



The relative correspondence of cranial and genetic distances in papionin taxa and the impact of allometric adjustments



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ABSTRACT

The reconstruction of phylogenetic relationships in the primate fossil record is dependent upon a thorough understanding of the phylogenetic utility of craniodental characters. Here, we test three previously proposed hypotheses for the propensity of primate craniomandibular data to exhibit homoplasy, using a study design based on the relative congruence between cranial distance matrices and a consensus genetic distance matrix (“genetic congruence”) for papionin taxa: 1) matrices based on cranial regions subjected to less masticatory strain are more genetically congruent than high-strain cranial matrices; 2) matrices based on cranial regions developing earlier in ontogeny are more genetically congruent than matrices based on regions that develop later; and 3) matrices based on cranial regions with greater anatomical/functional complexity are more genetically congruent than matrices based on anatomically simpler regions.

Morphological distance matrices based on the shape of 15 different cranial regions, delineated on the basis of previous catarrhine studies, were statistically compared to a matrix of known genetic distances in papionins. Since sexual dimorphism and allometry are known to characterize this clade, several analytical iterations were conducted: 1) mixed-sex, male-only, and female-only analyses and 2) with and without an allometric scaling adjustment. Across all datasets, the chondrocranium matrix was the most consistently correlated with genetic distances, which is also consistent with previous studies of cercopithecoïd taxa; however, there was no support for the internal predictions of the three hypotheses tested. Allometric scaling corrections had the largest impact on the genetic congruence of facial shape matrices, a result consistent with previous studies that have described facial homoplasy in papionin taxa. These findings differ from patterns described for hominoid taxa, suggesting that no single predictive criterion can explain phylogenetic utility of cranial datasets across catarrhine primate taxa. Many of the differences in morphological-genetic matrix correlations could result from different levels of phenotypic integration and evolvability in cercopithecoïds and hominoids, suggesting that further study of these phenomena in extant primates is warranted.

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1. Introduction

Accurate reconstructions and interpretations of the past, including the taxonomy, phylogeny, and evolutionary adaptations of fossil taxa require a thorough understanding of the biology of extant taxa. In particular, inferences regarding the hominin and non-hominin primate fossil records are dependent upon the development of an accurate inference model of primate

morphological diversity. The vast majority of the primate fossil record is composed of specimens for which direct DNA evidence is unattainable. Thus, morphological data must necessarily form the central basis for many phylogenetic, systematic, and evolutionary retrodictions. In primates, there is a general consensus that cranial morphology reflects genetic relationships among species and individuals to a reasonable degree; however, documented instances of homoplasy and phenotypic plasticity complicate such interpretations and result in potentially contradictory information among morphological datasets.

Most notably, [Collard and Wood \(2000\)](#) determined that several sets of craniomandibular and dental characters in hominoid and

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papionin species did not reflect the known phylogenetic relationships among these taxa, suggesting that craniodental characters may not be reliable indicators of phylogeny in the fossil record. Several subsequent studies have also revealed that different subsets of cranial data differ in their correspondence with genetic distances in human populations (Roseman, 2004; Harvati and Weaver, 2006; Smith, 2009; von Cramon-Taubadel, 2009a, b, 2011a, b), guenons (Cardini and Elton, 2008), and hominoid taxa (von Cramon-Taubadel and Smith, 2012). These findings highlight the importance of understanding the evolutionary basis for patterns of cranial variation across extant primate clades before they are extrapolated into the fossil record.

In the paleoanthropological literature, three major factors thought to predict the phylogenetic utility of different craniodental datasets have been suggested and widely discussed (for review see von Cramon-Taubadel, 2014). These factors comprise (1) the extent to which particular aspects of cranial morphology might be influenced by biomechanical (typically masticatory) strain, (2) the ontogenetic development and perceived “heritability” of cranial regions, and (3) the overall anatomical and functional complexity of particular cranial elements. Below we detail how these factors have been employed as a theoretical basis for proposed phylogenetic hypotheses and the outcomes of previous tests of these hypotheses.

1.1. Biomechanical strain

The “homoiology hypothesis” is predicated on the idea that skeletal regions that respond to non-genetic factors such as biomechanical stress (i.e., are subject to phenotypic plasticity) are more likely to result in homoplasies (“homoiologies”) than bones under reduced loading regimes (Collard and O’Higgins, 2001; Wood and Lieberman, 2001; Lycett and Collard, 2005; Collard and Wood, 2007). In other words, bones from higher strain regions should be more variable morphologically, and consequently are thought to be less reliable indicators of phylogeny, than those from lower strain regions (Lieberman, 1995). In the skull, the primary biomechanical stressors derive from the masticatory apparatus, including the strains experienced by the craniofacial bones during the chewing cycle, the forces resulting from muscle vectors in the temporalis, masseter, and pterygoid muscles, and the stress experienced via the load-bearing temporomandibular joint (Bouvier, 1986; Wall, 1999; Vinyard et al., 2003).

Wood and Lieberman (2001) compared levels of morphological variation in lower strain cranial regions (basicranium, neurocranium, upper face) to those that experience higher levels of masticatory strain (palate, mandible) in several catarrhine primates, and determined that on average, the higher strain regions were indeed more variable than lower strain regions. From this finding, they concluded that highly plastic characters, such as those of the masticatory complex, should be avoided in taxonomic evaluations of fossil hominin specimens due to their inherent variability and presumed unreliability (Wood and Lieberman, 2001). However, subsequent analyses directly comparing phylogenetic trees based on craniodental data and molecular genetic data found that despite elevated levels of variability, high strain cranial regions did not produce trees any less congruent with the molecular phylogeny than low strain regions in papionins (Lycett and Collard, 2005) or hominoids (Collard and Wood, 2007; von Cramon-Taubadel and Smith, 2012). In fact, in contrast to the homoiology hypothesis, several of the more phenotypically plastic regions were found to reflect the genetic relationships more reliably than those that remodel less in response to environmental stimuli (Collard and Wood, 2007).

Recently, the homoiology hypothesis was tested in hominoids using 3D landmark-based data and a morphological-genetic distance matrix correlation approach (von Cramon-Taubadel and

Smith, 2012). Morphological matrices based on the shape of the mandible and palatomaxilla matrices were found to be less strongly correlated with the genetic matrix than many of the other cranial regions; however, they still yielded morphological matrices that were significantly correlated with the genetic distances among taxa, albeit with lower correlation coefficients. Interestingly, other “masticatory” regions, such as the zygotemporal, were among the most strongly correlated cranial matrices with the genetic distance matrix (von Cramon-Taubadel and Smith, 2012). In guenons, the morphology of several masticatory regions, the mandible, oral cavity, and zygomatic region, all yielded morphological matrices significantly correlated with genetic distances among taxa, but the non-masticatory chondrocranium did so with a higher correlation coefficient (Cardini and Elton, 2008). Therefore, despite the intuitive link between masticatory strain, plasticity, and homoplasy, the relationship between these factors is complex, and this phenomenon does not necessarily negatively affect the correspondence between cranial morphology and genetic patterns (von Cramon-Taubadel, 2009b; Roseman et al., 2010).

The homoiology hypothesis has also been tested empirically in humans (von Cramon-Taubadel, 2009b). A comparison of cranial regions associated with masticatory function (palatomaxilla, zygotemporal) versus those that are unassociated with mastication (basicranium, neurocranium, upper face) in 12 human populations revealed that “masticatory” cranial regions are more variable in humans, as they are in other catarrhine species (von Cramon-Taubadel, 2009b). However, this increased phenotypic plasticity does not impact the extent to which these regions reflect past population history, because some masticatory and non-masticatory cranial regions were found to be equally genetically congruent when morphological and neutral, genetic, among-population distance matrices were compared (von Cramon-Taubadel, 2009b).

In humans, a number of studies have indicated that the morphology of the masticatory apparatus may be influenced by subsistence strategy (Larsen, 1997; González-José et al., 2005; Sardi et al., 2006; Lieberman, 2008, 2011; Pinhasi et al., 2008; Paschetta et al., 2010; Holmes and Ruff, 2011; von Cramon-Taubadel, 2011b). In particular, morphology of the mandible shows a weak correspondence with geographic distance (Nicholson and Harvati, 2006) and a lower correlation with neutral genetic distances than many other cranial regions (Smith, 2009). A comparison of the morphology of masticatory regions, such as the mandible and palatomaxilla, revealed that they co-vary with subsistence behavior among human populations (von Cramon-Taubadel, 2011a). Thus, it appears that the masticatory regions of the craniofacial complex in humans reflect a myriad of neutral and non-neutral evolutionary factors, thus influencing their covariation with inter-population genetic relationships.

1.2. Development and heritability

Several authors have also suggested a direct link between trait heritability, phenotypic plasticity, and developmental variation, such that presumably plastic and, therefore, variable traits are assumed to also exhibit lower heritability (Lieberman et al., 1996; Wood and Lieberman, 2001). The rationale behind this argument is similar to that of the homoiology hypothesis in that morphological regions thought not to be affected by phenotypic plasticity are predicted to more accurately reflect underlying “genetic” factors, rather than environmentally induced sources of variation during an organism’s lifetime.

In particular, it is often suggested that of the three major developmental complexes of the cranium—splanchnocranium, neurocranium, and basicranium—the endochondrally ossifying basicranium should be most developmentally stable (Olson, 1981;

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