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Craniofacial biomechanics and functional and dietary inferences in hominin paleontology

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A B S T R A C T

Finite element analysis (FEA) is a potentially powerful tool by which the mechanical behaviors of different skeletal and dental designs can be investigated, and, as such, has become increasingly popular for biomechanical modeling and inferring the behavior of extinct organisms. However, the use of FEA to extrapolate from characterization of the mechanical environment to questions of trophic or ecological adaptation in a fossil taxon is both challenging and perilous. Here, we consider the problems and prospects of FEA applications in paleoanthropology, and provide a critical examination of one such study of the trophic adaptations of *Australopithecus africanus*. This particular FEA is evaluated with regard to 1) the nature of the *A. africanus* cranial composite, 2) model validation, 3) decisions made with respect to model parameters, 4) adequacy of data presentation, and 5) interpretation of the results. Each suggests that the results reflect methodological decisions as much as any underlying biological significance. Notwithstanding these issues, this model yields predictions that follow from the posited emphasis on premolar use by *A. africanus*. These predictions are tested with data from the paleontological record, including a phylogenetically-informed consideration of relative premolar size, and postcanine microwear fabrics and antemortem enamel chipping. In each instance, the data fail to conform to predictions from the model. This model thus serves to emphasize the need for caution in the application of FEA in paleoanthropological enquiry. Theoretical models can be instrumental in the construction of testable hypotheses; but ultimately, the studies that serve to test these hypotheses – rather than data from the models – should remain the source of information pertaining to hominin paleobiology and evolution.

Introduction

Finite element analysis (FEA, interchangeably referred to as the finite element method or finite element modeling), has recently gained popularity as a technique for characterizing mechanical stresses, strains and forces in primate teeth and skeletons (Richmond et al., 2005; Panagiotopoulou, 2009). This mathematical technique, which was developed in the mid-20th century (Courant, 1943; Turner et al., 1956), has been employed for decades to investigate the mechanical behavior of biological tissues (Rybicki et al., 1972; Gupta et al., 1973; Thresher and Saito, 1973). Because FEA may be used to compare the mechanical behaviors of different designs of the same anatomical structure, it has become a powerful tool for testing biomechanical hypotheses with respect to postcranial bones, skulls and teeth (Richmond et al., 2005; Panagiotopoulou, 2009), and it has found increasing application in the biomechanical modeling and behavioral interpretation of extinct organisms (e.g., Macho et al., 2005; Rayfield, 2007; Wroe, 2008; Rayfield and Milner, 2008; Macho and Shimizu, 2010; Mazetta et al., 2009; Strait et al., 2009; Tseng, 2009).

The promise of FEA is a comprehensive accounting of the stress (and strain) field under specified loading conditions in any biological

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tissue of interest from tooth enamel (Spears and Macho, 1998) to skin (Dandekar et al., 2003). As was the case for multivariate statistics, the initial limiting factor for finite element studies was computational power. Because equilibrium equations must be solved for each element independently, computational processing time and data storage were at one time substantial impediments to analysis. Technological advances have rendered such concerns less immediate today, and several commercially-available packages exist that make FEA accessible to virtually any interested investigator. Thus, whereas the earliest mandibular finite element model consisted of 240 solid elements (Gupta et al., 1973), today a crude model of a primate jaw can have on the order of 10,000 (Hart et al., 1992; Marinescu et al., 2005), and a more realistic, but to some degree inaccurate, model of an anthropoid cranium may have well over 100,000 elements (Strait et al., 2007a,b).

With fewer operational challenges, it is not surprising that paleontological applications of FEA have been enthusiastically championed by functional morphologists interested in biomechanical modeling of extinct taxa (Macho et al., 2005; Rayfield, 2007; Rayfield and Milner, 2008; Wroe, 2008; Tseng, 2009; Mazetta et al., 2009). The potential of the method is vast, to the point that some have argued that the approach can model *in vivo* mechanical behavior in fossil hominins with considerable fidelity (Strait et al., 2009).

The purpose of the present contribution is to examine FEA applications in paleoanthropology through a brief discussion of general principles, and with the idea of gleaning generalities from particulars, we offer a detailed evaluation of a recent model put forward by Strait et al. (2009) pertaining to the cranium of *Australopithecus africanus*. It is our hope that interrogation of this FEA exemplar will serve to caution against the overenthusiastic application of such models in the interpretation of behaviors and possible adaptations of extinct hominins. We have chosen the research by Strait et al. (2009) over others not only because of its potential paleoanthropological impact, but also because of its general paleontological appeal. We examine a number of issues pertinent to this FEA, including the nature of the composite *A. africanus* cranium that was employed, the validation and parameters of the model, and the interpretation of the results. We also test the predictions made by Strait et al. (2009) concerning premolar use in *A. africanus* by examining postcanine tooth size, occlusal microwear and antemortem enamel chipping.

Although the veracity of the finite element model of trophic biomechanics and behavior in *A. africanus* is considered in some depth here, we also argue that FEA has fundamental limitations in its application to paleontological data, and caution, as did Jungers (1984: 78), with respect to the then-growing excitement over the "explanatory" power of allometric studies, that FEA is not a panacea for the challenges of functional inference in the fossil record. In the same way that scaling coefficients and exponents of allometry are simply a description of the numbers at hand, FEA is nothing more than a numerical accounting of the effects of a physical loading event.

Application of FEA in paleoanthropology

In the context of bones and teeth, FEA enables researchers to characterize the stress and strain tensors in structures of irregular geometry and complex material composition that would otherwise be either impossible to model by simple formulaic solutions, or would require simplified abstractions of the actual structure. While a number of experimental techniques can measure deformations directly in irregular structures, results are typically restricted to specific locations or surfaces. Assumptions of geometrical and material homogeneity, isotropy, and linearity – required for many simple mechanical models such as linear beam theory – can readily be bypassed by FEA, which will describe the loading state in a model that more closely approximates the geometry, structure and material composition of the actual specimen. This is accomplished in FEA by discretizing the bone as a mesh of geometrically regular subelements that can be analyzed separately through specification of appropriate equilibrium equations. Each of these elements can be assigned a specific set of material properties, such that spatial variations in stiffness can be incorporated into the model. The elements comprising the mesh structure can be varied in their geometry (e.g., brick elements and tetrahedrons) to further minimize any geometric differences between the model and the actual structure. This model is then constrained at certain nodes from spatial displacement in specific directions. Different types of loads can be placed at any element or node. These "boundary conditions," together with the geometric and material parameters of the model itself, define the displacement or the reaction forces of nodes from which the states of stress and strain at every element of the model are calculated. Although the precision with which the three-dimensional stress and strain fields can be specified is impressive, FEA should nevertheless "be understood as a method for finding an approximate solution for a simplified model" (Szabo and Babuska, 1991: 4).

Other than the recent development of finite element models of anthropoid crania (Ross et al., 2005; O'Higgins et al., 2005; Richmond et al., 2005; Strait et al., 2005, 2007a,b; Kupczik et al., 2007, 2009), skeletal FEA in biological anthropology has largely focused on mandibles (Korioth et al., 1992; Chen and Chen, 1998; Marinescu et al., 2005) and teeth (Spears and Macho, 1998; Macho et al., 2005; Shimizu and Macho, 2007), with more limited postcranial investigation (Richmond, 2007). Some of these studies have been nearly exclusively methodological in their focus, investigating the effects of boundary conditions or material property assignment on model performance (Chen and Chen, 1998; Strait et al., 2005; Ross et al., 2005; Marinescu et al., 2005; Kupczik et al., 2007). Other investigations have focused on using FEA to infer the adaptive or functional utility of variables such as palatal thickness (Strait et al., 2007a,b), the "anterior pillars" of *A. africanus* (Strait et al., 2009), the supraorbital torus (Kupczik et al., 2009), molar cusp morphology (Spears and Macho, 1998) and the arrangement of enamel prisms (Macho et al., 2005).

These different foci of finite element investigations – methodological concerns on the one hand and the inference of adaptive or evolutionary significance on the other – represent two important challenges for FEA applications in the context of extinct species. Methodological concerns include the issue of validation: what steps must be taken before one can have confidence that a finite element model of a fossil reflects biomechanical behavior as experienced by the organism in question? Interpretive concerns include the issue of evaluating the very large quantity of resulting data to generate hypotheses of function, adaptation or paleoecology.

Validation in FEA has a specific meaning: the physical behavior of a valid model is similar to that of the object being modeled. Complete validation, as defined by an agreement of spatial stress and strain distribution throughout a model, is neither the objective, nor it is technically possible for complex structures. Indeed, such data from the object under study would obviate FEA. Instead, the goal of a validation study is to ensure that the model behaves congruently with respect to independent experimental data under conditions similar to those the model is intended to mimic. A model that incorporates significant errors in material property assignment and/or boundary conditions can be expected to fail a rigorous (and often elusive) test of validation. What qualifies as legitimate validation, however, is open to question, because no universal standard is recognized. Unfortunately, in functional morphological investigations, any kind of validation is carried out infrequently (Richmond et al., 2005).