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Basicranium and face: Assessing the impact of morphological integration on primate evolution

Dimitri Neaux [a, *, 1], Gabriele Sansalone [a, b, c, 1], Justin A. Ledogar [a], Sarah Heins Ledogar [d], Theodora H.Y. Luk [a], Stephen Wroe [a]

[a] *Function, Evolution & Anatomy Research Lab, Zoology Division, School of Environmental and Rural Science, University of New England, NSW, 2351, Armidale, Australia*
[b] *Department of Sciences, Roma Tre University, Largo San Leonardo Murialdo 1, I-00146, Rome, Italy*
[c] *Center for Evolutionary Ecology, Largo San Leonardo Murialdo 1, I-00146, Rome, Italy*
[d] *Department of Archaeology & Palaeoanthropology, School of Humanities, University of New England, NSW 2351, Armidale, Australia*

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ABSTRACT

The basicranium and facial skeleton are two integrated structures displaying great morphological diversity across primates. Previous studies focusing on limited taxonomic samples have demonstrated that morphological integration has a significant impact on the evolution of these structures. However, this influence is still poorly understood. A more complete understanding of craniofacial integration across primates has important implications for functional hypotheses of primate evolution. In the present study, we analyzed a large sample of primate species to assess how integration affects the relationship between basicranial and facial evolutionary pathways across the order. First, we quantified integration and modularity between basicranium and face using phylogenetically-informed partial least squares analyses. Then, we defined the influence of morphological integration between these structures on rates of evolution, using a time-calibrated phylogenetic tree, and on disparity through time, comparing the morphological disparity across the tree with that expected under a pure Brownian process. Finally, we assessed the correlation between the basicranium and face, and three factors purported to have an important role in shaping these structures during evolution: endocranial volume, positional behavior (i.e., locomotion and posture), and diet. Our findings show that the face and basicranium, despite being highly integrated, display significantly different evolutionary rates. However, our results demonstrate that morphological integration impacted shape disparity through time. We also found that endocranial volume and positional behavior are important drivers of cranial shape evolution, partly affected by morphological integration.

1. Introduction

1.1. Morphological integration and cranial shape evolution

There is a considerable cranial morphological diversity across the nearly 500 species, and more than 70 genera, of extant primates (Mittermeier et al., 2013; Rylands and Mittermeier, 2014). Much of this variation is located in the basicranium and in the facial skeleton (Fleagle et al., 2010, 2016; Bennett and Goswami, 2012). Previous studies suggest that these two structures evolved in a coordinated fashion in *Homo* (Bastir and Rosas, 2006, 2016; Gkantidis and Halazonetis, 2011), in the Hominoidea (Singh et al., 2012; Neaux et al., 2013; Neaux, 2017), and in the Platyrrhini (Marroig and Cheverud, 2001; Marroig et al., 2004; Makedonska, 2014), indicating they may be morphologically integrated. This coinheritance of character complexes (Cheverud, 1995) has been described as the consequence of shared genetic processes, developmental pathways, functional selective pressures, and/or phylogenetic constraints (Lieberman, 2011; Marcucio et al., 2011; Parsons et al., 2011, 2015; Bastir and Rosas, 2016; Martínez-Abadías et al., 2016).

Morphological integration between biological structures is purported to have a significant impact on the evolution of new morphologies (Wagner and Altenberg, 1996; Schlosser and Wagner, 2004; Klingenberg, 2005). When the covariation level is high, the

* Corresponding author.
E-mail address: dimitrineaux@gmail.com (D. Neaux).
[1] Dimitri Neaux and Gabriele Sansalone should be considered co-first authors.

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integration between traits is strong. In this case, morphological variation is constrained and channeled into specific directions of phenotypic space, corresponding to paths of least resistance (Marroig et al., 2004; Wagner et al., 2007; Klingenberg, 2010; Goswami et al., 2014; Evans et al., 2017). Conversely, when covariation is lower between traits than within traits (i.e., traits constitute different modules), constraints on morphological variation are reduced. In this case, specialization of traits is facilitated, as the different structures can respond independently to selective forces.

In addition to phenotypic diversity, integration may also affect the rate at which morphologies evolve, i.e., evolutionary rates. A strong integration among structures, limiting the ability of a particular structure to respond to selective pressures, or the magnitude of that response, may lead to a reduction in rates of evolution for this specific structure (Goswami et al., 2014).

Previous studies underline the key role of morphological integration in shaping the phenotypic diversity of the primate basicranium and face, notably in hominoids (Strait, 2001; Bastir and Rosas, 2006, 2016; Gkantidis and Halazonetis, 2011; Singh et al., 2012; Neaux et al., 2013; Neaux, 2017). However, a comprehensive understanding of the impact of covariation on the evolution of these structures across primates is lacking. The present study is designed to assess how morphological integration affects the relationship between primate basicranial and facial evolutionary pathways. First (objective #1), we will quantify integration and modularity between these structures across the primate clade. Then (objective #2), we will assess the extent of correlation between primate basicranial and facial shapes, and three of the main factors purported to have played an important role in shaping these structures during primate evolution (i.e., endocranial volume [ECV], positional behavior, and diet). Finally (objective #3), we will define the influence of morphological integration on shape disparity through time and rates of evolution for the basicranium and face.

1.2. Objectives of this study

Objective #1 The basicranium and face have been previously described as integrated structures in different primate clades (Marroig and Cheverud, 2001; Marroig et al., 2004; Bastir and Rosas, 2006, 2016; Gkantidis and Halazonetis, 2011; Singh et al., 2012; Neaux et al., 2013; Makedonska, 2014; Neaux, 2017). Yet, studies of modularity in primates (Esteve-Altava et al., 2013, 2015; Esteve-Altava, 2017), and at higher taxonomic levels (Goswami, 2006, 2007; Goswami and Polly, 2010), have revealed that the basicranium and face can also be considered as two partially decoupled modules. In the present study, we will, for the first time, test for both integration and modularity between the basicranium and face across primates, including all the major clades.

Objective #2 Alongside morphological integration, multiple factors influence the development and evolution of the basicranium and face. The ECV and positional behavior (i.e., locomotion and posture) are among the main features influencing basicranial shape. Previous studies suggest that variation in morphology and flexion of the basicranium are mainly structural responses to generate enough space in the braincase for an enlarged brain (Biegert, 1957; Ross and Ravosa, 1993; Spoor, 1997; Lieberman et al., 2000b; Bastir et al., 2010). Additionally, it has been hypothesized that primate species with more upright, or orthograde, positional behaviors exhibit an anteriorly positioned foramen magnum and corresponding modifications to the morphology of the basicranium (Dean and Wood, 1981; Russo and Kirk, 2013, 2017). Orthograde posture might also influence aspects of facial prognathism and orientation (Sirianni and Swindler, 1979; Ross, 1995; Zollikofer et al., 2005; Lieberman, 2011). Further, diet is considered to be a major factor affecting facial shape evolution in primates (Anapol and Lee, 1994; Spencer, 1999). In particular, bite force efficiency is considered to be adaptively significant (Ross and Iriarte-Diaz, 2014; Smith et al., 2015).

If morphological integration impacts the way ECV, positional behavior, and diet influence basicranial and facial shapes, changes in one of these features (ECV, positional behavior, and/or diet) are likely to influence both structures (face and basicranium). Specifically, ECV and positional behavior, linked to basicranial shape, should also influence facial shape. Conversely, diet, related to the morphology of the face, should also impact the basicranium. In order to assess the impact of morphological integration, we define the relationship between ECV, positional behavior, and diet on one hand, and between the 'basicranium-face complex' (BFC; i.e., the association of basicranial and facial structures), basicranium, and face on the other hand. We test the hypothesis that ECV, positional behavior, and diet significantly influence the shape of both the basicranium and the face.

Objective #3 As previously suggested, morphological integration can affect both shape disparity and rates of phenotypic evolution (Goswami et al., 2014). In the present study, we test the influence of integration on the evolution of the basicranium and face by assessing shape disparity through time and rates of evolution in the BFC, the basicranium, and the face. These analyses aim to determine how morphological integration impacts the evolution of the basicranium and face. If integration impacts shape disparity and evolutionary rates, the two studied structures should behave as an almost uniform system (Klingenberg, 2008, 2014). We will, thus, test the hypothesis that shape disparity and rates of evolution are similar in the BFC, the basicranium, and the face.

2. Material and methods

2.1. Sample

The sample consists of 141 crania of extant primates belonging to 54 different species (Table 1), constituting a representative sample of the diversity of the order, i.e., ~75% of the recognized extant genera (Groves, 2001). One to three individuals, depending on the availability of the specimens, represent each species. The sample includes males and females for each species wherever possible. We chose to include a great number of species rather than a great number of specimens for each species, as our study focuses on integration at the interspecific level. The list of specimens, including museum catalog number and location, can be found in the Supplementary Online Material (SOM) Table S1. Computed tomography (CT) scans were obtained from the Morphosource [dataset] (Aguilar et al., 2017a, 2017b; Allen and Schaeffer, 2017; Copes et al., 2017) and the National Museum of Natural History (http://humanorigins.si.edu/evidence/3d-collection/primate) digital repositories. They belong to the collections of the Museum of Comparative Zoology at Harvard University (Cambridge, USA), the National Museum of Natural History (Washington, USA), the Natural History Museum (London, UK), and the Duke Lemur Center (Durham, USA). All specimens were determined to be adults based on the full eruption of the third molars. We created three-dimensional (3D) virtual representations in PLY file format from CT scans with pixel size and slice thickness adjusted according to the cranial size of each specimen ranging from 0.3 mm to 1 mm. We subsequently edited the surfaces with Geomagic v.2014 software (3D Systems, 2014) to have access to internal basicranial structures.