Models in palaeontological functional analysis

Models are a principal tool of modern science. By definition, and in practice, models are not literal representations of reality but provide simplifications or substitutes of the events, scenarios or behaviours that are being studied or predicted. All models make assumptions, and palaeontological models in particular require additional assumptions to study unobservable events in deep time. In the case of functional analysis, the degree of missing data associated with reconstructing musculoskeletal anatomy and neuronal control in extinct organisms has, in the eyes of some scientists, rendered detailed functional analysis of fossils intractable. Such a diagnosis may indeed be realized if palaeontologists attempt to recreate elaborate biomechanical models based on missing data and loosely justified assumptions. Yet multiple enabling methodologies and techniques now exist: tools for bracketing boundaries of reality; more rigorous consideration of soft tissues and missing data and methods drawing on physical principles that all organisms must adhere to. As with many aspects of science, the utility of such biomechanical models depends on the questions they seek to address, and the accuracy and validity of the models themselves.

Keywords: palaeobiology; biomechanics; function; feeding; locomotion

1. INTRODUCTION

Biological systems are invariably complex, consisting of multiple interdependent parameters with nonlinear relationships. Such systems can be prohibitively difficult to replicate completely for experimental or analytical purposes, so creating a simplified model allows the system to be investigated more easily. By their nature, models can also deal with uncertainty in the parameters of a system. This is especially important to palaeontologists, who are often missing important data (Figure 1). A key advantage of modeling in palaeobiology is the ability to construct models focusing on specific aspects of a system, holding constant or simplifying parameters which are unknown or of no interest, and permitting sensitivity analyses of how certain variables affect the outcome of the model. Figure 2 outlines examples of different model types of utility to palaeontology.

2. APPLYING MODELS IN PALAEOONTOLOGY

(a) Validation

Models are simplifications of reality, so it is important to have a strong understanding of the modelling parameters. In palaeontology, a great deal of data may be incomplete (such as muscles, material properties and neurological data). These issues can cause major errors in functional analyses performed using fossil data [5], particularly, where palaeobiologists are attempting to perform similar mechanical analyses to biologists [6].

Analysis of the sensitivity and the validity of models is therefore crucial. Approaches such as calculating moment arms of muscles [7], bending and torsion resistance in bone [8] and the use of experimental techniques such as wind tunnels [9] rely on the fact that all organisms respond to similar physical principles, and such approaches have been used successfully for many years to deduce extant organismal function. It is well known how output parameters from these models, such as mechanical advantage and coefficients of lift and drag, relate to organismal performance. For computational models such as finite-element analysis (FEA) and computational fluid dynamics (CFD), sensitivity analysis involves modifying parameters in the model to see how they influence results. Models can be validated using experimental data; comparing performance in extant taxa with a best-fit computational model. FE skull models created with a paucity of input data can generally reproduce patterns and orientations of bone strain but tend to poorly estimate absolute numerical values [10,11], yet those with more precise input data become more accurate [12]. Unless the input parameters are confidently known, palaeontological FE models are likely to be most useful for comparing relative rather than absolute performance.

(b) What questions can we address with models in palaeontology?

Palaeontological models can address questions of varying complexity at numerous hierarchical levels [6]. The majority of studies focus on specimen-specific questions, in part owing to the time required to construct some computational models. These studies address ‘classic’ functional questions: how hard could an animal bite [13], how fast could it run [14] or even how crinoids were able to support themselves in the water column [15]. A fruitful line of enquiry is comparative analyses of form–function, such as analysing changes in posture across therapsid groups [16] and three-dimensional dynamic projections of locomotion in extinct vertebrates [17]. By virtually manipulating geometry in computer-based FE models, researchers may make morphological changes whose effects on model performance can be evaluated [18]. This can involve the simple addition or removal of features such as sutures or fenestrae in a skull [19] or altering the morphology to mimic that of closely related groups [20]. It is also possible to create idealized models which can be modified one parameter at a time to explore morphospace [21]. Some workers have used FEA to pare down a generic block of material into a skull shape based solely on optimization for dealing with functional stresses [22]. Similarly, other workers have created theoretical morphospaces encompassing all possible morphologies of a system, then used biomechanical theory to eliminate untenable forms until a range of possible functions remains [23].
These virtual modelling approaches permit user control over input variables, which can be advantageous over traditional comparative analyses that must focus solely on taxonomic variation.

A more recent development uses models to derive functionally relevant measures that can be applied as data points in large-scale palaeontological analyses. Some recent examples include extinction selectivity across the...
Cretaceous–Tertiary boundary (K–T) [24], functional disparity of placoderm faunas [25], jaw diversity in the earliest radiation of gnathostomes [26], bite force evolution in theropods [27] and morphofunctional evolution of crocodilians [28]. In all these studies, the data are simple biomechanical metrics but future advances will incorporate biomechanical data from more complex models (FEA and CFD). Here, we can study the evolution of functional diversity on a temporal scale, within sister groups or across clades.

3. OPPORTUNITIES FOR THE FUTURE

Increases in computing capability are streamlining the construction of palaeontological models, allowing scientists to analyse large amounts of three-dimensional digital data in relatively short amounts of time. This presents the opportunity for larger scale comparative studies based on sophisticated techniques like FEA or CFD and opens the door to comparative functional analyses.

It is becoming possible to combine functional models with other techniques to answer new questions. Geometric morphometrics can be combined with FEA, where shape variation is analysed for variation in mechanical behaviour [1,4]. In this way, existing and hypothetical morphologies can be assessed for their structural performance. FE models can also be linked to multibody dynamic analyses to incorporate kinematics and muscular loads [29]. CFD [30] has been used very little in palaeontology yet has the potential to inform on the performance of extinct animals in aerial and aquatic habitats as well as respiratory anatomy or pneumatization. Similarly, fracture models [31] have not been extensively used, yet they can aid in understanding dental evolution and development. Phylogenetic methods offer the potential to assess historical constraint from form–function relationships, reconstruct ancestral function and to assess temporal and evolutionary trends in functional behaviour.

Many of the new techniques employed in palaeontological functional analysis are shifting emphasis away (i) from a qualitative assessment of function by analogy with morphology, and (ii) from a paradigm-based approach [32] in which function is predicted by the best-fit match to a selection of model systems. The new techniques focus on quantitative analysis: models are testable and repeatable, numerical results are generated and sensitivity analysis of parameters can be performed. Yet aside from the perennial problem of missing data, the ‘black-box’ nature of some techniques can be misleading and seductive as it can produce visually impressive results with little understanding of model process or input parameters. To use this new breed of methodologies, it is important for researchers to define and stay focused on particular questions or hypotheses, and to recognize the sophistication of model required to address palaeontological questions in the full.

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