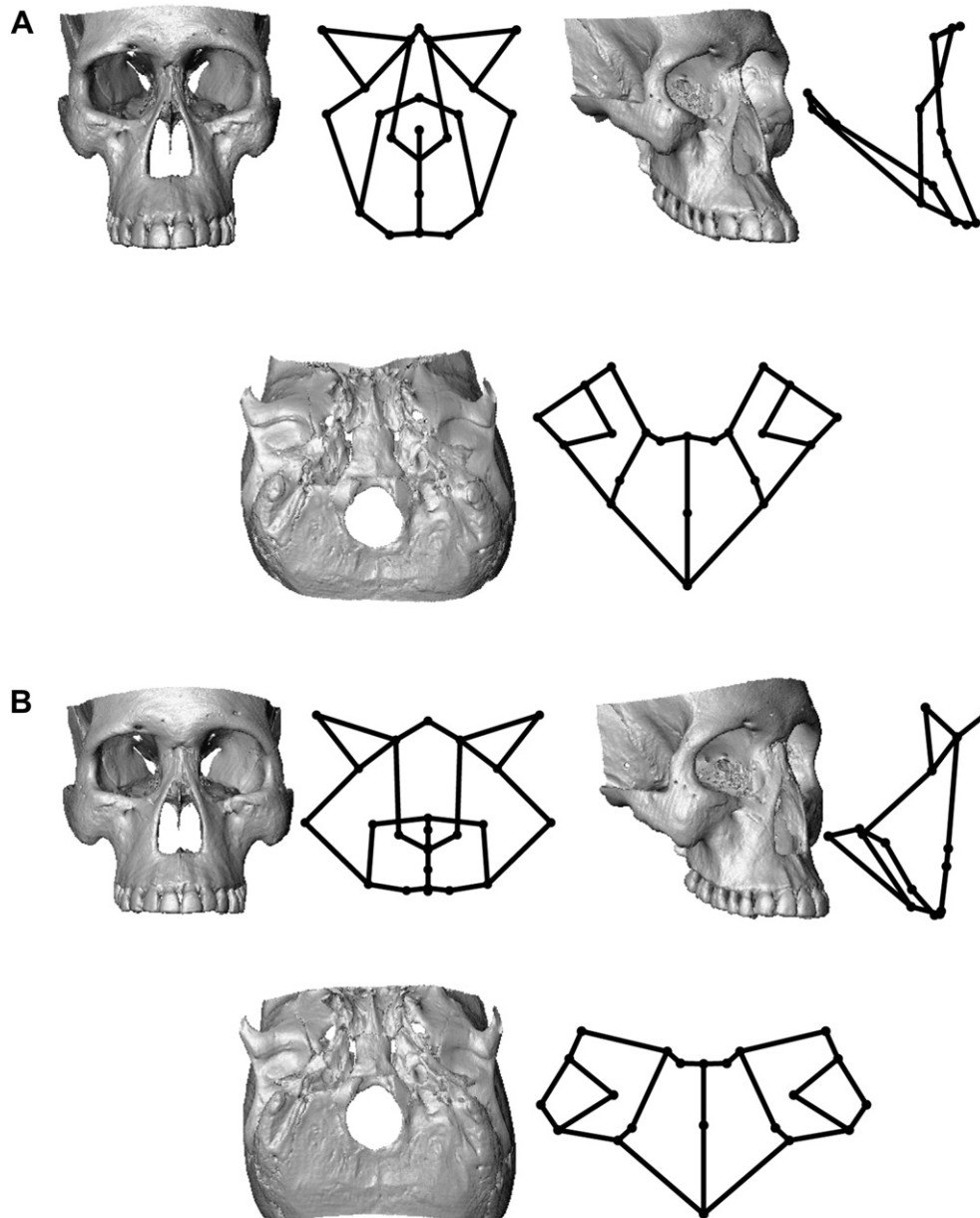


Figure 3. Two-block PLS analysis of the face vs. basicranium. Shape changes along PLS 1 from the lower (A) to the higher (B) scores corresponding to the PLS plot in Fig. 2. The surface morphs and wireframe diagrams of the face (anterior and lateral views) and basicranium (inferior view) illustrate the associated shape changes between the two regions. Only the landmarks shown in Fig. 1 are included in the warping.

a downwardly deflected face relative to the basicranium, a condition called klinorhynch. Studies on non-human apes (Delattre and Fenart, 1956; Enlow, 1975) have shown that the main structural difference between African and Asian ape crania is in the position and not the overall form of the face relative to the basicranium (Shea, 1985). The aspects of cranial integration explored in this study are mainly related to the associated shape changes between the different cranial structures and not their relative positioning, and indicates that cranio-facial traits that distinguish *Pongo* from the other hominoids do not result from a different pattern of integration between the face and the other cranial structures. However, the species-specific differences among the taxa, particularly orangutans, are reflected in the within-block shape changes along PLS 1 (Fig. 5), ranging from a relatively short and wide face, with a broad inter-orbital distance and an elongated face with a narrow inter-orbital distance, as in orangutans. Moreover, orangutans show a larger within-species

variance than the other taxa, especially in the face and cranial vault, and the basicranium and cranial vault analyses (Fig. 2). Similarly, chimpanzees also show more variation than the other taxa in between-block comparisons with the cranial vault (Fig. 2). Overall shape changes in the vault (Figs. 4 and 5) are more pronounced compared with the face and cranial base, especially in the supra-orbital region. The higher variance seen among chimpanzees, but not the other taxa, could be due to more variability in brow ridge morphology of chimpanzees (Figs. 4 and 5), ranging from markedly prominent to gracile, than gorillas that mainly have large tori or humans that are the least developed in this feature.

While it is clear that hominoids have distinct cranial morphologies, they exhibit strong similarities in the pattern of covariation between the face, basicranium and cranial vault. Similarities in these patterns have been largely attributed to shared developmental processes (Klingenberg et al., 2003; Marroig et al., 2004;

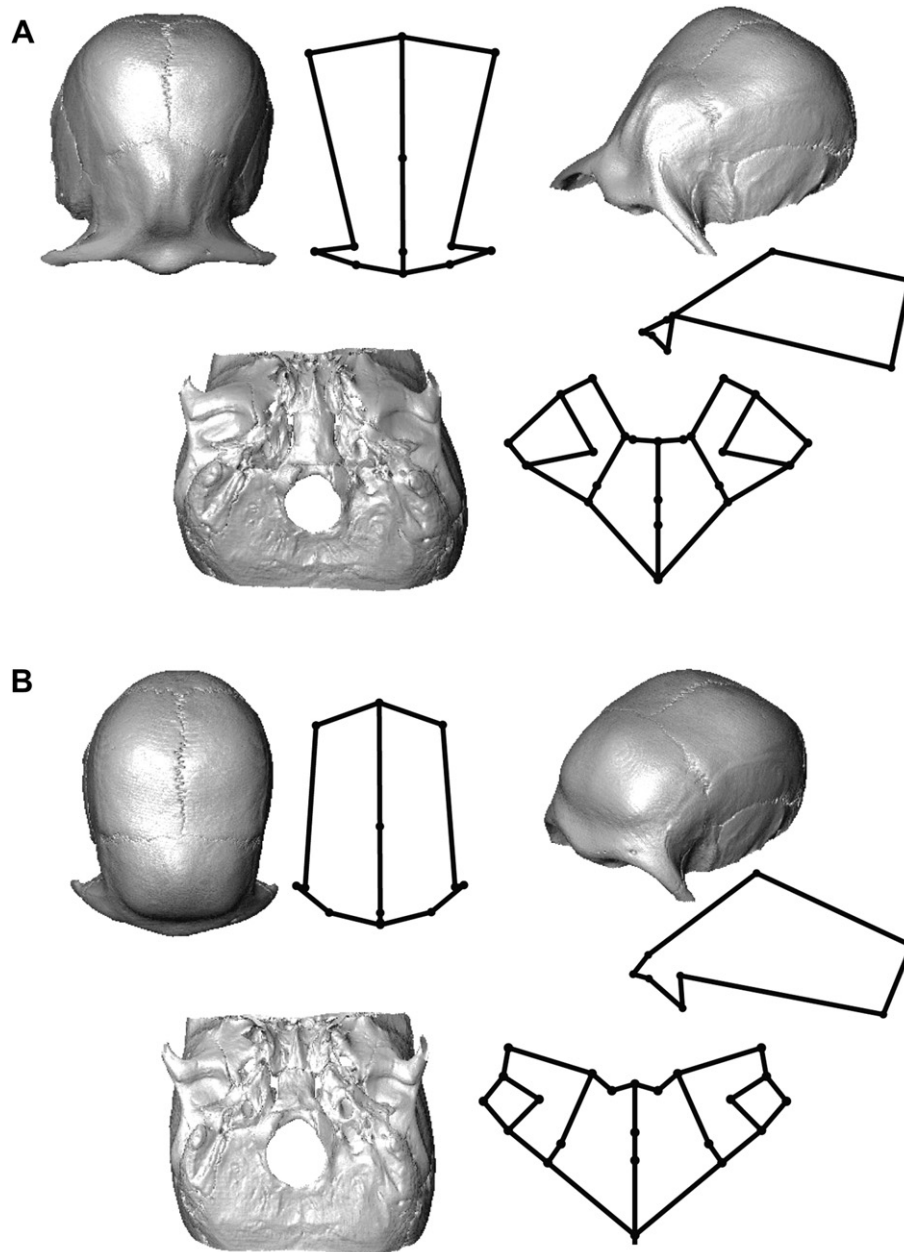


Figure 4. Two-block PLS analysis of the cranial vault vs. basicranium. Shape changes along PLS 1 from the lower (A) to the higher (B) scores corresponding to the PLS plot in Fig. 2. The surface morphs and wireframe diagrams of the cranial vault (superior and lateral views) and basicranium (inferior view) illustrate the associated shape changes between the two regions. Only the landmarks shown in Fig. 1 are included in the warping.

Hallgrímsson et al., 2007a) or ‘common factors’ (Mitteroecker and Bookstein, 2008). For instance, single mutations, developmental buffering mechanisms, cartilage growth, interactions of muscles and bones, and brain growth can influence covariation among morphological traits/units. An example of how different morphologies may arise from shared developmental and/or functional mechanisms is the supraorbital torus. Modern humans differ from other apes in lacking a large, well-developed supraorbital torus. Shape changes seen in Figs. 4 and 5 illustrate this feature from being prominent and ape-like to less developed and human-like. The frontal bone comprises an inner and outer table of bone. Growth and remodeling in the inner and outer tables of the frontal bone occur the same way across primates, through a process called drift (Duterloo and Enlow, 1970; Lieberman, 2000). In the supra-orbital torus, drift involves osteoclasts resorbing bone from the

posterior surface of the growth fields and osteoblasts forming bone in the anterior surface of the growth fields (Duterloo and Enlow, 1970). Given that the general distribution of the growth fields in the frontal bone is the same among primates, Lieberman (2000) concluded that the disparity in supraorbital morphology is a consequence of differences in the amount of bone resorption and deposition, rather than the process of drift itself. Mitteroecker and Bookstein (2008) referred to such shared genetic and developmental processes as ‘common factors’ that contribute to similarities in cranial integration patterns among humans, chimpanzees and gorillas. These ‘common factors’ refer to genes with wide pleiotropic effects or developmental events affecting many parts of the organism.

Integration studies are key in understanding whether the underlying developmental and functional interactions are

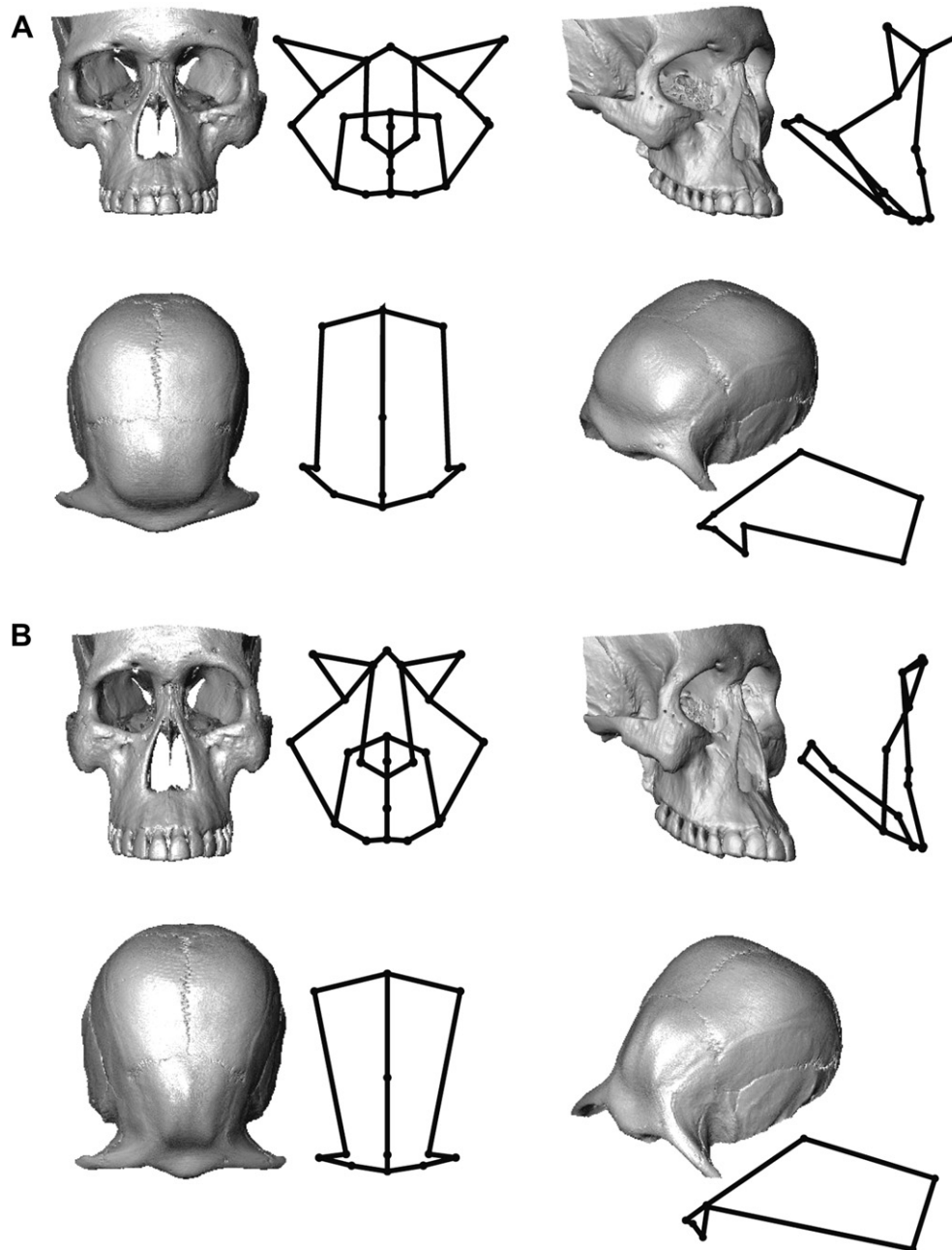


Figure 5. Two-block PLS analysis of the face vs. cranial vault. Shape changes along PLS 1 from the lower (A) to the higher (B) scores corresponding to the PLS plot in Fig. 2. The surface morphs and wireframe diagrams of the face (anterior and lateral views) and cranial vault (superior and lateral views) illustrate the associated shape changes between the two regions. Only the landmarks shown in Fig. 1 are included in the warping.

conserved or evolvable across phylogenies on a macroevolutionary time scale. One of the objectives of this study was to evaluate whether patterns of cranial integration have a tendency to evolve or whether they are constraint across extant hominoids. Evolvability is the tendency or potential of populations to respond to natural selection and evolve through adaptive evolution, or nonadaptive evolution such as genetic drift (Wagner and Altenberg, 1996; Klingenberg, 2005). Another property of evolvability is the ability to give rise to novel phenotypes. Constraint restricts evolvability by biasing evolutionary change in a specific phenotypic direction, thereby conserving aspects of the phenotype (Klingenberg, 2005). Identifying possible factors that generate and/or constrain phenotypic covariation is essential for interpreting the

results of such studies. Thus, the question that then arises is, what maintains covariation patterns? Experimental studies (Jamniczky and Hallgrímsson, 2009) comparing cranial covariance structures between wild and mutant mice show that wild murids tend to have more stable phenotypic covariance structures than mutant populations. Jamniczky and Hallgrímsson (2009) found that laboratory mice were more susceptible to the effects of single mutations on covariance generating processes such as developmental mechanisms. Specifically, they found that changes in the variance of underlying developmental interactions altered the patterning of covariation within and between structures in the laboratory mice. Conversely, stability or conservation of covariance patterns observed in wild populations was largely attributed to stabilizing

selection acting on the effects of developmental processes preserving such patterns (Jamniczky and Hallgrímsson, 2009).

The role of stabilizing selection in conserving and maintaining covariance structures in natural populations, including primates, has also been proposed by other authors (Cheverud, 1982; Ackermann, 2002; Hallgrímsson et al., 2009; Roseman et al., 2011). Stabilizing selection reduces variability or the potential to vary within a population, but favors the average or common traits in a population, conserving aspects of development and/or function across evolutionary time. Effects of selection on ‘common factors’ (Mitteroecker and Bookstein, 2008), particularly on developmental factors, may be one the determinants that conserve covariance structures despite the evolution of distinct phenotypes. Even though it is extremely difficult to isolate one evolutionary process over another to provide an explanation for the evolution of covariance patterns across phylogenies, similarities in patterns of integration among species that have been evolving independently across a macroevolutionary time scale strongly imply that stabilizing selection on common developmental factors may be important in maintaining these patterns.

Finally, as a caveat, a potential problem for studies on cranial integration and inferring patterns of integration is sample size. Ackermann (2002, 2005) pointed out that differences among species could be influenced by sample structure and size. Small and/or unevenly distributed samples, such as combining sub-species, may potentially bias the results. In this study, only the chimpanzee sample had three different sub-species. We accounted for possible sub-species, population and sex differences by conducting pooled within-group analyses for each species, as previously mentioned. This subtracts possible mean differences that arise from sex, population and/or sub-species differences within species, thus facilitating near equal comparisons between taxa. Small sample sizes are especially problematic for integration studies when trying to incorporate fossils. Therefore, the majority of the studies, including the present one, use extant analogs to examine phenotypic integration patterns because larger sample sizes are available and covariation patterns of extant taxa can be used as proxies for their closely related ancestors (Ackermann, 2002). However, caution has to be exercised in terms of which reference extant sample to use when approximating covariance patterns for fossils (Ackermann, 2009).

To summarize, this study is one of the few to include *Pongo* and not just *Gorilla*, *Pan* and *Homo* (Ackermann, 2002; Polanski and Franciscus, 2006; Mitteroecker and Bookstein, 2008), diversifying the sample of great apes previously investigated in the context of morphological integration. Orangutans being particularly distinct from the other apes (Groves, 1986, 2001; Röhrer-Ertl, 1988; Aiello and Dean, 1990; Cray et al., 2010) in their cranio-dental morphology provide additional insight into the patterns of cranial shape integration across all extant human and non-human apes. In terms of covariation patterns, shape changes in the face and cranial vault capture the most ‘uniform’ pattern of covariation across taxa. Integration patterns among these taxa are by and large similar, suggesting that these patterns are conserved across hominoids, at least in aspects of the face, basicranium and cranial vault. Future investigations on the influence of developmental processes and selection on covariance structures will greatly enhance our understanding of factors that influence phenotypic variability and morphological evolution.

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