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Evolutionary insights into global patterns of human cranial diversity: population history, climatic and dietary effects

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Summary – *The study of cranial variation has a long, and somewhat difficult, history within anthropology. Much of this difficulty is rooted in the historical use of craniometric data to justify essentialist typological racial classification schemes. In the post-war era of the 'New Physical Anthropology' (sensu Washburn, 1951), anthropologists began to analyse human variation in an explicitly populationist and evolutionary philosophical and analytical framework. However, even within recent decades, substantially different approaches have been employed; some advocate a focus on the analysis of individual traits or clines, while others are explicitly adaptationist, with a focus on natural selection as the preeminent force of phenotypic diversification. In recent years, a series of studies have analysed craniometric data in an explicitly quantitative genetic framework, which emphasises the importance of neutral forces such as migration, gene flow and genetic drift in creating global patterns of phenotypic diversity. This approach has revealed that global patterns of cranial variation can largely be explained on the basis of neutral theory. Therefore, human cranial data can be productively employed as a proxy for neutral genetic data in archaeological contexts. Moreover, there is a growing recognition that regions of the cranium differ in the extent to which they fit a neutral model of microevolutionary expectation, allowing for a more detailed assessment of patterns of adaptation and phenotypic plasticity within the human skull. Taking an historical perspective, the current state of knowledge regarding patterns of cranial adaptation in response to climatic and dietary effects is reviewed. Further insights will be gained by better incorporating the study of cranial and postcranial variation, as well as understanding the impact of neutral versus non-neutral evolution in creating among-species diversity patterns in primates more generally. However, this will most effectively be achieved when comparative anatomy studies are situated within an explicitly quantitative genetic evolutionary framework.*

Keywords – *Cranial variation, Population History, Adaptation, Quantitative Genetics, Microevolution*

Introduction

This review has a number of separate yet interconnected goals. Primarily, the aim is to review the current state of knowledge regarding the microevolutionary history of global patterns of craniometric variation. Much of this microevolutionary history is neutral; that is, the result of the stochastic processes of past mutation, gene flow, and genetic drift. Some aspects of craniometric variation may be attributed to the actions of past diversifying selection, particularly in relation to climatic and dietary factors. However, these adaptations have affected different globally distributed populations to varying degrees and appear to only affect specific anatomical regions of the cranium. Importantly, these evolutionary insights depend upon the application of an explicitly quantitative genetic analytical framework, which places emphasis on a null hypothesis of neutral evolutionary expectation that must first be rejected prior to testing specific adaptive hypotheses (Roseman & Weaver, 2007). Hence, this review also has a secondary aim; to illustrate, by way of an historical perspective, the underlying principles of an explicitly microevolutionary approach to understanding global patterns of phenotypic variation. Utilising this conceptual and analytical framework allows for the past action of neutral and selective evolutionary forces to be disarticulated, and advocates for the statistical control of the stochastic patterns of past (neutral) population history when testing the predictions of adaptive hypotheses.

Historical perspective

The form of the human cranium has long been the focus of attention in anthropological studies. Much of this association rests with the historical use of craniometric data to create and justify essentialist racial classifications (Gould, 1981; Molnar, 1983). Starting with the work of Johann Blumenbach (1752-1840) in the 18th century (Blumenbach, 1795), collections of crania were amassed with the express purpose of devising more accurate means of measuring cranial variation and/or to create typological racial taxonomies for modern humans (e.g., Morton, 1839, 1844; Broca, 1861, 1875; Topinard, 1890; von Török, 1890; Fawcett & Lee, 1902; Duckworth, 1904a,b). Particular emphasis was placed on the shape and size of the cranium given its association with the brain and the prevailing assumption that brain form and size were directly related with intelligence (see e.g., review and critique by Tobias, 1970). In particular, the work of Franz Joseph Gall (1758-1828) and Johann Gasper Spurzheim (1776-1832) provided the basis for the popular nineteenth pseudoscience of 'phrenology' (Gall & Spurzheim, 1810, 1812; Spurzheim, 1832), which advocated that the external features of the skull provided direct insight into a person's inherent talents and personality (Brace, 2005).

In the late nineteenth century, precipitated by the work of Anders Retzius (1796-1860), the 'cranial index' became a popular measure in 'racial' studies, whereby the relative length and width of the skull allowed individuals to be characterised as doliocephalic (long, narrow head), mesocephalic (intermediate) and brachycephalic (short, wide head). In addition, based on work by Pieter Camper (1722-1789) in the eighteenth century (Camper, 1791), facial form was characterised according to the angle at which the face projected in front of the braincase (Brace, 2005). Orthognathic (steep facial angle) indicated 'superior' racial form, while more prognathic (projecting face) was used to imply inferior (more primitive) racial types (e.g., Morton, 1839; Nott & Gliddon, 1854). There was also a widely held belief that cranial form was resistant to change and, therefore, that cranial features would provide an accurate description of fixed 'racial' affinities. Franz Boas provided empirical evidence to the contrary (Boas, 1899, 1912) demonstrating that the cranial shape differed in children born to immigrant groups in the U.S.A. compared to children from the same countries in Europe. His results suggested that environmental influences on cranial shape could occur and, therefore, argued against the prevailing view of the fixity of cranial form within and between races (see also Sparks & Jantz, 2002; Gravlee *et al.*, 2003; Relethford, 2004b).

As physical anthropology began its divorce from racially-motivated research in the second half of the twentieth century, the study of craniometric variation underwent several philosophical and theoretical shifts. However, of particular interest here is the increased application over recent decades of an explicitly microevolutionary analytical framework based on population and quantitative genetic theory (Roseman & Weaver, 2007). This analytical framework differs from alternative approaches in two key respects; the use of an operationalized taxonomic unit (i.e. the 'population') to delineate and compare groups of humans at a global level, and the use of population variance and covariance patterns to statistically relate population affinities with models of microevolutionary expectation. This approach, therefore, allows for the testing of specific hypotheses regarding past population history and instances of adaptation. Here, an historical overview of this analytical approach is provided, and thereafter, current knowledge regarding global patterns of cranial variation is reviewed in order to offer new insights into the evolution of patterns of global craniometric diversity.

New theoretical and methodological approaches

The 'population' as the unit of analysis

The call for a 'New Physical Anthropology' (Washburn, 1951) in post-war anthropology signalled a shift away from deterministic typological thinking and racial description, and a move towards the application of neo-Darwinian principles to the analysis of human variation (Washburn, 1963). Perhaps more importantly, it signalled a shift towards replacing 'race' concepts with 'population' concepts (e.g., Thieme, 1952). The effects of the 'modern synthesis' (*sensu* Huxley, 1942) began to permeate anthropology in terms of understanding evolutionary change as a dynamic process of changing allele frequencies *within* species (microevolution), ultimately leading to the creation of new species (macroevolution) (e.g., Fisher, 1930; Wright, 1931; Haldane, 1932; Dobzhansky, 1937; Huxley, 1942). As early as 1942, anthropologist Ashley Montagu was advocating the use of 'populations' as the analytical unit of human variation and argued against the "artificial" and "confusing" typological concept of 'race':

> *"If it can be agreed that the human species is one and that it consists of a group of populations which, more or less, replace each other geographically or ecologically and of which the neighbouring ones intergrade and hybridize wherever they are in contact, or are potentially capable of doing so [Mayr, 1941a, 1941b], then it should be obvious that the task of the student interested in the character of these populations must be to* study the frequency distribution of the genes which characterize them – not entities which are purely imaginary.*" (Montagu, 1952, pp. 41-42, my emphasis).*

As noted by Mayr (1976, p. 28), the views of the typologist and the populationist are diametrically opposed, both philosophically and methodologically. The populationist's view is that "[a]ll organisms … are composed of unique features and … form populations of which we can determine only the arithmetic mean and the statistics of variation. … For the typologist, the type (*eidos*) is real and the variation an illusion, while for the populationist the type (average) is an abstraction and only the variation is real". Therefore, a population approach to understanding the evolution of continuous variation within the human species relies on a statistical and analytical approach based on the comparisons of variance/covariance patterns for understanding the causal link between genetic evolution and phenotypic changes in populations over time.

Seemingly, for some biologists and anthropologists, the incorporation of evolutionary theory and methods into anthropology could be quite simply achieved by using 'population' as a synonym of 'race', with the recognition that the new analytical framework was fundamentally different from the old pre-Mendelian essentialist racial typologies. For example, Dobzhansky (1944) defines (human) races as "populations differing in the incidence of certain genes, but actually exchanging or potentially able to exchange genes across whatever boundaries (usually geographic) separate them" (p. 252). Dobzhansky was quite comfortable with the conception of races as 'subspecies' (1944, p. 252) and indeed viewed 'races' as dynamic units of incipient speciation (Dobzhansky, 1937; Lewontin, 2003). However, Dobzhansky's employment of the term 'race' as a synonym for subspecies in relation to the question of *human* variability could be considered naïve given the history of prejudice and fallacy surrounding the use of the term in anthropology (Livingstone, 1962). It is for precisely this reason that Julian Huxley, Ashley Montagu and others (e.g., Huxley & Haddon, 1935; Huxley, 1941, 1942; Montagu 1942) advocated dropping the term 'race' altogether from the anthropological literature in favour of the "noncommittal phrase" (Huxley, 1941, p. 126) of 'ethnic group'. Montagu (1952) defined ethnic group as representing "…one of a number of populations, which together comprise the species *Homo sapiens*, but individually maintain their differences, physical and cultural, by means of isolating mechanisms such as geographic and social barriers” (pp. 87-88). The key issue for evolutionary-minded anthropologists was that a conceptual separation was required between the “materials” (Montagu, 1952, p. 38) that make up human variation (i.e. genetic, phenotypic, social and cultural factors) and the theoretical tools used to understand that variation. However, various essentialist concepts continued to be used to create typologies of race within anthropology for several decades (e.g., Coon *et al.*, 1950; Garn & Coon, 1955; Garn, 1961; Coon, 1962) although many empirical studies began to focus more on genetic as opposed to morphological or phenotypic data (e.g., Boyd, 1950). Hence, it is important to realise that craniometry is often viewed, for historical reasons, as synonymous with the construction of essentialist typological racial categories (e.g., Gould, 1981), yet it is not the data themselves that are the problem but the theoretical and analytical framework within which these data were understood and interpreted (Weiss & Fullerton, 2005).

During the 1960s and 70s, there was a shift in focus from ‘populations’ or ‘races’ as the units of analysis and an increased emphasis on the geographic patterns created by individual genetic or phenotypic traits (e.g., Livingstone, 1962; Brace, 1964, 1980; Krantz, 1980). This framework argued that no satisfactory entity could adequately be defined to describe the actual global patterns of variation for continuous traits in humans. The focus was placed instead on the description and interpretation of clinal patterns of genetic and phenotypic variation (Caspari, 2003; Mielke *et al.*, 2006). Also important in this context are the empirical findings of Lewontin (1972) who demonstrated that much more genetic variation existed *within* groups classically attributed to major geographic ‘races’ than lay between these groups. This has subsequently been (somewhat erroneously) interpreted as meaning that any two individuals drawn at random from the same group were more likely to differ from one another genetically than two individuals drawn at random from two different groups (Edwards, 2003; Witherspoon *et al.*, 2007). Lewontin was making the point that overall genetic variation apportioned in such a way that most of the variability actually lies within populations, rather than between populations (Barbujani *et al.*, 1997; Jorde *et al.*, 2000; Bamshad *et al.*, 2004; Rosenberg *et al.*, 2005). This finding was used by Lewontin (1972) to argue that the classic *typological* concept of non-overlapping races was of no taxonomic value and should be abandoned. In that sense Lewontin’s argument was entirely correct and worth making, especially given the historical context of typological thinking within anthropology. However, his emphasis on taxonomic significance detracted from the real problem, which was not that patterns of human genetic (and indeed phenotypic) variation have no value in terms of understanding the evolutionary *relationships* between human populations (Rosenberg *et al.*, 2002; Edwards, 2003; Long & Kittles, 2003; Hunley *et al.*, 2009; Long *et al.*, 2009; Rosenberg, 2011, see also Howells, 1973; Cavalli-Sforza *et al.*, 1988; Lahr, 1996; Cavalli-Sforza, 1997), but rather that the preconceived theoretical construct of human racial taxonomy was flawed.

A quantitative genetic framework for the analysis of craniometric variation

In the 1980s, largely driven by the work of John Relethford and colleagues, anthropometric (including craniometric) data began to be analysed in an explicitly quantitative genetic framework (e.g., Relethford, 1980; 1982, 1988; Relethford *et al.*, 1980, 1981; Relethford & Lees, 1982; Rogers & Harpending, 1983; Williams-Blangero, 1990; Williams-Blangero & Blangero, 1989, 1990; Blangero, 1990). This body of work applied population and quantitative genetic theory and methods (e.g., Fisher, 1930; Wright, 1951; Falconer, 1960; Crow & Kimura, 1970; Cavalli-Sforza & Bodmer 1971; Crawford & Workman, 1973; Morton, 1973; Mielke & Crawford, 1980) to classic anthropological data. These studies served to illustrate that when analysed under explicit conditions, anthropometric data were useful proxies for genetic data in terms of estimating population structure and history, modelling the effects of past gene flow and the effects of various microevolutionary forces such as genetic drift and natural selection (see also e.g., Lande, 1976, 1977, 1979; Cheverud 1982, 1988; Lynch & Hill, 1986; Lynch, 1989, 1990). The framework developed by Relethford and Blangero (1990) is particularly important as it provided a model-bound means of using continuous quantitative traits (such as craniometric data) to derive measures of population affinities and distance under varying assumptions of heritability. Their framework extended that of Harpending and Ward (1982) for use with genetic data, which modelled the expected heterozygosity (variance) for populations within a geographic region as a function of the total heterozygosity, and the distance of the population from the regional centroid of allele frequencies (i.e. the average allele frequencies of the whole region). Populations who were experiencing greater than average gene flow from outside the region (i.e. outbreeding) would exhibit greater heterozygosity than expected by their distance to the centroid, and populations experiencing less than average gene flow from outside the region (i.e. inbreeding) would exhibit less variance than predicted on the basis of their distance to the centroid.

Relethford & Blangero (1990) extended this principle for use with multiple quantitative traits, under the assumption of an equal (no dominance effects) and additive (no epistatic effects) effects model for the relationship between genotype and phenotypic expression of quantitative traits [See Box 1]. That is, phenotypic variances are assumed to be proportional to additive genetic variances and environmental effects across traits were considered equal (Williams-Blangero & Blangero, 1989). In addition, Relethford & Blangero (1990) developed methods for estimating genetic relationship matrices from quantitative traits. These relationship or R-matrices describe the pairwise affinities of populations in a relative manner, with positive values in the matrix indicating that two populations are more similar than on average and negative values indicating populations are more different than on average (Relethford *et al.*, 1997). Relationship matrices can then be employed to calculate genetic (and phenotypic) distance matrices (Harpending & Jenkins, 1973), which describe the pairwise affinities of populations in terms of their absolute differences. The assumption that quantitative traits exhibit variance patterns proportional to additive genetic variances may not be unrealistic (e.g., Cheverud, 1988; Konigsberg & Ousley, 1995), despite the fact that phenotypic variances are potentially affected by many other environmental factors (Relethford & Harpending, 1994). Numerous studies have employed phenotypic variance patterns to estimate the underlying genetic variance patterns (e.g., Relethford & Blangero, 1990; Sciulli & Mahaney, 1991; Konigsberg & Blangero, 1993; Relethford & Harpending, 1994; Varela & Cocilovo, 2002) and have concluded that provided that trait heritabilities are not too low (i.e. $h^2 < 0.2$), the proportionality of genetic and phenotypic affinity matrices holds true (Cheverud, 1988). Phenotypic variances are always greater than their analogous genetic variances and, therefore, population distances based on phenotypic traits under the assumption of complete heritability (i.e. $h^2=1.0$) are by definition *minimum* estimates of genetic distances.

Building on this framework developed in the 1980s and 90s, a body of literature employing explicitly quantitative genetic approaches to understanding modern human craniometric evolution has emerged over the last 25 years (e.g., Lynch, 1989; Konigsberg, 1990; Relethford, 1994, 2001, 2002, 2004a, 2010; Ackermann & Cheverud, 2004; González-José *et al.*, 2001, 2004; Roseman, 2004; Roseman & Weaver, 2004; Harvati & Weaver, 2006a,b; Martínez-Abadías *et al.*, 2006, 2012; Manica *et al.*, 2007; Perez *et al.*, 2007; Weaver *et al.*, 2007, 2008; von Cramon-Taubadel & Lycett, 2008; Betti *et al.*, 2009, 2010; Hubbe *et al.*, 2009; Perez & Monteiro, 2009; Smith, 2009, 2011; von Cramon-Taubadel 2009a,b, 2011a,b; Strauss & Hubbe, 2010). The importance of the quantitative genetic framework lies in the ability to model the dynamic processes of past evolution from phenotypic traits, and thereby distinguish between neutral evolution (*sensu* Kimura, 1968, 1983, 1989) due to mutation, genetic drift and gene flow, and diversifying microevolutionary change due to natural selection (Box 1; Roseman & Weaver, 2007; Weaver & Roseman, 2008). In cases where neutral forces can be assumed to be the major evolutionary factors creating patterns of phenotypic variation, quantitative traits can be used to infer past population history or population phylogenies (von Cramon-Taubadel & Weaver, 2009). Also, in order to identify non-neutral processes effectively, the null expectation of neutral evolution must first be rejected or controlled (Roseman & Weaver, 2007).

A consensus view has emerged that global patterns of human cranial variation are primarily shaped by neutral evolutionary forces. This consensus is strengthened by the fact that studies have employed different craniometric datasets and analytical approaches drawn from the quantitative genetic framework [See Box 2]. Firstly, numerous studies have demonstrated that global cranial variation apportions in a similar manner to presumed neutral genetic loci (e.g., Relethford, 1994, 2002, 2004a; González-José *et al.*, 2004; Roseman & Weaver, 2004; Hubbe *et al.*, 2009). This finding is particularly striking when compared against the apportionment of global skin colour variation, which show the exact opposite pattern (low within-population and high between-population variation) as expected for adaptive phenotypes that have been shaped by long-term diversifying selection. Another group of studies have statistically compared population distance matrices based on craniometric data against analogous matrices based on neutral genetic data. In all cases, neutral genetic and craniometric matrices were shown to be highly congruent (Roseman, 2004; Harvati & Weaver, 2006a,b, Smith, 2009; von Cramon-Taubadel, 2009a,b, 2011a,b).

A third approach has been to test whether craniometric data fit a model of iterative founder effects from an African origin as has been demonstrated for several neutral genetic datasets (e.g., Prugnolle *et al.*, 2005; Ramachandran *et al.*, 2005; Liu *et al.*, 2006; Jakobsson *et al.*, 2008; Li *et al.*, 2008; Hunley *et al.*, 2009). Several studies have found that, as is the case with neutral genetic data, within-population cranial variation is negatively correlated with geographic distance from sub-Saharan Africa (Manica *et al.*, 2007; von Cramon-Taubadel & Lycett, 2008; Betti *et al.*, 2009). This work is important in that it lends further empirical support to the 'Out-of-Africa' model for modern human origins (Eriksson *et al.*, 2012; Henn *et al.*, 2012) and also clarifies the relationship between craniometric distance and geographic distance found in other studies (e.g., Relethford, 2004a). A correlation between craniometric (or indeed genetic) distance and geographic distance is to be expected given that contiguous populations are more likely to share a recent common ancestor and experience intensive gene flow than populations that are geographically separate (e.g., Kimura and Weiss, 1964; Relethford, 2004a). However, the data congruence itself does not allow for a clear distinction between a classic model of 'isolation-by-distance' (*sensu* Wright, 1943; Malêcot, 1973) as opposed to a geographically-mediated model of nested serial founder effects from a common point of origin (e.g., Ramachandran *et al.*, 2005; Hunley *et al.*, 2009). It has recently been shown that a model combining serial population fissions, population bottlenecks, long range migration plus short-range gene flow (Hunley *et al.*, 2009) best explain global patterns of genetic diversity. This migration and gene flow history results in a nested hierarchical model of modern human genetic structure (e.g., Cavalli-Sforza & Piazza, 1975; Hunley *et al.*, 2009; Long *et al.*, 2009).

Finally, craniometric data have been shown to have a similar fit to theoretical patterns of neutrality (e.g., Lande, 1976, 1977, 1979, 1980; Lynch, 1989) as neutral genetic loci (e.g., Weaver *et al.*, 2007, 2008; Smith, 2011). Lande's (1977) approach is based on the statistical association of within- and between-population variance-covariance (V/CV) matrices. Under a null (neutral) expectation, these matrices are predicted to be proportional to one another, providing a simple yet powerful test of neutral evolution. Significant deviations from a proportionate within-between population V/CV pattern indicates substantial non-neutral effects such as diversifying natural selection. One of the key advantages of this approach is that it allows for the assessment of genetic drift in populations at differing points in time, as the pattern of within-between V/CV is expected to remain consistent through time under neutral conditions. Therefore, this approach has been applied to fossil taxa such as the Neanderthals (e.g., Weaver *et al.*, 2007, 2008) or the australopithecines and early *Homo* (e.g., Ackermann & Cheverud, 2004) to assess whether random evolutionary processes alone could explain observed patterns of morphological diversity amongst taxa.

While all of these studies make slightly different use of available cranial datasets and available analytical techniques, the empirical findings are remarkably consistent regarding the overall neutrality of the modern human cranium. This has a number of important ramifications. Firstly, it implies that we can use cranial shape variation to model past population history and demography in the absence of genetic data. This is especially important in the case of human prehistory and palaeoanthropology, where direct genetic data are unlikely to be abundant. Secondly, it underscores the importance of controlling for the effects of shared ancestry (i.e. population history) when attempting to uncover past instances of diversifying selection. While 'Galton's Problem' (Naroll, 1961) is most often associated with inference problems when studying cultural attributes in geographically spaced human societies, the same problem arises in the association between phenotypic attributes and presumed forces of adaptive change. The clearest example of this being climatic conditions, which (as discussed in further detail below) are spatially autocorrelated at a global level. Phenotypic (and genetic) traits are also spatially autocorrelated with geography, so correlations between climatic conditions and phenotypic traits cannot be taken as evidence for a *causal* association between the two. Galton's insight in 1889 (Naroll, 1961) is as relevant today as it was then. That is, in order to infer a true causal association between a spatially autocorrelated environmental factor and phenotypic patterns of variation, it is first necessary to control for the effects of shared ancestry (e.g., Roseman, 2004; von Cramon-Taubadel, 2009a, 2011b; Betti *et al.*, 2010).

Is the human cranium more than the sum of its parts?

It is clear, therefore, that multiple independent studies using slightly different methodological approaches and focusing on different morphological datasets have all suggested that *overall* cranial shape variation patterns can be explained as being the result of neutral microevolutionary population history. However, this is not the end of the matter, as the cranium is a complex mosaic structure comprising different anatomical regions, with differing embryological origins, ossification patterns, and functional attributes (e.g., Lieberman, 2011). Therefore, a key question arises: Is the cranium more than the sum of its parts? Do different cranial regions, defined on the basis of specific criteria differ in the extent to which they reflect this neutral past population history? Are some regions more likely to display divergent morphological patterns that are the signature of past directional selection? In contrast with some polygenic morphological traits such as skin colour, which are essentially 'univariate' being primarily attributable to relative levels of epidermal melanin (e.g., Relethford, 1997, 2002; Parra, 2007; Jablonski & Chaplin, 2010), cranial shape variation is a multivariate phenomenon. Therefore, there exists the potential that the cranium may be decomposed into regions or units that differ in the extent to which they reflect neutral population history.

Understanding the relative neutrality of individual regions of the cranium is important for two main reasons. Firstly, any action of past selection is likely to have only affected specific aspects of cranial morphology (and perhaps only in specific populations) and will, therefore, be 'swamped'

BOX 1: The Basic Principles of Population and Quantitative Genetics

In **population genetics**, the 'population' is the evolutionary unit of statistical analysis. Species are rarely single panmictic[1] groups and can, therefore, be analytically subdivided into 'populations' to account for the structured patterns of mating and gene flow within a species. Populations are also sometimes referred to as 'demes'. Within populations, evolution occurs via a change in allele *frequencies* from one generation to the next. The four major ways by which allele frequencies can be altered through time are:

- Mutation: introduction of new alleles
- Gene flow: introduction of new alleles through individual movement from outside of the population/deme
- Drift: stochastic loss of alleles through random sampling of alleles from one generation to the next
- Selection: differential reproductive success (fitness) of specific genotypes/phenotypes.

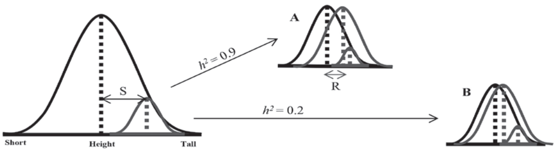
The key point is that some forces (mutation and genetic drift) occur **stochastically** and, therefore, affect allele frequencies in a random/neutral manner with respect to fitness. Selection, on the other hand, can affect allele frequencies in a **deterministic** way through the fitness differentials associated with particular genotypes/phenotypes.

Quantitative genetics extends the basic principles of population genetics to model the inheritance and evolution of continuous phenotypic characteristics (e.g., height, weight, skin pigmentation, craniometric data etc.). Quantitative traits are more difficult to model than simple Mendelian phenotypes because of the many factors contributing to overall phenotypic variance (**VP**$_{\text{henotype}}$). In any given population, **VP** can be decomposed into genetic (**VG**$_{\text{enetic}}$), environmental (**VE**$_{\text{nvironment}}$) and genotype-environment interaction (**VG/E**) components: **VP = VG + VE + VG/E**

However, genetic variance can be further decomposed into three potential sources of variation. Because continuous traits are **polygenic** (coded for by many different genetic loci), the actual genetic information inherited (additive, **VA**) does not map directly onto variation in the phenotype. Alongside additive genetic variance, there is the variance due to dominance effects at particular loci (**VD**) plus the effects that gene loci have upon each other in terms of gene expression (epistatic effects, **VI**). Additional to these genetic sources of variation, there is potential for environmental variability due to the differential expression of the same genotype in different environments (**VE**) and variable interactions between genotypes and particular environmental factors (i.e. **VG/E**).

Heritability is the proportion of phenotypic variation that is attributable to variation in heritable genetic material. While narrow-sense heritability (h^2) refers only to the proportion of phenotypic variation attributable to additive genetic variation (i.e. **VA/VP**), generally speaking only broad-sense heritability is estimated with any reasonable degree of accuracy (i.e. **VG/VP**). Heritability is sometimes misinterpreted as referring to the degree to which a phenotypic trait is genetically *determined*. However, it is a really a measure of how likely it is that a particular phenotype might respond to selection. For example, low heritability (close to 0) implies that most of the population phenotypic *variance* is due to *variance* in the environment. Very high heritability would suggest that most of the phenotypic variance is due to underlying genetic variability. Hence, heritability is a population- and trait-specific statistic and can change through time as additive genetic variance increases or decreases.

The importance of heritability in quantitative genetics is best illustrated by reference to the **Breeder's Equation ($R = h^2 S$):**



For any given quantitative trait, the response to selection (R) is a function of the heritability (h^2) and the selection differential (S). The selection differential is a measure of the strength of selection (i.e. the difference between the means of the reproductively active section of the population and the mean of the parental population). In the example above, there is strong positive directional selection in favour of tall individuals, such that only a sample of the tallest individuals (grey insert) will reproduce in any given generation. The likelihood that the daughter population will be significantly taller than the parental generation is dependent on the heritability of height. If height is highly heritable (A) then the response to selection will be strong, leading to a significant increase in height over time. If height is not very heritable (B) then the response to selection will be weak resulting in little change between the parental and daughter populations.

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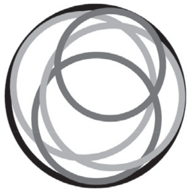
[1] **Panmictic/Panmixia**: A group of sexually-reproducing individuals (species, population etc.) in which any two members are equally likely to mate and interbreed. This notion of **random mating** is central to population genetic theory and species are rarely actually randomly mating.

BOX 2: Testing the neutral theory of phenotypic evolution using craniometric data

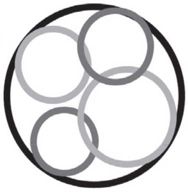
The use of population and quantitative genetic theory to model phenotypic evolution under neutral conditions (i.e. due only to mutation, gene flow and genetic drift) results in explicit empirical expectations regarding within- and between-population affinity patterns that can be tested using craniometric data. Here are examples of three empirical predictions of neutrality that have been tested using datasets of global craniometric variation.

1. **Variance apportionment within- and between-populations:** Human neutral genetic variances apportion at a global level such that most of the variance is found *within* rather than *between* populations. This is based on Sewell Wright's fixation indices (commonly referred to as F_{st}). Under panmictic conditions, heterozygosity (genetic variance) should be equivalent at the species level and at the population level (i.e. there is no genetic substructure). F_{st} measures the deviation from this prediction: $F_{st}=(H_T–H_s)/H_T=1$, where H_T=total heterozygosity, H_S=sub-population heterozygosity. Hence, low F_{st} is consistent with little substructure (high gene flow, no selection), while high F_{st} suggests high internal sub-structure (low gene flow or diversifying selection). In the diagram **A** is consistent with low F_{st} whereby four populations have high internal variance and relatively low between-group variance. This is the pattern of variance apportionment expected under neutral conditions in humans, and what is found using neutral genetic and craniometric data. In the case of **B**, populations have relatively restricted within-group variances and high between-group variance, as would be expected under non-neutral conditions. This is the pattern found for phenotypes such as skin colour that have been subject to strong natural selection. Example studies: Relethford (1994, 2002; Roseman & Weaver, 2004).

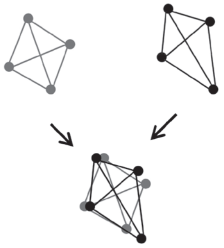
A



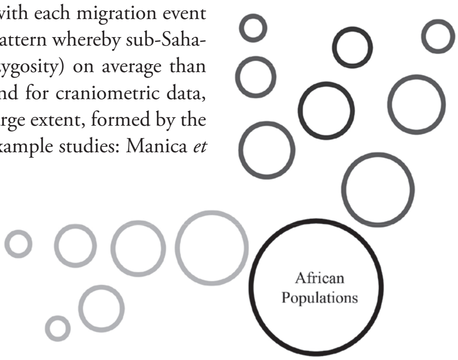
B



2. **Proportionality of neutral genetic and craniometric distance matrices:** Under neutral conditions, it would be expected that pairwise population distance matrices, based on matched neutral genetic and craniometric data, be highly congruent. Relethford and Blangero (1990) provide a framework for estimating phenotypic distance (Q_{st}) under varying assumptions of heritability. Matrices based on Q_{st} can be compared to analogous genetic matrices (based on F_{st}) using Mantel tests (Mantel, 1967). Example studies: Roseman (2004; Harvati & Weaver, 2006a; Smith, 2009; von Cramon-Taubadel, 2009a).



3. **Fit to a model of serial founder effects from point of origin:** Analyses of global datasets of autosomal neutral genetic markers have shown a strong negative relationship between within-population genetic variance (heterozygosity) and geographic distance from sub-Saharan Africa (e.g., Prugnolle *et al.*, 2005; Ramachandran *et al.*, 2005). This is consistent with a model of serial founder effects, whereby each successive migration event in human prehistory involved a substantial founder effect as humans migrated from Africa to eventually colonise all of the major landmasses. Founder effects are the consequences of intense genetic drift, as the effective population size decreases with each migration event resulting in reduced genetic variance. This results in a genetic pattern whereby sub-Saharan African populations have higher genetic variance (heterozygosity) on average than populations outside of Africa. The same pattern has been found for craniometric data, suggesting that global craniometric variance patterns are, to a large extent, formed by the demographic signature of past (neutral) population history. Example studies: Manica *et al.* (2007; von Cramon-Taubadel & Lycett, 2008; Betti *et al.*, 2009).



by the largely neutral effects shaping global patterns of overall cranial shape variation. Secondly, given our reliance on skeletal morphology for reconstructing fossil hominin phylogeny, we need to better understand the relative influence of neutral versus non-neutral evolutionary forces in generating patterns of morphological covariation in extant primate taxa. As modern humans are the only extant hominin species, any increased understanding that we might gain regarding the microevolutionary history of the human skeleton will aid our ability to accurately reconstruct fossil hominin phylogeny. However, in order to do so, we need to first overcome some methodological and conceptual stumbling blocks.

Methodologically, the accurate morphometric delineation of specific cranial regions has been greatly aided by the development of geometric (landmark-based) morphometric methods. Geometric morphometrics is a specific branch of statistical shape analysis that relies on the identification of homologous co-ordinate points in two- or three-dimensions, called 'landmarks'. There are various mathematical techniques for analysing and comparing the geometric properties of objects using landmarks (e.g., Bookstein, 1991; Dryden & Mardia, 1998; Adams *et al.*, 2004; Slice, 2005; Zelditch *et al.*, 2012). While traditional morphometric schemes for measuring cranial variation (e.g., Martin, 1928; Howells, 1973, 1996; Lahr, 1996) can accurately capture overall cranial form variation, landmark-based schemes offer a more flexible approach to quantifying the shape and size of individual cranial regions. In addition, landmarks can be captured on certain parts of the cranium inaccessible to traditional calliper measurements. One of the advantages of using a landmark-based morphometric system for quantifying cranial form is the ability to partition the cranium into constituent regions, while still maintaining a high number of measureable traits. While some parts of the skull may have more traditional anatomical landmarks than others, it is possible to use semilandmarks (e.g., Gunz *et al.*, 2005) to define the shape of regions devoid of traditional points (e.g. vault bones). In contrast, traditional measurement schemes generally cut across different cranial regions, making it more difficult to define individual units that are equally well quantified in terms of numbers of traits. Therefore, it is not surprising that the increased application of geometric morphometrics for quantifying human cranial data over the past 15 years (e.g., Hennessey & Stringer, 2002; Strand Viðarsdottir *et al.*, 2002; Harvati, 2003a; Martínez-Abadías *et al.*, 2006; Perez *et al.*, 2007; Nicholson & Harvati, 2006; Nikita *et al.*, 2012) led also to the publication of various studies directly comparing the relative genetic congruence of individual cranial regions (e.g., Harvati & Weaver 2006a,b; Perez *et al.*, 2007; Smith, 2009; von Cramon-Taubadel, 2009a,b, 2011a,b).

Harvati & Weaver (2006a,b) were the first to conduct empirical comparisons of three-dimensional cranial region shape and size affinity patterns against published neutral genetic data. They compared global population distance matrices based on facial, neurocranial (vault) and temporal bone shape and size against distance matrices based on neutral genetics, latitude, and climatic factors such as mean annual temperature. Broadly speaking, their results consistently found that vault and temporal bone shape was highly congruent with neutral genetic data, while facial shape was more reflective of temperature variation, as might be expected under thermoregulatory adaptation (Franciscus & Long, 1991; Roseman, 2004; Hubbe *et al.*, 2009; Noback *et al.*, 2011). Interestingly, both vault and temporal bone size were found to be related with climatic factors (Harvati & Weaver, 2006a), which is also consistent with thermoregulatory adaptation related to isometric scaling (e.g., Beals *et al.*, 1983; Smith *et al.*, 2007). In the second study (Harvati & Weaver, 2006b), it was found that overall cranial shape was correlated with both neutral genetic data and climatic data, however, the correspondence with climatic data was not statistically significant when the only Inuit (cold-adapted) population was removed from the analysis. This is important as it suggests that some relationships between cranial shape and climate are driven solely by the inclusion of extreme cold-adapted populations (see also Roseman, 2004; von Cramon-Taubadel, 2009a). Smith (2009) published a more extensive comparison of cranial regions, using a different craniometric dataset of 14 globally distributed human populations. Here, she compared the shape of the basicranium, temporal bone, cranial vault, upper face, upper jaw, mandible (lower jaw) alongside the shape of the entire cranium. The results found that all regions except for the mandible, upper jaw and vault were significantly correlated with neutral genetic data, although Dow-Cheverud tests (Dow & Cheverud, 1985) found no statistical difference in the strength of the genetic congruence of the basicranium, temporal bone, upper face or entire cranium.

The results of the two studies differ in their conclusions regarding the relative neutrality of the cranial vault, but they also differ in the numbers and positions of the landmarks used to delineate comparable cranial regions, the geographical locality of the populations employed, and the matches made between morphological and genetic samples. On the other hand, the studies did show remarkable consistency regarding the neutrality of the temporal bone, which had independently been suggested as a reliable candidate region for conducting phylogenetic and taxonomic analyses (Lockwood *et al*., 2004; Harvati, 2003b; Terhune *et al*., 2007; Smith *et al*., 2007). In order to make sense of these empirical findings, it is first necessary to tackle the conceptual hurdle of how we logically delineate comparable cranial regions.

To split or not to split?

The endeavour of assessing the relative influence of neutral versus non-neutral forces on regions of the cranium is only justified if it is possible to decompose the cranium into semi-discrete evolutionary units. As reviewed by Cheverud (1982), there is the philosophical view that evolution acts upon the whole phenotype and that, therefore, it is the total genotype that evolves (Mayr, 1963; Lewontin, 1974; Wright, 1980). If this holistic view of organismal phenotypic structure were true, then the endeavour of splitting the human cranium into constituent regions would be without theoretical merit. In essence, this would imply that if population history/phylogeny cannot be reliably reconstructed from the entire morphology (phenotype) of the taxa under consideration, then no separate element of the phenotype could offer a more reliable estimate of phylogeny. Given that most quantitative traits such as craniometric dimensions are polygenic (i.e. many loci code for a single phenotypic trait) and most loci contributing to the genetic variation of quantitative traits are pleiotropic (i.e. each locus affects many individual traits) (Lynch & Walsh, 1998), it seems reasonable to assume that genotypes and phenotypes are highly integrated systems with evolutionary forces affecting the entire organism in a systematic manner.

In contrast, theories of phenotypic integration (e.g., Olson & Miller, 1958) would posit that it is possible to detect, describe and interpret the small morphological changes that occur throughout the evolution of species and populations. This implies that there is a hierarchy of connectedness between various elements of the phenotype (Wagner & Altenberg, 1996; Chernoff & Magwene, 1999; Bastir & Rosas, 2005; Mitteroecker & Bookstein, 2007; Klingenberg, 2013) and that these connections vary in their nature and intensity depending on the extent to which they are developmentally and functionally related. Olson & Miller's (1958) method involves grouping quantitative measurements by the extent to which they are expected (on theoretical or experimental grounds) to relate to a similar biological function (F-sets), and based on the statistical association between measurements (P-sets). Equivalence between F- and P-sets implies that the hypothesis of morphological integration is supported (i.e. that morphological characters that are highly correlated tend to relate to integrated functional biological units) (Olson & Miller, 1958; Cheverud, 1982; Wilmore *et al*., 2007). These structures are sometimes referred to as 'modules', which are characters or sets of characters that are more tightly integrated internally than they are with other characters (Wagner, 1996; Hallgrímsson *et al.*, 2004; Mitteroecker & Bookstein, 2008; Klingenberg, 2013). Indeed, the concept of integration has been expanded beyond the level of the individual to include the concept of evolutionary integration (Cheverud, 1996; Marroig & Cheverud, 2001; Mitteroecker & Bookstein, 2008; Klingenberg, 2013). That is, the interaction between the genome and the phenotype via pleiotropy and linkage disequilibrium results in the coordinated evolution of traits over time, through the inheritance of genetically and developmentally integrated phenotypic structures (Cheverud, 1982).

Evidence for 'modules' in the primate cranium

Assuming that a complex phenotype such as the human cranium is composed of evolutionary modules makes plausible the hypothesis that individual regions (modules) of the cranium have been affected by neutral and non-neutral forces to varying extents. Based on integration theory, the expectation is that evolutionary modules can be defined on the basis of shared developmental, functional and positional information (González-José *et al.*, 2004; Willmore *et al.*, 2007). Functional matrix analysis (van der Klaauw, 1948-1952; Moss & Young, 1960; Moss, 1971) provides a framework for identifying functional and developmental relationships within the cranium. Within this framework, the cranium is considered an amalgamation of connected units (known as functional components) each of which perform semi-independent functions such as inspiration, vision, olfaction and sensory processing (e.g. Moss, 1954; Young, 1957, 1959; Moss & Salentijn, 1969). The two major components are the 'neurocranial' and the 'orofacial' components, whose skeletal elements approximately correspond with the cranial vault and the face/mandible, respectively. Each of these major components also contains several submatrices, as reviewed in detail by Cheverud (1982) (see also Fig. 1). Further empirical support for the existence of functional modules has been found in Rhesus macaques (Cheverud, 1982), saddle-back Tamarins (Cheverud, 1995), New World monkeys (Marroig & Cheverud, 2001), catarrhines (de Oliveira *et al.*, 2009), hominoids (Ackermann, 2002; Polanski & Franciscus, 2006; Singh *et al.*, 2012) and modern human populations (González-José *et al.*, 2004).

Criteria employed to delineate cranial 'modules'

The studies by Harvati & Weaver (2006a,b) and Smith (2009) demonstrate that cranial regions do indeed differ in the extent to which they reliably reflect the neutral genetic affinities between samples of globally distributed human populations. Subsequently, a number of studies (von Cramon-Taubadel, 2009a,b, 2011a) examined the issue of cranial regions in further detail by employing three distinct philosophical criteria for delineating cranial regions or 'modules'. The collective aim of these studies was two-fold; in each case to test specific hypotheses regarding the genetic congruence of particular cranial modules and, secondly, in so doing to assess the soundness of the *logic* used to delineate individual modules. In brief, the logic used to define and quantify individual cranial regions revolved around (1) the identification of the external morphology of individual cranial bones, (2) comparing levels of within-population variability (as a measure of phenotypic plasticity) against genetic congruence, and (3) delineating modules on the basis of developmental and functional criteria.

An assessment of the relative genetic congruence of individual cranial bones (von Cramon-Taubadel, 2009a) was carried out specifically to test the hypothesis advocated by Lockwood *et al.* (2004) and others that the shape of the temporal bone was a particularly reliable indicator of past population history/phylogeny (Harvati, 2003b; Harvati & Weaver, 2006a,b; Terhune *et al.*, 2007; Smith *et al.*, 2007; Smith, 2009). Two main rationale were given for this efficacy; that the functional and anatomical complexity of the temporal bone would minimise the likelihood that it be affected by (homoplastic) convergent adaptation (Lockwood *et al.*, 2004), and/or that its anatomical position in the general architecture of the basicranium would render it less prone to homoplastic changes, given the general (presumed) reliability of the basicranium for reflecting the genetic relationships amongst taxa (Olson, 1981; Lieberman *et al.*, 1996; 2000a,b; Wood & Lieberman, 2001; Harvati & Weaver, 2006a,b; Smith, 2009). A systematic comparison of the external shape of the temporal bone against the shape of six alternative cranial bones (see Fig. 2) found that the temporal, sphenoid, parietal and frontal bones were all equally strongly correlated with neutral genetic data, while the occipital, zygomatic, and (to a lesser extent) the maxilla were all less reliable for reconstructing population history. Also, it was found that the four 'good' bones were all statistically as reliable as using data encompassing the entire cranium. Therefore, the results supported the empirical findings of earlier studies suggesting that the temporal bone is a reliable aspect of cranial morphology for reconstructing phylogeny. However, the results did not support the theoretical assumptions underlying earlier studies, in that neither anatomical complexity nor inclusion in the basicranium could explain the results obtained. The frontal and parietal bones are, arguably, the least morphologically or functionally complex bones in the human cranium being flattened 'eggshell-like' components of the cranial vault. Similarly, the occipital bone, which forms a relatively large component of the basicranium, was found to be statistically less reliable than all other bones except for the zygomatic.

Another study (von Cramon-Taubadel, 2009b) focused specifically on testing the 'homoiology hypothesis' using modern human population data. The homoiology hypothesis was originally devised by Lieberman (1995, 1999, 2000), subsequently tested by others (Lieberman *et al.*, 1996; Collard & Wood, 2001, 2007; Lycett & Collard, 2005), and derives from the general observation that osseous growth is affected by the biomechanical environment, such that mechanical stress can influence resultant bone shape, size and strength properties (e.g., Herring, 1993; Lieberman, 1995, 1997, 1999, 2000, 2011; Skerry, 2000). Given that regions of the skeleton are likely to be affected by biomechanical factors to differing extents, it can reasonably be predicted that; (1) skeletal traits subject to intense biomechanical stress will exhibit significantly higher within-taxon variation, and that (2) these more variable traits will also be less reliable for reconstructing phylogeny than non-stressed (less variable) regions. Therefore, the homoiology hypothesis makes a direct conceptual link between the potential for phenotypic plasticity, within-group variability and the relative phylogenetic efficacy of anatomical structures. In the case of the cranium, the most likely candidate for causing significant differences in biomechanical stress across primate species is masticatory function. Wood and Lieberman (2001) established the empirical connection between variability and masticatory-induced phenotypic plasticity, by showing that masticatory traits were indeed more variable within-taxa (as measured by the Co-efficient of Variation) than non-masticatory traits. Thereafter, the predictions of the homoiology hypothesis were tested using papionin (Lycett & Collard, 2005) and hominoid (Collard & Wood, 2007) taxa. In both cases, the

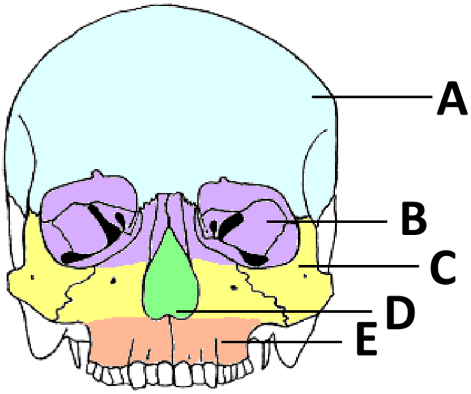


Fig. 1 - Skeletal units associated with the 'orofacial' matrix. According to the Functional Matrix Hypothesis (e.g., Moss & Young, 1960), the 'orofacial' component can be further subdivided into (A) Frontal, (B) Orbital, (C) Masticatory, (D) Nasal and (E) Oral components. The frontal bone also contributes to the 'neurocranial' matrix, which approximates the cranial vault, illustrating the lack of strict concordance between cranial bones and functional components. Redrawn following Cheverud (1982).

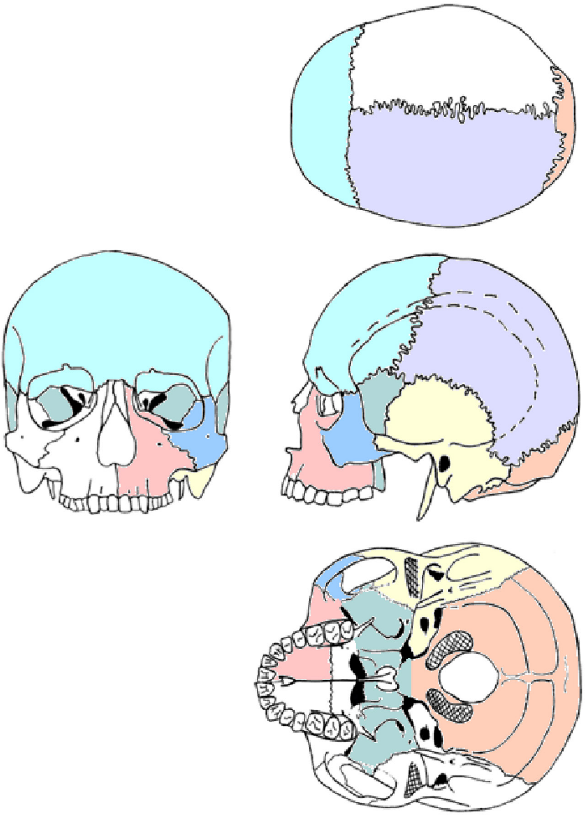


Fig. 2. Seven individual cranial bones tested against neutral genetic and climatic data (von Cramon-Taubadel, 2009a). Frontal (turquoise), parietal (purple), occipital (orange), temporal (yellow), sphenoid (green), zygomatic (blue) and maxilla (pink).

results found that the first prediction (osseous masticatory traits are more variable) to be supported but no support for the second prediction regarding phylogenetic efficacy. That is, traits with increased within-taxon variability were no less reliable for recovering the correct molecular phylogenies of either group of primates. However, Lycett & Collard (2005) did suggest that homoiologies may confound attempts to recover intraspecific phylogenetic relationships and, therefore, the homoiology hypothesis ought to be tested using an intraspecific approach.

This suggestion was followed by a test of the homoiology hypothesis using modern human craniometric variation (von Cramon-Taubadel, 2009b). Here, two three-dimensional cranial regions related to masticatory function – the zygotemporal and the palatomaxilla – were compared against three non-masticatory regions of the skull – the cranial vault, basicranium and the upper face. As in the case of the papionins and the hominoids, the masticatory regions were statistically more variable in shape within-populations than the three non-masticatory regions. However, this difference in within-population variability did not translate into genetic congruence. All cranial regions were found to be equally reliable for recovering the genetic relationships between populations, with the exception of the palatomaxilla region. Taken together with the results of Lycett and Collard (2005; Collard & Wood, 2007), the empirical conclusions undermine the theoretical assumptions of the homoiology hypothesis. In addition, Roseman *et al.* (2010) found that genetic and environmental variation of individual cranial traits were randomly distributed across different cranial regions, irrespective of levels of biomechanical strain experienced, in a large sample of pedigreed baboons. Effectively, biomechanical stress (such as masticatory function) may lead to increased within-species and within-population variation, however, this increased variability does not predict the phylogenetic efficacy or 'taxonomic valance' (Wood & Lieberman, 2001) of particular craniodental characters. While the heritability of individual characters may be affected by phenotypic plasticity, it is difficult to assess whether increased phenotypic variance is actually the result of increased genetic or environmental variance. More importantly, increased phenotypic variance will not affect estimations of among-taxon (or among-population) distances if the mean phenotype is not affected. Thus, while phenotypic plasticity may increase the *potential* for homoplastic responses in different lineages, it does not in and of itself predict the liability for homoplasy.

Two further sets of logic used to predict the phylogenetic efficacy of cranial regions were tested by von Cramon-Taubadel (2011a) under the general auspices of functional and developmental criteria. Here, the developmental criterion related to regions of the vertebrate cranium with differing phylogenetic origins, as measured by differing modes of ossification. In brief, the human cranium retains evidence of the vertebrate chondrocranium (basicranium) and dermatocranium (vault and face) distinguishable via their differing modes of ossification (Scheuer & Black, 2000). The chondrocranium ossifies endochondrally, while the dermatocranium ossifies intramembranously. The dermatocranium can be further sub-divided into the neurocranium (vault) and the viserocranium (face) under functional criteria consistent with the Functional Matrix framework (Moss & Young, 1960). Also, using the logic of functional autonomy, three further modules were delineated corresponding with the sensory functions of vision (orbits), olfaction (nasal cavity) and audition (petrous region of the temporal plus the external auditory meatus). As shown in Figure 1, these modules have been identified previously (e.g., Cheveurd, 1982) given that developmental precursors are known to arise early during development (Kjaer 1990; Lieberman *et al.*, 2000b).

Using these delineated modules, two distinct hypotheses and two aspects of logic were tested. First, the 'basicranial hypothesis' predicts that the endochondrally ossifying basicranium (chondrocranium) will be a more reliable indicator of genetic relationships than the intramembranously ossifying dermatocranium (Lieberman *et al.*, 1996, 2000a,b). The logic underlying this hypothesis being that the early establishment of the basicranial architecture in cartilage, together with the functional constraints placed upon it, would render the chondrocranium immune to subsequent potential homoplastic changes. Secondly, the 'single function hypothesis' predicts that relatively simple cranial modules that are primarily associated with a single function (e.g., vision) will be relatively less congruent with neutral genetic data than anatomically and functionally complex modules. The underlying logic here being the inverse of that applied by Lockwood *et al.* (2004) to the temporal bone, i.e. that anatomically complex regions involved in multiple functions would limit the potential for homoplasy (see also Perez *et al.*, 2007). Hence, application of the reverse logic would imply than relatively simple, unifunctional anatomical structures would be more prone to the effects of convergence and, therefore, be less genetically congruent.

The results (von Cramon-Taubadel, 2011a) found that the predictions of the basicranial hypothesis were not supported for modern human populations, as the dermatocranium and the chondrocranium were both equally congruent with the neutral genetic data. Therefore, at least in the case of human populations, mode of ossification does not accurately predict the phylogenetic efficacy of individual cranial regions. There was some empirical support for the predictions of the 'single function hypothesis' in that two of the three sensory-defined modules (orbits and auditory region) were less genetically congruent than complex multi-functional regions such as the

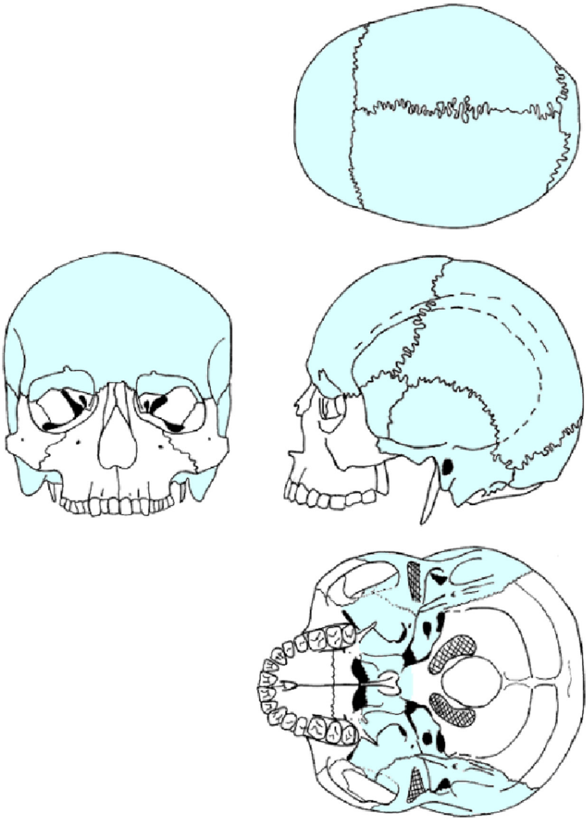


Fig. 3 - Regions of the human cranium found to have overall 'good' versus 'bad' phylogenetic efficacy. Regions of the cranium found to fit a neutral model of evolutionary expectation better than the baseline are highlighted in blue. The remainder of the cranium (in white) was found to depart from neutrality relative to the entire cranium.

vault, face and basicranium. However, when Inuit populations were excluded from the analysis, the nasal region was statistically less congruent than all three complex modules. This suggests that the performance of the nasal region had less to do with it being a unifunctional or anatomically simple region and more to do with its likely involvement in thermoregulatory activities (Franciscus & Long, 1991) as well as olfaction and inspiration. Moreover, the shape of the nasal saddle and the nasal opening contribute substantially to the overall shape of the human face, therefore making it difficult to disarticulate the shape of the nasal region from the overall shape of the face.

In combination, what the results of these three studies suggest is that while integration theory may be a good conceptual means of identifying and delineating cranial 'modules', it does not provide a mechanism for predicting the relative genetic congruence of cranial modules, thus defined. Of all the logical criteria applied – anatomical complexity, functionality, ossification patterns, individual bones, and within-group variation patterns – none have operated as predictive criteria in a consistent manner. This seemingly negative conclusion needs to be put into perspective, however. In the case of all individual cranial regions tested, all were found to be statistically significant in terms of their congruence with neutral genetic affinity patterns. Therefore, on the whole, cranial shape *is* a reliable indicator of past population history. In fact, it is probably easier to identify specific criteria that predict which cranial regions will perform less well (see Fig. 3). von Cramon-Taubadel (2009a) found that the entire cranium performed significantly better than the maxilla, zygomatic and occipital bones. There is also a strong overlap between these bones and the palatomaxilla region defined in von Cramon-Taubadel (2009b), which was found to be less genetically congruent than all other regions tested. These anatomical areas have certain characteristics in common, in that they are either the sites of major muscle attachments (e.g., nuchal, masseter, pterygoid) and/or are related to overall facial morphology.

Although a null model of microevolutionary neutrality cannot be rejected entirely for the regions shown in white in Figure 3, the consistency with which some aspects of cranial anatomy appear in studies of climatic and dietary adaptation (e.g., Hylander, 1977a; Carey & Steegmann, 1981; Beals *et al.*, 1983, 1984; Larsen, 1997; Franciscus & Long, 1991; Lieberman *et al.*, 2004; González-José *et al.*, 2005; Sardi *et al.*, 2006; Hubbe *et al.*, 2009; Noback *et al.*, 2011) suggests that non-neutral or selective factors are, at least partially, responsible for shaping global patterns of human craniometric diversity in some regions of the cranium. The two most likely sources of directional diversifying selection on the human cranium are climatically-driven adaptation and responses to changes in dietary behaviour. In both cases, the shape of the face is inherently involved, as will be discussed in further detail below.

Climatic Adaptation

Historically, analyses of climatic adaptation largely took place in the absence of any consideration of potential underlying neutral population history effects (e.g., Thomson and Buxton, 1923; Davies, 1932; Weiner, 1954; Coon, 1955; Beals, 1972; Beals *et al.*, 1973, 1984; Carey & Steegman, 1981; Crognier, 1981). For example, average population cephalic index (head breadth as a ratio of head length), used as a measure of average sphericity or elongation of head shape, was compared against four main types of climatic conditions (Beals, 1972). These four zones of ‘climatic stress’ referred to areas of extreme dry-heat, wet-heat, dry-cold and wet-cold conditions. The results, based largely on visual comparison of descriptive statistics, found a general trend toward higher cephalic indices (relatively broader crania) in cold climatic conditions. However, Beals (1972) also noted differences in the average cephalic indices of major continental groupings, with Africa and Oceania having the lowest indices, and Europe, Asia and the New World having higher indices. While these continents do differ in their average climatic conditions, the results cannot adequately distinguish between climate and global geography in being the main determinant of average population cephalic index.

In the historical context of shifting paradigms in craniometric studies, it is instructive to read how Beals (1972) implements his hypothesis-testing framework. His null-hypothesis is that if cephalic index is selectively neutral it should be statistically equivalent in all parts of the world; “… if head form is selectively neutral, there would be no reason to expect the means of groups living in hot or cold climates to deviate significantly from the neutralized world mean. But if there is a detectable selective advantage according to climate, then we should expect the mean of cold adapted populations to be higher than the world mean” (Beals 1972, p. 88). The second prediction of the hypothesis is based on Bergman’s (1847) and Allen’s (1877) thermoregulatory rules, which would foresee a more spherical (higher cephalic index) head shape in cold conditions, as this would minimize heat loss relative to head size. However, the first prediction of the hypothesis is theoretically flawed, as it assumes that evolutionary neutrality will always generate patterns whereby all populations are equivalent in mean form. Stochastic evolutionary processes such as genetic drift lead to random patterns of population covariation such that neutral genetic (and by extension morphological) traits can be used to infer past population history. Therefore, there is clear distinction between the likely covariance patterns generated under neutral conditions and the evolutionary 'stasis' predicted here (which would more likely be the result of strong stabilising selection).

Given the historical connections between craniometric assessment and the development of racial typologies reviewed earlier, this (albeit erroneous) theoretical expectation is perhaps a natural outcome of the application of the 'New Physical Anthropology' (*sensu* Washburn, 1951) during the post-war era. Indeed, Beals and colleagues inadvertently hint at this explanation in saying, for example; "The historically important assumption that head shape was a nonadaptive trait (and hence indicative of racial affinity) is no longer tenable. Furthermore, there is no reason to believe the trait serves any better for taxonomic diagnosis." (Beals *et al.*, 1983, p. 435). Later, the authors write; "The implication is that if head shape is included among the traits used for taxonomic assessment, some adjustment for the effect of climate must be made." (p. 435). These statements make clear the theoretical framework being assumed; neutrality (non-adaptive) is equivalent to a 'racial' trait, and if indeed aspects of morphology might tell us about taxonomy (population affinities), we must first account for the effects of natural selection. And so, in attempting to banish the racial demons from physical anthropology, the cart was placed before the proverbial horse in assuming that adaptation (via natural selection) would account for any significant variation between populations (Washburn, 1963), and that the effects of selective factors such as climate would need to be 'controlled for' prior to investigating population affinity patterns (see also comments by Bennett Blumenberg and Robert Sokal on Beals *et al.*, 1984).

These early studies of cranial shape and climatic selection serve merely as one example of how adaptationist reasoning has muddied the waters in terms of understanding global patterns of human craniometric variation. It is easy to criticise this theoretical stance in hind-sight, but given the historical development of biological anthropology, it is probably fair to say that this framework was entirely a product of its time. However, as early as 1979, Guglielmino *et al.* published a population-based analysis that attempted to investigate the phylogenetic signal in craniometric data, while controlling for the effects of climate. The authors recognised the importance of integrating the study of environmentally-driven adaptation with considerations of the underlying population phylogenetic structure. Indeed, the paper by Steegmann (1970) is noteworthy in considering non-selective mechanisms for altering cranial and facial shape, such as drift, founder effects and plasticity, alongside selective explanations. With the increased awareness of the need to control for, and indeed reject, a null model of neutrality (e.g., Roseman 2004; Roseman & Weaver, 2007), recent studies have now tested for climatic effects within an explicitly quantitative genetics framework (Roseman, 2004; Harvati & Weaver, 2006a,b, Hubbe *et al.*, 2009; von Cramon-Taubadel, 2009a; Betti *et al.*, 2010).

Hubbe *et al.* (2009) conducted a large-scale global analysis of climatic congruence for the whole cranium, the neurocranium (vault) and the face. As also suggested by previous studies (Roseman, 2004; Harvati & Weaver, 2006a,b; Betti *et al.*, 2010), Hubbe *et al.* (2009) found a strong association between cranial shape (especially facial shape) and mean annual temperature, when extreme high-latitude populations were also considered. The authors go further in suggesting possible convergences in the facial morphology of cold-adapted populations from North America, Europe and North East Asia. They note that in all three continents, the nasal index (nasal breadth relative to nasal height) is minimised, with all populations having relatively narrow noses. However, the manner in which this is achieved differs in that European populations have absolutely narrower noses, while Asian and New World populations have absolutely taller nasal cavities (Franciscus & Long, 1991). Hubbe *et al.*

(2009) also discuss the implications of the finding that northernmost populations tend to have absolutely wider neurocrania (Roseman, 2004) as being the result of a trend towards increasing the overall *size* of the vault and, therefore, in line with Bergman's (1847) rule. In essence these empirical findings are consistent with those presented by Beals (1972; Beals *et al.*, 1983, 1984) who argued that increased brachycephalisation was a means of increasing overall cranial size in response to cold stress. However, this conclusion needs to be considered with some caution, as Harvati & Weaver (2006b) found no association between cranial *size* and temperature, even when cold adapted populations were included. Harvati & Weaver (2006a), on the other hand found a significant relationship between neurocranial (vault) size and temperature with the cold-adapted Greenland Inuit population having the absolutely largest vault. However, confusingly, Greenland Inuit have relative narrow (doliocephalic) crania, highlighting the mismatch between the explanations of brachycephalisation and cranial size for understanding adaptation to heat stress (Roseman, 2004). As no study has yet directly controlled for geographic or genetic distance when comparing aspects of vault form against climate, it is not possible to definitely distinguish between the effects of shared ancestry or climate in generating neurocranial shape and size patterns. However, taken together the current evidence suggests that neurocranial *shape* patterns are most likely primarily the outcome of neutral population history (Harvati & Weaver, 2006a,b; von Cramon-Taubadel, 2009a,b, 2011a), while aspects of neurocranial *size* differences could be related to climatic adaptation, especially in high latitude populations.

The case for climatic adaptation in the facial, and especially nasal region, is much better supported by current independent lines of evidence. Several studies have reported a relationship between nasal dimensions and measures of temperature and humidity (e.g., Thomson & Buxton, 1923; Davies, 1932; Weiner, 1954; Wolpoff, 1968; Crognier, 1981). Carey & Steegman (1981) also investigated the relationship between nasal protrusion and various environmental and climatic factors, and found that the strongest relationships were between absolute nasal projection and humidity during the coldest months of the year. Nasal projection was found to increase in dryer climatic conditions. Even though the authors confirmed a relationship between nasal index and temperature, their results suggest that humidification of inspired air is as important in driving potential nasal adaptation as the temperature of the air *per se*. Franciscus & Long (1991) make the point that simply demonstrating significant correlations between measures of external nasal morphology and climatic factors was not a substantive test of climatic adaptation as they do not necessarily demonstrate the mechanisms by which fitness advantages are conferred by differing morphologies. Given that the most persuasive adaptive explanations for nasal morphology relate to the physiology of inspired air humidification and thermoregulation, Franciscus & Long (1991) suggest that future studies need to relate the shape and size of the external (skeletal) morphology with internal nasal morphology, as the majority of moisture and heat exchange actually occurs in the interior nasal cavity. Yokley (2009) found that there was no straight-forward relationship between nasal index and internal nasal cavity size, although he did find consistent statistical differences between African and European samples in both measures of nasal dimensions. Churchill *et al.* (2004) used physical models to experimentally test some of the airflow dynamic predictions relating to internal nasal morphology and the physiological adaptation to air temperature and humidity. Their results support a model of turbulence, as opposed to laminar flow, for the passage of inspired air in humans. Unfortunately, their models were based on 10 'Caucasian' cadavers, thus limiting ethnic diversity in the sample. Hence, the results could not speak directly to the potential physiological impact of large-scale global variation in nasal cavity and external morphology.

Recently, Noback *et al.* (2011) employed 3D geometric morphometrics to quantify the shape of the overall external and internal nasal cavity for 10 globally-distributed human populations. They employed partial least squares analyses to compare patterns of morphological variability against measures of climate such as temperature and humidity. Their results found a strong association between the shape of the nasal capsule and both temperature and vapour pressure. Interestingly, their results did show a slightly different pattern of climatic congruence for the external nasal morphology (related with differences in temperature) and internal nasal capsule shape (related to humidity). What remains to be tested now is the extent to which these climatic congruence patterns remain once population history is controlled for. While the strength of evidence is in favour of an (at least partial) adaptive explanation for shape variation in the human nose, the extent to which this is accounted for by directional selection in extreme cold or extreme dry climatic conditions only, or whether diversifying selection on nasal morphology is a ubiquitous phenomenon in the human species, remains to be fully tested.

Dietary Adaptation

Dietary-related adaptation has also long been studied in the human cranium. This research relates to two main aspects of masticatory behaviour. At a mechanical level, there is a large body of work investigating the morphological effects of masticatory stress (Lieberman, 2011) in order to better understand how phenotypic plasticity (osseous remodelling) due to masticatory forces influences the size and shape of the cranium. Most of this work has been conducted either experimentally in non-human primates (e.g., Hylander, 1977b, 1979; Hylander & Johnson, 1994, 1997; Ravosa *et al.*, 2013) or by using Finite Element Analysis (FEA) to model the morphological effects of different masticatory loading regimes (e.g., Richmond *et al.*, 2005; Strait *et al.*, 2009; Wroe *et al.*, 2010; Fitton *et al.*, 2012). While this research is important for understanding the anatomical effects of chewing behaviour on cranial form, I will focus here on our current understanding of how dietary behaviour affects patterns of cranial form between-populations of *Homo sapiens*. In particular, a significant body of work has investigated the potential anatomical differences between human populations broadly defined as hunter-gatherer-foragers and populations who primarily operate an agricultural or pastoralist subsistence strategy. Given that the shift towards agriculture signals such a dramatic shift in modern human prehistory, not only in terms of overall diet, but also population demography, health, and growth patterns (e.g., Gignoux *et al.*, 2011; Pinhasi & Stock, 2011), systematic differences in cranial anatomy due to subsistence behaviour between human populations might be expected.

Bioarchaeologists and biological anthropologists have long hypothesised that there may be an important interaction between subsistence behaviour and the growth/development of the skull and lower jaw (e.g., Larsen, 1995, 1997; Lieberman, 2008, 2011). Empirical evidence comes from a body of work based on Old World (e.g., Carlson, 1976; Carlson & Van Gerven, 1977, 1979; Pinhasi *et al.*, 2008) and New World (e.g., González-José *et al.*, 2005; Paschetta *et al.*, 2010) populations, which suggests that major changes in cranial robusticity and shape accompanied the shift from hunting-gathering to farming. This is explained on the basis that agriculturalists, on average, have a softer and more processed diet than hunters and gatherers, which in turn places less mechanical stress on the masticatory apparatus. Carlson and colleagues referred to this as the ‘masticatory-functional’ hypothesis (Carlson, 1976; Carlson & Van Gerven 1977, 1979). The hypothesis contends that as populations transitioned from a hunting and gathering lifestyle (i.e. in the Mesolithic) to a fully agricultural strategy through the Neolithic and beyond, their masticatory apparatus experienced less neuromuscular stress, thereby altering the pattern of growth in the lower face and jaw. This was accompanied by a change in the flexion of the basicranium, leading to a more acute basicranial angle and a more globular neurocranium. Thus, on average, agricultural populations were found to have smaller and less prognathic faces, and more globular brain cases.

These empirical findings are further supported by evidence from in vivo experiments carried out using rats (e.g., Kiliaridis *et al.*, 1985; Yamada & Kimmel, 1991), pigs (Ciochon *et al.*, 1997), hyraxes (Lieberman *et al*,. 2004) and primates (Corruccini & Beecher, 1982, 1984) fed on hard and soft diets. In all cases, the animals fed on harder diets had larger and more robust lower jaws (mandibles) and/or faces than those fed on soft diets. The hyraxes, in particular, make an interesting case study when trying to understand human facial form, as they have a relatively short snout. Lieberman *et al*. (2004) found that hyraxes fed a soft diet had approximately 10% less growth in the lower face and lower jaw than those fed on hard diets.

A global comparison of cranial and mandibular shape variation in populations defined as broadly agriculturalist or hunter-gatherer (von Cramon-Taubadel, 2011b) found consistent differences in mandibular (lower jaw) and, to a lesser extent, upper jaw shape between subsistence groups, even after having controlled for the potentially confounding effects of population phylogeny, geography and climate. While the results of this study are largely congruent with the expectations of the 'masticatory-functional' hypothesis, there are important differences in the conclusions reached. The global analysis, which also controls for neutral population history as well as geographic and climatic effects, did not find any consistent relationship between subsistence behaviour and the shape of either the cranial vault or the basicranium. Moreover, the mandible, vault and basicranium were all statistically significantly related with geographic distance and climatic differences. However, the relationship with climate disappeared for all morphological regions once the effects of neutral population history were controlled.

The effects of 'Galton's Problem' are clearly highlighted here in so far that virtually all cranial regions tested have a significant relationship with geographic distance, yet the reason for this relationship differs depending on the anatomical region in question. In the case of the mandible, the relationship is driven by subsistence economy, which is itself related to geography to a certain extent. In the case of the 'neutral' cranial regions such as the vault and basicranium, the relationship with geography is the result of patterns of shared ancestry and ancient population demography. In essence, as discussed earlier, when dealing with *global* patterns of genetic and phenotypic population affinities, geography can be viewed as a potential proxy for several different neutral and adaptive factors. Global climatic patterns are to some extent mediated by geography, subsistence strategies are related with local ecology and climate, which in turn is mediated by geography, and the neutral population history of the human species has been mediated by geography, via the processes of iterative founder effects out of Africa alongside subsequent patterns of short-range gene flow and population isolation (e.g., Hunley *et al.*, 2009).

Taken together, current research does suggest a link between subsistence behaviour and the morphology of the lower jaw and to some extent, the shape of the lower face. von Cramon-Taubadel (2011b) also found consistent patterns of morphological similarity in the lower jaw of agriculturalists and hunter-gatherers, broadly defined. Farming/pastoralist populations tended to have relatively shorter mandibles from front to back with relatively longer rami (lever linking the lower jaw to the base of the skull) with the opposite anatomical pattern in hunter-gatherers, irrespective of which continent the populations came from. This finding has two ramifications; firstly it suggests that the mechanism of change is phenotypic plasticity (Lieberman, 2011) as opposed to natural selection and, secondly, it provides an explanation for the onset of dental malocclusion and crowding with the shift from hunting-gathering to farming in prehistory (Corrucini & Beecher, 1982; Corrucini, 1984; Varrela, 1990; Kaifu *et al.*, 2003). What is still less clear, however, is whether the phenotypic plasticity is necessarily *entirely* explained by the biomechanical action of mastication (i.e. more mechanically challenging regimes lead to longer and more robust mandibles), or whether other differences between these populations might also play a role. Given that all modern human populations cook or process food to some extent, it is not entirely certain that all hunter-gatherers necessarily subsist on a more mechanically intensive diet than all agriculturalists. One potential issue that does warrant further exploration is that all hunter-gatherer societies tend to wean their children later than farming communities (e.g., Sellen & Smay, 2001), despite the wide-spread availability of suitable soft weaning foods. This extended childhood breastfeeding behaviour may also impact the growth and development in the lower jaw and face in ways that might explain the systematic differences in masticatory anatomy between agricultural and hunter-gatherer communities worldwide.

Future directions and concluding remarks

Anthropology has come a long way in terms of how craniometric data are analysed, interpreted and employed in studies of human evolution and variation. A growing and consistent body of literature now exists to support the notion that global patterns of modern human variation fit a largely neutral microevolutionary model for the overall shape of the human skull. This implies, therefore, that in the absence of direct genetic information concerning specific population affinities, cranial variation can (under reasonable quantitative genetic assumptions) be used as a proxy for genetic data. Therefore, we can confidently apply craniometric data to answer questions regarding past population history, model specific dispersal events and establish patterns of population affinity (e.g., González-José *et al.*, 2001; Pinhasi & von Cramon-Taubadel, 2009; Hubbe *et al.*, 2010; von Cramon-Taubadel & Pinhasi, 2011). While some specific regions of the human cranium have been found to support this neutral model more accurately than others, no consistent ‘rules’ have emerged to define the criteria of what makes a particular ‘reliable’ region in terms of phylogenetic efficacy. Indeed, it is probably easier to consistently identify those regions of the human cranium that are less neutral (face, occipital and mandible). Once a largely neutral model is rejected for some cranial regions, non-neutral explanations begin to emerge. In the case of the occipital a likely non-neutral explanation is the extent to which this bone is shaped by large muscle (nuchal) attachment sites. However, given the strong integration between the occipital squama and the parietal and temporal bones (e.g., Gunz & Harvati, 2007), a distinction should be drawn between the neurocranial and basal portions of the occipital bone. The shape of the mandible appears to be heavily influenced by differences in subsistence behaviour. However, it should be noted that within subsistence categories, the mandible carries a relatively strong geographic signal (Nicholson & Harvati, 2006) suggesting that a rejection of the neutral pattern may only be true when considering both agriculturalist and non-agriculturalist groups at the same time. Finally, the face is the region of the cranium that is most likely to exhibit a non-neutral pattern of variation, especially when cold-adapted populations are considered. Both the shape of the nasal region and the shape of the upper jaw (maxilla and palate) have been shown to diverge from a neutral model of expectation. Although climatically-driven adaptation does not occur in all populations or in all climatic conditions, on balance, the face is the region of the skull most likely to reflect patterns of past diversifying selection (e.g., Roseman, 2004; Harvati & Weaver 2006a,b; Smith, 2009; von Cramon-Taubadel, 2009a). Having said that, it is important to remember that cranial shape taken as a whole is largely congruent with neutral expectation and, therefore, future studies should not shy away from using craniometric data from the whole cranium when addressing specific questions of past population history, especially in bioarchaeological or fossil contexts where data are fragmentary or poorly preserved (e.g., Pinhasi & von Cramon-Taubadel, 2009; von Cramon-Taubadel & Pinhasi, 2011).

More information is required regarding the ontogeny of population-specific affinity patterns within modern humans. While numerous studies have compared ontogenetic trajectories between modern humans and other species such as the Neanderthals (e.g., Ponce de Leon & Zollikofer, 2001; Williams *et al*., 2002; Krovitz, 2003; Bastir *et al*., 2007) or taxa referred to as 'archaic' *Homo sapiens* (e.g., Lieberman *et al*., 2002), relatively little is known about differences in developmental trajectories between populations of *Homo sapiens.* Studies of cranial ontogeny within modern humans have suggested that population-specific affinity patterns arise early in development (e.g., Strand Viðarsdóttir *et al*., 2002; Krovitz, 2003; Gonzalez *et al*., 2010, 2011; Sardi & Ramírez Rozzi, 2012) but different cranial regions are subject to differing pre- and post-natal growth trajectories (e.g., Bastir *et al*., 2006; Morimoto *et al*., 2008). This is important as it allows for the identification of differing population covariance patterns throughout ontogeny (Mitteroecker and Bookstein, 2009), which could impact the potential response to selection of particular cranial regions. In addition, a better understanding of population-specific ontogenetic allometry could help identify patterns of phenotypic plasticity resulting from biomechanical stress throughout post-natal growth (e.g., Barbeito-Andrés *et al*., 2011).

While this review is limited to discussing cranial variation, a number of studies have begun to address the question of the relative importance of neutral versus non-neutral factors in determining human postcranial variation. In particular, Betti and colleagues have found that global patterns of shape variation in the major pelvic bone (os coxae) appear to be largely driven by neutral evolutionary processes (Betti *et al*., 2012, 2013), in contrast with long bone morphology, which appears to primarily reflect non-neutral forces such as thermoregulatory adaptation and plasticity (Betti *et al*., 2012). While traditionally the entire human postcranium has largely been conceived of as shaped by the action of various selective or biomechanical factors (e.g., Trinkaus, 1981; Holliday, 1999; Ruff, 1994, 2002; Ruff *et al*., 2006; Stock, 2006; Stock *et al*., 2011; Cowgill *et al*., 2012), this new body of literature is beginning to decipher the relative importance of neutral and selective evolutionary forces in shaping global patterns of postcranial variation.

Another avenue for further enquiry is the extent to which patterns of cranial neutrality might be reflected in non-human primates more generally. This question is key if we are to employ the knowledge gained from understanding craniometric variation in modern humans to the fossil hominin record more generally (e.g., Harvati & Weaver, 2006a; Smith, 2009; von Cramon-Taubadel, 2011a; von Cramon-Taubadel & Smith, 2012). To date, however, there are no obvious 'rules' for consistently identifying cranial characters that are particularly reliable indicators of taxonomic or phylogenetic affinity (Collard & Wood, 2001; Lycett & Collard, 2005; von Cramon-Taubadel & Smith, 2012). However, it is likely that neutral and selective forces are operating to different extents depending on the taxonomic scale of the analysis, and therefore, more detailed studies operating at intra-specific and intra-generic scales are required. Indeed, the study of Ackermann and Cheverud (2004) showcases a framework for investigating the extent to which hominin diversity might be explained on the basis of neutral and selective forces. Future work should focus on specific instances of divergence between molecular and morphological estimates of phylogeny in order to gain insight into the detailed microevolutionary history of the primates more generally (e.g., Ackermann & Cheverud, 2002; Marroig & Cheverud, 2004).

Given the large collections of human and non-human primate crania available worldwide, there is a rich resource available to anthropologists to directly study humanity's evolutionary history. Despite the ever-growing amount of DNA information available, certain questions regarding human prehistory and hominin evolution will always rely on the analysis of morphological data. Great improvements in understanding have been, and continue to be, made on the basis of explicitly evolutionary analyses of craniometric data. However, future studies will need to place human craniometric studies within the context of the entire skeleton, and also forge stronger empirical connections between intra-specific and inter-specific cranial variation across the primates, more generally. This can be achieved by situating all comparative anatomy studies within the theoretical and conceptual framework of quantitative genetic and evolutionary theory.

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