VIRTUAL ANTHROPOLOGY AND THE STUDY OF SKELETAL FORM AND FUNCTION

RICARDO MIGUEL GODINHO University of York, Department of Archaeology and Hull York Medical School, ricardomiguelgodinho@gmail.com

RESUMO A paleoantropologia estuda frequentemente a relação entre forma e função. Tradicionalmente, esses estudos usam morfometria convencional para medir a forma e simplificações geométricas para analisar a função mecânica. A antropologia virtual reúne um conjunto de avanços tecnológicos e disciplinas para melhorar o conhecimento da morfologia esquelética e da sua função mecânica. A morfometria geométrica é já uma área implementada, e frequentemente utilizada na antropologia virtual, que apresenta múltiplas vantagens relativamente à morfometria convencional. A análise de elementos finitos não é normalmente integrada na antropologia virtual mas é crescentemente utilizada em paleoantropologia. Permite simulações mecânicas complexas em esqueletos cujos resultados são decisivos na compreensão de como o esqueleto responde a cargas mecânicas. Este manuscrito apresenta uma revisão geral das técnicas tradicionalmente utilizadas em estudos paleoantropológicos de forma-função e como a antropologia virtual pode melhorar o conhecimento nesta área.

PALAVRAS CHAVE **Antropologia virtual, morfometria geométrica, análise de elementos finitos, forma-função, paleoantropologia**

ABSTRACT Many paleoanthropology studies examine skeletal form and function. Those studies have traditionally used conventional morphometrics to measure form and geometrical simplifications to assess mechanical function. Virtual anthropology (VA) gathers a set of technological advances and disciplines to augment understanding of skeletal morphology and mechanical function. Geometric Morphometrics is now a well-established morphometric approach, and commonly used in VA, that offers clear advantages over traditional morphometrics. Finite Element Analysis is not integrated in VA, but has recently started being used in paleoanthropology. It allows complex simulations of mechanical loading, thus providing important insights about how skeletal elements respond to loading. This paper provides a general overview of traditional approaches in paleoanthropology to studies of skeletal form and function and how VA is able improve such approaches.

KEYWORDS **Virtual anthropology, geometric morphometrics, finite element analysis, form-function, paleoanthropology**

INTRODUCTION

Paleoanthropology has compared cranial form between populations (Coon, 1962; Howels, 1973; Lahr, 1996). When morphological dissimilarities are identified they are often associated with mechanical loading, which has been shown to impact skeletal form (Currey, 2006). Thus, paleoanthropology often focuses mechanical function (Rak, 1983; Russell, 1985; Rak, 1986; Demes, 1987; Trinkaus, 1987; Demes and Creel, 1988; Ruff, 2007). Traditionally, such studies used conventional morphometrics to measure form and geometrical simplifications to measure mechanical function. Virtual anthropology (VA) uses a set of computer based approaches to augment assessment of skeletal form. Instead of examining physical bones, VA uses three dimensional surfaces or volumes to perform analyses that allow comprehensive morphological studies and visualization of internal structures that are physically inaccessible without sectioning bone/teeth (Weber, 2015). Morphological analysis in VA typically uses Geometric Morphometrics (GM) to allow a better understanding of morphological variance (Weber, 2015). Moreover, by integrating other techniques currently used in virtual functional morphology, such as Finite Element Analysis (O'Higgins *et al.*, 2011), VA may also enhance the study of human skeletal mechanical function.

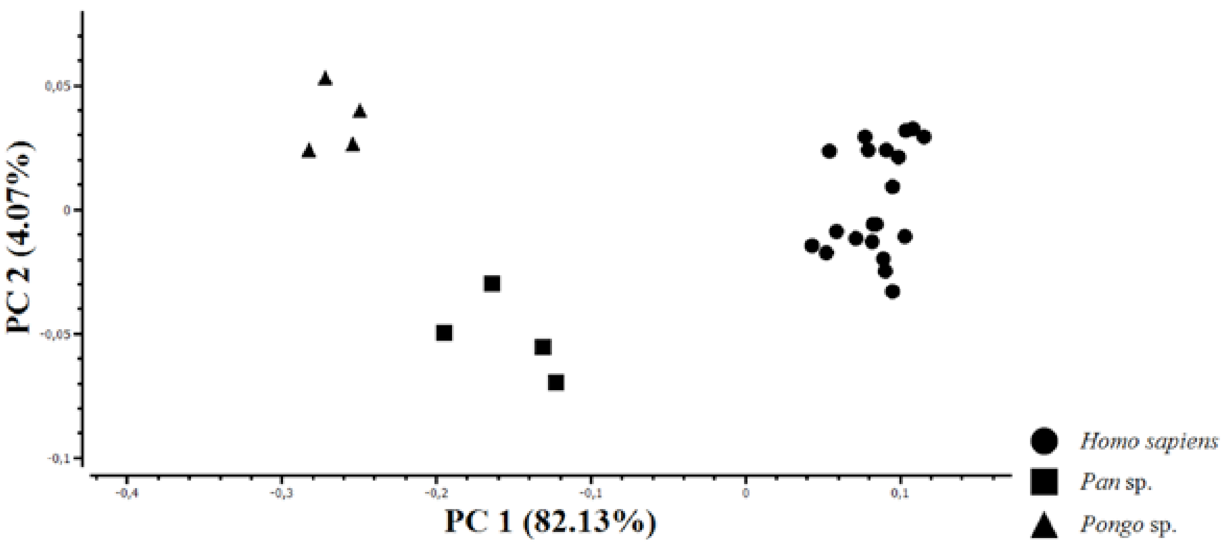
Thus, this paper presents an overview of how paleoanthropology typically measured form-function and how VA may improve studies of skeletal form and function.

MEASURING FORM

Measurement of human form has typically relied on linear measurements, which are basically measures of size. Even though size and shape are intimately linked in biological processes, theory of shape states that form integrates size *and* shape (Zelditch *et al.*, 2004). This

partitioning is relevant when considering the impact of size on shape. The former is a scalar and can be measured in multiple ways. Shape is defined as the geometrical information that is invariant to location, orientation and scale (Zelditch *et al.*, 2004). Thus, in order to examine shape, researchers started using ratios and angles in addition to lengths (Slice, 2005) and traditional morphometrics combined those measurements with multivariate statistics to analyze morphology. However traditional multivariate morphometrics has statistical limitations, does not allow complete encoding of geometry and does not allow visualization of morphology (Adams *et al.*, 2004). To overcome those limitations, morphometrics underwent a revolution in the 1980s and several new techniques were created, of which GM became the most popular (Adams *et al.*, 2004; Slice, 2005).
GM has been defined as the statistical analysis of covariation between shape and other causal variables (Bookstein, 1997). To capture form GM relies on landmarks, which are homologous points between specimens assumed to have biological equivalence and relevance (O'Higgins, 2000). However there are not many classical landmarks that can be used to map morphology. Hence, researchers developed sliding semi-landmarks (Gunz and Mitteroecker, 2013), which are geometrically homologous points that allow dense coverage of regions that lack classical landmarks, such as curves and surfaces (figure 1).
The first step in GM is, thus, acquisition of geometry through landmarking, which is commonly done virtually using 3D surfaces. Once landmarking is complete landmark coordinates are submitted to Generalized Procrustes Analysis, which removes the effects of location, scale and orientation (Zelditch *et al.*, 2004). Scaling removes size information and leads to analysis of shape, but size and shape are intimately linked in biological processes. Thus, several approaches have been used to account for size *and* shape (Mitteroecker *et al.*, 2004; O'Higgins and Milne, 2013). After registration, analysis is based on multivariate statistics of the shape variables. A standard practice is to perform a principal component analysis, investigate morphological variance (figure 2) and visualize morphological differences using the Thin Plate Spline (TPS) function to warp reference specimens along principal components. This approach has been used to investigate intra and inter-specific morphological differences (Delson *et al.*, 2001; Bastir *et al.*, 2007; Harvati *et al.*, 2010; Baab *et al.*, 2013) and ontogenetic patterns (Collard and O'Higgins, 2001; Cobb and O'Higgins, 2004, 2007; Bastir *et al.*, 2008; Freidline *et al.*, 2012). Multivariate regression has been used to

1. Example of reconstructed fossil hominin (Kabwe 1) with 71 classical landmarks (dark grey) and 350 sliding semi-landmarks (light grey).



2. Example of PCA examining morphological variance in Homo sapiens, Pan sp. and *Pongo* sp.

examine the impact of size on shape (Mitteroecker *et al.*, 2004; Franklin *et al.*, 2007) and of age on mandibular shape (Franklin *et al.*, 2007). Partial least squares has been used in integration and modularity studies (Bastir and Rosas, 2005; Mitteroecker and Bookstein, 2008; Neaux *et al.*, 2015), and to determine the relevance of biomechanical (Noback and Harvati, 2015b; Noback and Harvati, 2015a) and ecological (Monteiro *et al.*, 2003; Noback *et al.*, 2011) factors on form.

RECONSTRUCTING INCOMPLETE FORMS

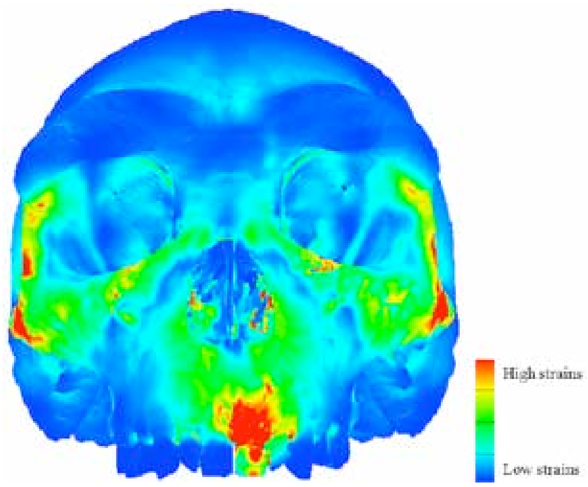
Paleoanthropology frequently deals with skeletal elements that are distorted and fragmented. This severely constrains morphology studies, thus researchers have reconstructed incomplete specimens to enable further research. However, physical reconstruction has proved itself detrimental for preservation of fossils (e.g. the Le Moustier Neanderthal cranium). Furthermore, it is a subjective process that involves assumptions and relies on anatomical expertise (Tattersall and Sawyer, 1996; Gunz *et al.*, 2009). This impacts on later research because studies often use casts of those reconstructions (Gunz *et al.*, 2009). VA allows more objective approaches to reconstruction of incomplete specimens and the advantage of being performed virtually, thus not requiring any handling of specimens (Weber, 2015). Virtual reconstruction approaches depend on the aim of subsequent research. When research only requires estimation of missing landmarks this can be done using statistical or geometric based reconstruction. The former uses multivariate regression, which is based on existing landmarks to estimate missing points. Geometric based landmark reconstruction uses the TPS function to estimate missing landmarks (Gunz *et al.*, 2009). However, FEA studies simulating function require complete specimens (see below). In such cases it is necessary to fully reconstruct the missing elements. Symmetry may be used and existing contralateral elements reflected to replace missing structures. Furthermore, because no skeletal structures are perfectly symmetrical, TPS may be used to warp reflected elements to existing structures, thus accounting, to some extent, for asymmetry. When no contralateral elements are present it is possible to use portions of other specimens and warp them to the morphology of the target specimens (Gunz *et al.*, 2009).

MEASURING MECHANICAL FUNCTION

Several paleoanthropology studies have focused on assessing how skulls resist biting. Such studies have, until recently, used geometrical simplifications of crania (Rak, 1983; 1986; Demes, 1987; Trinkaus, 1987). Direct strain measurement using strain gauges in other primates (Hylander *et al.*, 1991; Ross and Hylander, 1996; Ravosa *et al.*, 2000a; Ross, 2001) has also been used to infer hominin cranial mechanical function (Ravosa *et al.*, 2000b). Although these approaches are informative and provide insights about how hominin crania resisted biting, they do not allow assessment of experienced deformations. Thus, with increasing computational power, researchers started using FEA to predict stresses and strains experienced by crania during biting (Strait *et al.*, 2007; Strait *et al.*, 2009; Strait *et al.*, 2010; Wroe *et al.*, 2010; Benazzi *et al.*, 2015; Smith *et al.*, 2015b; Ledogar *et al.*, 2016).

FEA is a numerical tool for solving engineering or mathematical physics problems (Logan, 2007) that has recently been applied to hominin biomechanics to analyze how skeletal elements resist loading (Strait *et al.*, 2007; Strait *et al.*, 2009; Strait *et al.*, 2010; Wroe *et al.*, 2010; Benazzi *et al.*, 2015; Smith *et al.*, 2015b; Ledogar *et al.*, 2016).

FEA requires creation of a model that is divided (discretized) into a set of elements. Models can be based on surface or volume scans and computer-aided design (Richmond *et al.*, 2005), but CT-based models have been recognized as most reliable (Marinescu *et al.*, 2005). Such CT-based models are built through a segmentation process that uses differences in bone density to extract relevant structures from the scanned volume (Weber and Bookstein, 2011). Once the model is created material properties are allocated, forces applied and the model constrained in space. These boundary conditions impact on how the model responds to loading and the strains it experiences. After all boundary conditions are applied the model is solved and resulting displacements calculated. Stresses and strains are commonly used to assess how models respond to loading (figure 3). However, FEA is only useful if results approximate reality, thus a validation phase should also be included when possible (Richmond *et al.*, 2005; Kupczik, 2008). Despite all progress FEA allows in mechanical simulations there is significant debate about what biologically meaningful information may actually be inferred from FEA studies (Weber *et al.*, 2011; Daegling *et al.*, 2013; Strait *et al.*, 2013). Hence, interpretation should be cautious not to assume erroneous conclusions.



3. Example of a solved FE model of a hominin fossil (Kabwe 1) cranium.

VIRTUAL EXPERIMENTAL MORPHOLOGY

Creation of FE models is an extremely time consuming process. Thus, transforming an existing model into a target form is of significant interest. This can be achieved with good results by densely landmarking an original specimen and warping it into a target that was landmarked similarly (Stayton, 2009; O'Higgins *et al.*, 2011). This approach can also be applied to create models that represent extremes of morphological variance within a taxon. Those models can then be used to simulate mechanical loading and examine how intraspecific morphological variance impacts on mechanical function (Smith *et al.*, 2015a).

Modification of discrete anatomical regions allows creation of experimental specimens that may be of interest (O'Higgins *et al.*, 2011). For example, Strait *et al.* (2007) experimentally thickened the hard palate of a *Macaca fascicularis* and measured resulting strains to infer the relevance of thick palates in Austalopiths. Fitton *et al.* (2009) reconstructed a gracile *Australopithecus* and warped the zygomatic arch to that of a *Paranthropus* while maintaining the remaining anatomy constant. This allowed assessing how changing this region would impact on stresses and strains.

FINAL REMARKS

With increasing computing power and new technologies VA is able to bring together a set of techniques (e.g. GM and FEA) that augment insights on form and function when compared to traditional paleoanthropology studies. GM allows a deeper understanding of morphology and how it varies intra and inter-specifically. Furthermore, it is also fundamental in the reconstruction of incomplete specimens. FEA allows complex simulations of mechanical function that account for gross morphological complexity, material properties of skeletal structures, force magnitudes and directions of muscles. Thus, by combining these and other computerized techniques VA provides new insights about form-function in paleoanthropology.

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