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DOI:

[10.1111/pala.12501](https://doi.org/10.1111/pala.12501)

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Document Version

Publisher's PDF, also known as Version of record

Citation for published version (Harvard):

Lautenschlager, S 2020, 'Multibody dynamics analysis (MDA) as a numerical modelling tool to reconstruct the function and palaeobiology of extinct organisms', *Palaeontology*, vol. 63, no. 5, pp. 703-715.
<https://doi.org/10.1111/pala.12501>

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MULTIBODY DYNAMICS ANALYSIS (MDA) AS A NUMERICAL MODELLING TOOL TO RECONSTRUCT THE FUNCTION AND PALAEOBIOLOGY OF EXTINCT ORGANISMS

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Typescript received 18 March 2020; accepted in revised form 23 June 2020

Abstract: Recent advances in computer technology have substantially changed the field of palaeontology in the last two decades. Palaeontologists now have a whole new arsenal of powerful digital techniques available to study fossil organisms in unprecedented detail and to test hypotheses regarding function and behaviour. Multibody dynamics analysis (MDA) is one of these techniques and although it originated as a tool used in the engineering and automotive industry, it holds great potential to address palaeontological questions as well. MDA allows the simulation of dynamic movements in complex objects consisting of multiple linked components. As such, this technique is ideally suited to model biological structures and to obtain quantifiable results that can be used to test the function of musculoskeletal systems rigorously. However, despite these advantages, MDA has seen a slow

uptake by the palaeontological community. The most likely reason for this lies in the steep learning curve and complexity of the method. This paper provides an overview of the underlying principles of MDA and outlines the main steps involved in conducting analyses. A number of recent studies using MDA to reconstruct the palaeobiology of fossil organisms are presented and the potential for future studies is discussed. Similar to other computational techniques, including finite element analysis and computational fluid dynamics, the non-invasive and exploratory power of MDA makes it ideally suited to study the form and function in vertebrates for which no modern analogues exist.

Key words: numerical modelling, palaeobiology, multibody dynamics, fossil, functional morphology, biomechanics.

OVER the last two decades, novel computational applications and technologies have increasingly found their way into palaeontological and biological sciences. First and foremost, digital visualization techniques, such as computed tomography (CT) scanning, laser scanning, and photogrammetry have substantially changed the way how fossil organisms can be studied and characterized in unprecedented detail (Cunningham *et al.* 2014; Sutton *et al.* 2014). The potential of these methods to generate high-resolution and accurate three-dimensional (3D) digital models has itself triggered a further surge in downstream analyses to study the functional morphology and biomechanical behaviour of fossil and extant taxa (Anderson *et al.* 2012; Cunningham *et al.* 2014). Among these mechanical analysis techniques originally developed in the engineering and biomedical industry, finite element analysis (FEA) has become a popular tool in palaeontology to calculate the distribution of stress, strain, and deformation of geometrically complex

structures such as vertebrate skulls, limb bones or other skeletal elements (Rayfield 2007; Bright 2014). First applied to fossil organisms in the 1980s, technological advances have made FEA a mainstay tool in palaeontology for studying the functional morphology of individual fossil organisms and large-scale evolutionary transitions, as well as for the exploration of the function of hypothetical models. (Anderson *et al.* 2011; Lautenschlager *et al.* 2016; Lautenschlager, 2017a; Taylor *et al.* 2017). Similarly, palaeontologists have started to explore the use of computational fluid dynamics (CFD) (sometimes also referred to as finite volume method) as a powerful tool to simulate fluid flow around and within fossil morphologies (Bourke *et al.* 2014; Rahman 2017; Gutarra *et al.* 2019). In contrast to FEA, CFD has yet to experience the same broad applications in palaeontology, presumably due to the perceived complexity of the method. However, both methods have impressively demonstrated the ability to study and quantify fossil

form/function relationships and the potential of reconstructing palaeobiology.

Multibody dynamics analysis (MDA, sometimes also MBDA or referred to as multibody system dynamics, MSD), is a further computational tool originally invented for applications in the engineering sciences to simulate and study the behaviour of mechanical systems (Shabana 2020). A multibody dynamics system is defined as an assembly of solid (rigid) components that are connected by joints (kinematic constraints) that restrict the relative motion of the system when subjected to internal and/or external forces (Fig. 1A). Since the 1970s, MDA has been primarily used in engineering sciences, construction and the automotive industries to conduct motion analyses of complex mechanical setups for which the kinematic behaviour and the resulting generated loads on each component are challenging to predict. MDA non-invasively simulates and tests different scenarios and complex designs and therefore has increasingly been co-opted by other fields. For example, in the medical sciences, MDA has been applied to investigate human jaw movement (Koolstra & van Eijden 1995), to study the behaviour of arterial systems (Shin *et al.* 2005), and to reconstruct and assess the effects of accidents (O’Riordain *et al.* 2003; Rueda & Gilchrist 2009). In the biomedical industry, MDA has predominantly been used for implant design and analysis (Middleton *et al.* 1999; Sherman *et al.* 2011; Williams & Goma 2013), and has been applied to simulate the impact of exercise and sports-related activities on the human body (Celigieta 1996; Liu *et al.* 2011; Skals *et al.* 2017). More recently, MDA has also been discovered by biologists and functional morphologists studying the kinematic and biomechanical behaviour of vertebrates (Langenbach *et al.* 2002 and references therein; Curtis *et al.* 2008; Moazen *et al.* 2008). As the vertebrate skeleton also represents a complex system of inter-connected rigid bodies (i.e. bones) linked by kinematic constraints (i.e. joints) and experiencing loads (i.e. muscle forces) (Fig. 1B), MDA is ideally suited to study animal motion. Although not restricted to extant animals, MDA has, to date, been employed only rarely in palaeontology. As with FEA and CFD, the reasons behind the initially slow uptake of MDA probably lie in the steep learning curve and complexity of the method, whereas non-automated applications of MDA have used custom programming and algorithms that may not translate readily for all researchers (Hutchinson & Garcia 2002, Snively & Russell 2007). Furthermore, suitable digital datasets and models may not be available, although technological advances in digitization, and the publication and dissemination of existing datasets is increasingly abating this problem (Davies *et al.* 2017).

To facilitate the dissemination and application of MDA, I will present the general fundamentals and main steps involved in MDA in this paper. Basic requirements

and possible research applications based on published examples will be introduced and advantages and disadvantages will be discussed. It is hoped that this contribution will allow other researchers to use MDA as a quantitative tool to test the functional morphology of fossil organisms and to reconstruct their palaeobiology.

CONDUCTING MULTIBODY DYNAMIC ANALYSES

Requirements

As MDA is a computational analysis technique it requires (just as FEA and CFD) the simulated object to be available as a digital representation (Fig. 2). A variety of different approaches exist to generate digital models of fossil or extant specimens (Sutton *et al.* 2014). Most commonly, models derived from computed tomography (CT) scanning are used as these generally offer the highest fidelity and resolution and are able to capture internal structures of specimens, such as cavities housing soft tissues (e.g. brain, neurovascular structures, sinuses) and different bone types (i.e. cortical and trabecular bone). However, as internal properties can play a relatively minor role in the functional behaviour of MDA models, surface-based digitization techniques, including laser-scanning and photogrammetry, can be used to create digital models, which become useful if computed tomography is not an option (e.g. large specimens, fossils as part of museum exhibitions, etc.) Similarly, digital models can be created using box-modelling (Rahman & Lautenschlager 2016; Morales-García *et al.* 2019) which involves creating complex morphologies in a fully digital environment by the repeated addition and modification of simple shapes to produce a final model. In particular, for incomplete, inaccessible, or lost fossil specimens, this approach offers the possibility to replicate models based on published photographs and figures. Similarly, for the generation of a large number of models, this approach can provide an alternative option to more conventional approaches as digitization times are drastically reduced (e.g. 2–6 h for most models/morphologies) (Rahman & Lautenschlager 2016).

When working with fossil specimens, further processing of the digital models may be required (Fig. 2) because taphonomic deformation and disarticulation of fossils often prevent their immediate use for computational analysis. Digital restoration and retrodeformation steps will be necessary to correct for these artefacts, but can often be performed in the same software used for creating the digital models (e.g. VSG Avizo, Materialise Mimics, Synopsis Simpleware, Blender) (Lautenschlager 2016a, 2017b, table 1).

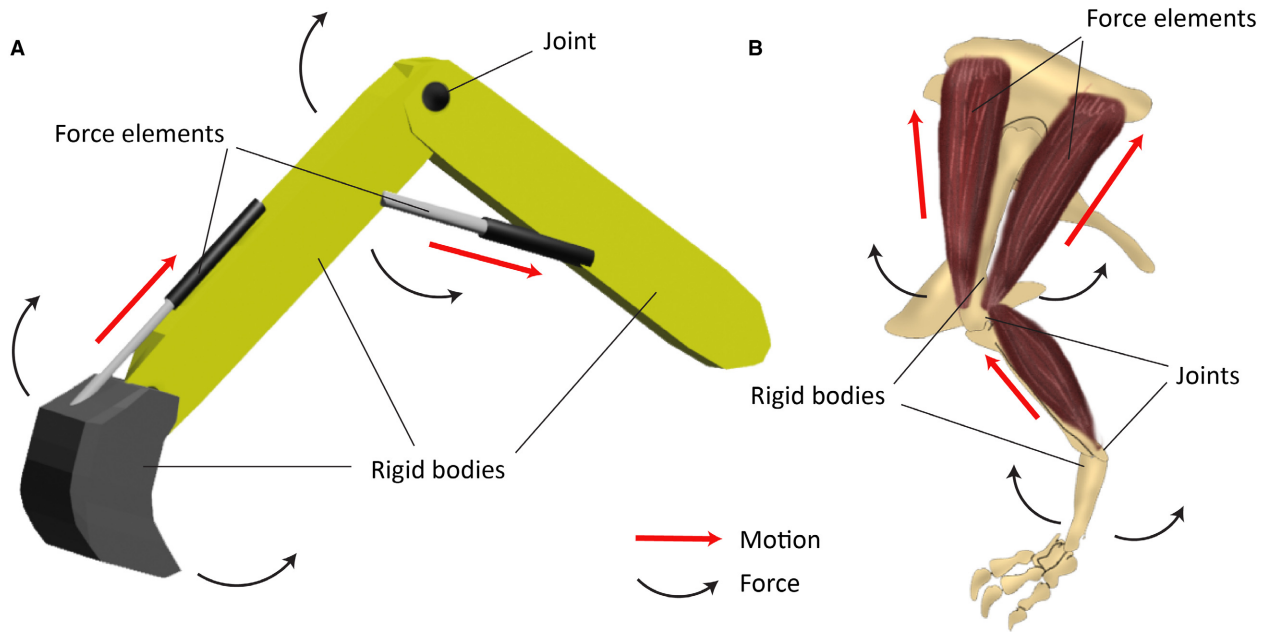


FIG. 1. Schematic illustration of multibody dynamics models and components exemplified by: A, a hydraulic excavator; B, a theropod hindlimb.

Depending on the analysis type and the hypothesis to be tested, additional soft-tissues will have to be reconstructed (Fig. 2). For fossil vertebrates, these are primarily the musculature and keratinous structures which have not been preserved. For the musculature, it can be enough to identify the insertion and origin areas on the bone, which will then be used to attach artificial muscles to in the analysis setup. However, calculating muscle volume, cross-sectional area and forces requires the three-dimensional reconstruction of the musculature (Lautenschlager 2013, 2016b). For models of extant species, or to estimate soft-tissue properties which are not readily available in fossils, these data can also be obtained using contrast-enhanced CT scanning (Lautenschlager *et al.* 2014; Gignac *et al.* 2016). However, care should be taken using properties from contrast-enhanced specimens as shrinkage of soft-tissues can occur during the staining process.

Software and file formats

A variety of software packages, both commercial (e.g. MSC Adams) and open source (e.g. OpenSim, Gait-Sym) (Table 1), exist to perform MDA. While the workflow and analysis setup are comparable for most, they can vary in their user interface, functionality, supported file types and cost. The majority of these packages will support the import of standard 3D file types, such as STL, OBJ or PLY. However, if accurate interaction between two or

more rigid bodies is to be simulated, a file format supporting so-called collision detection is required. Collision detection is commonly used in the development of video games, robotics and physical simulations to identify the intersection of two or more objects (Jiménez *et al.* 2001; Redon *et al.* 2002). For MDA, such intersections occurring between objects are relevant when the behaviour and movement of the rigid bodies or the force output are affected. For example, the relative motion of two bones connected by a specific joint type (i.e. ball-and-socket joints) will be dependent on whether the two bones can intersect or whether one constrains the movement and range-of-motion of the other (i.e. articular surface of the jaw joint). Similarly, interactions with non-skeletal components, such as simulated food items or ground topography (Fig. 3A), require collision detection to calculate (ground) reaction forces.

Generally, most MDA software has collision detection capabilities for in-built geometries included. These geometries consist of simple shapes, such as boxes, spheres or cones for which intersections can quickly be calculated via their bounding boxes (an artificial box encompassing all points of an object used to describe its location and dimensions). For more complex objects, including skeletal components, the bounding box does not accurately describe the object's morphology and will result in inaccurate collision detection. To generate objects which are detectable, the parasolid file format (extension *.X_T* or *.X_B*) is required. However, the parasolid

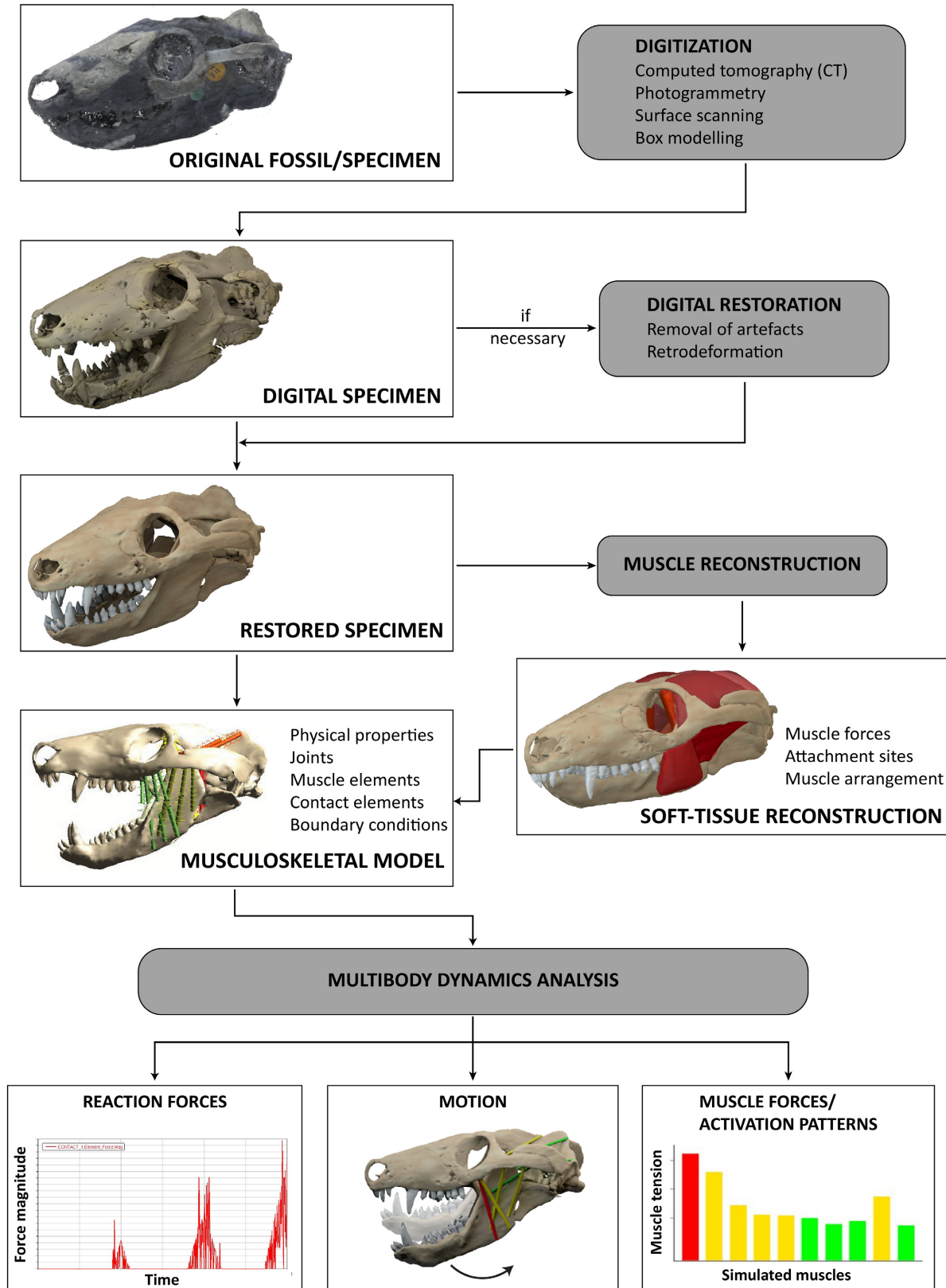


FIG. 2. Workflow and main steps in an MDA exemplified by a model of the cynodont *Thrinaxodon liorhinus*.

format is proprietary, not vendor-neutral, and commercial software (e.g. SolidWorks) is required for its generation. While parasolid files have full collision detection capabilities, they have a large resolution/file size ratio. This can either lead to large file sizes for complex geometries (e.g. up to 1 GB for a skull model based on a surface model with c. 500 000 faces) or low-resolution models to allow realistic analysis and processing times for MDA. It is recommended that models containing the lowest possible number of faces without loss of morphological detail are created and processed (e.g. by moderate smoothing, retopologizing) before converting to parasolid format and importing into MDA software.

A practical workaround for this problem can be to use a standard file format (e.g. STL) to visualize the geometry and to link it to a detectable object. This can be either a simple geometric object from the software's in-built library (e.g. sphere capable of collision detection attached to the tip of a tooth in feeding simulations) or a sub-region of the model converted to parasolid file (e.g. high-resolution model of a joint surface). A typical pitfall using this approach is that the detectable object is not registered to the main model and therefore the movement is not inherited.

Analysis setup

The first step in setting up an MDA is to import the previously generated and prepared digital model(s) into the used software package and to correctly scale and align it with the local coordinate system. In most software, alignment and scaling are not a necessity as the relative motion between components and kinematic behaviour

are not affected by either. However, to obtain correct absolute output values and magnitudes scaling the model to its accurate (life-sized) dimensions is a prerequisite. Reorienting the model will further facilitate interrogating the specimen if it is aligned with the global axes. A common problem is the use of different reference coordinate systems in different software (e.g. point of origin of the spatial axes, bounding box centre of models, or other) which can create substantial errors during the subsequent analyses. Most MDA software will allow defining a local coordinate system specific to the model. It is important to align the newly defined coordinate system with the software-specific global coordinate system so that the relative movement of the model is correctly registered.

In the next step, the mass properties of the models can be assigned. Depending on the software this can be done by defining the specific tissue density or material type (for example from an in-built library with pre-defined properties) based on which the mass and inertial properties are then automatically calculated for the analysis. As the volume of the digital model is used to calculate the mass, differences in the digitization process of the model could potentially lead to different properties at this point. High-resolution models incorporating detailed fidelity of the internal and inter-trabecular cavities will result in a slightly lower mass than models derived from surface-based digitization methods which are lacking this information. For models with a low percentage of internal cavities the resulting differences are likely to be minor. However, varying bone density (and therefore overall mass) has been shown to have a considerable effect on inertial properties (Snively *et al.* 2013). The necessity to include such details will mostly depend on questions addressed with the analysis and the taken approach

TABLE 1. Commonly used software packages used for model processing and multibody dynamics analysis of fossils.

Software package	Source	Example
Model pre-processing		
Amira (http://www.amira.com)	Commercial	Gunz <i>et al.</i> (2009)
Avizo (http://www.vsg3d.com)	Commercial	Lautenschlager (2016a)
Blender (http://www.blender.org)	Freely available	Lautenschlager (2016a)
GeoMagic Studio (http://www.geomagic.com)	Commercial	Tseng & Wang (2010); Whitenack <i>et al.</i> (2011)
Autodesk Maya (http://usa.autodesk.com/maya)	Commercial	Molnar <i>et al.</i> (2012)
MeshLab (https://www.meshlab.net)	Freely available	White <i>et al.</i> (2013)
VG Studio Max (https://www.volumegraphics.com)	Commercial	O'Hara <i>et al.</i> (2019)
Multibody dynamics analysis		
AnyBody Modeling System (http://www.anybodytech.com)	Commercial	David <i>et al.</i> (2016)
ArtiSynth (http://www.artisynth.org)	Freely available	Blasi <i>et al.</i> (2019)
GaitSym (http://www.animalsimulation.org)	Freely available	Sellers <i>et al.</i> (2009); Bates & Falkingham (2012)
MSC Adams (http://www.mscsoftware.com)	Commercial	Snively <i>et al.</i> (2013); Lautenschlager <i>et al.</i> (2018)
OpenSim (https://opensim.stanford.edu)	Freely available	Domalain <i>et al.</i> (2017)
SIMM (Software for Interactive Musculoskeletal Modeling) (https://www.motionanalysis.com)	Commercial	Hutchinson <i>et al.</i> (2005); Klinkhamer <i>et al.</i> (2018)

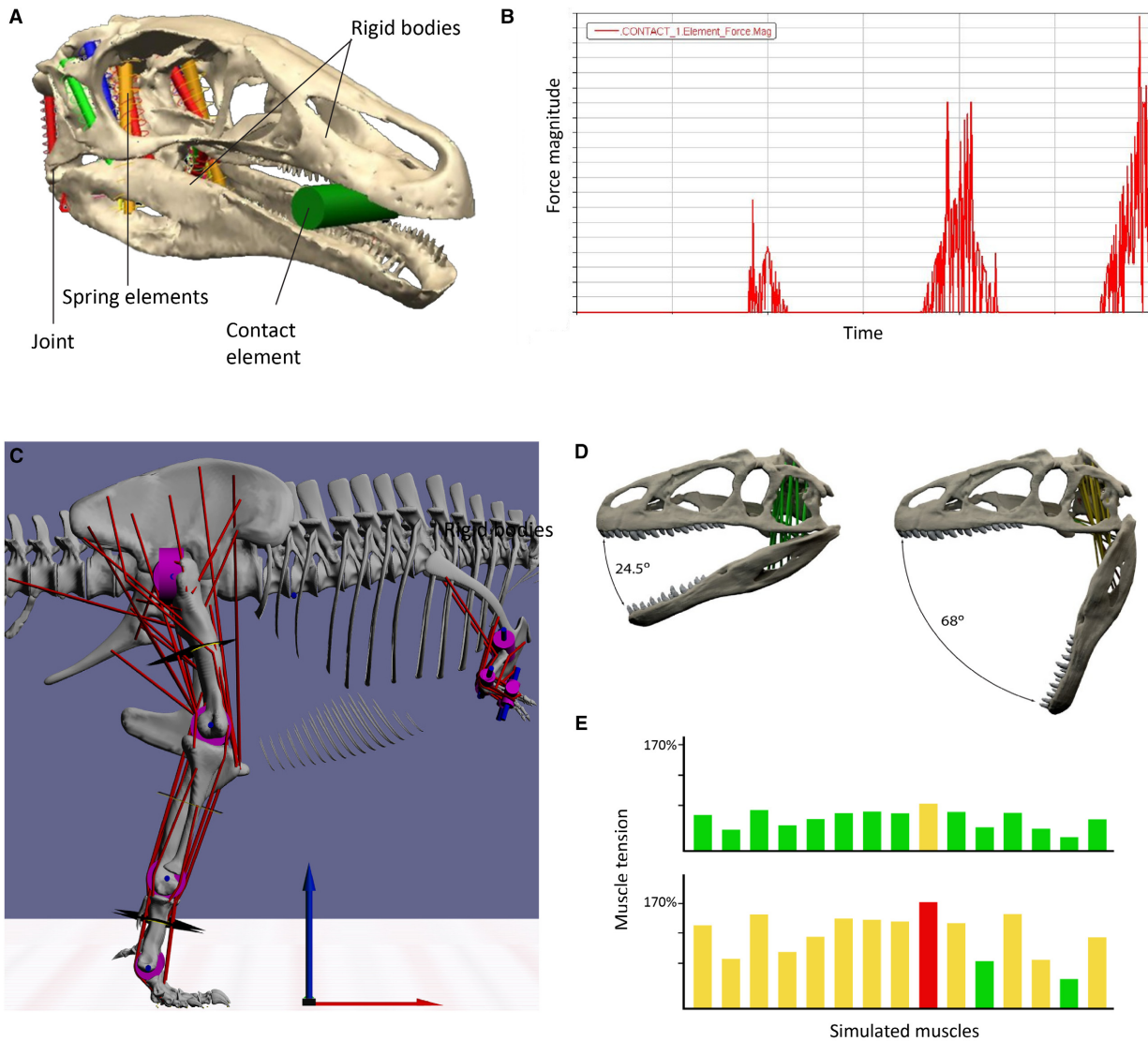


FIG. 3. Examples of MDA used to address palaeontological questions. A, MDA model of the therizinosaur dinosaur *Erlikosaurus andrewsi* to calculate: B, bite forces at different tooth positions (as used by Lautenschlager *et al.* 2016). C, MDA model and musculoskeletal setup for the analysis of locomotory behaviour of the theropod dinosaur *Tyrannosaurus rex* (modified from Sellers *et al.* 2017, fig. 2, CC BY 4.0). D–E, musculoskeletal model of the theropod dinosaur *Allosaurus fragilis* at different gape angles (D) based on muscle strain results (E) (as used by Lautenschlager 2015).

(comparative across a wider range of different models vs single models). For the study of single models, it is, therefore, advisable to perform sensitivity testing to estimate parameter effects (Snively *et al.* 2013).

Next, boundary conditions controlling the kinematic constraints need to be defined. These include external conditions acting upon the model and internal conditions representing constraints due to the relative motion of the model components. External conditions include constraints fixing a component from movement. This is

necessary for simulations of components which would be largely restrained from movement due to being attached to other parts, but which are not simulated. For example, for the analysis of a feeding cycle in vertebrates, the skull would be constrained from movement as it would be attached to the vertebral column thereby limiting its movement while the vertebrae themselves are not part of the simulation. In this, the setting of constraints in MDA is comparable to the requirements for FEA (Bright 2014) (although, constraints also form part of the displacement

analysis in FEA, which is not the case for MDA). Constraints can be applied to restrain movement only along selected axes, such as allowing anteroposterior movement but no transverse movement of a vertebrate mandible. In addition, further external boundary conditions can be set for components undergoing movement, such as assigning gravity. Including gravity in an analysis will lead to increased or decreased acceleration of components depending on the direction of movement.

Internal boundary conditions are mostly represented by how different components are allowed to move relative to each other. This can be achieved by using different joint types. For example, a hinge-type joint might be most appropriate to model the jaw joint of most archosaurs allowing only movement of the jaw along the sagittal plane, whereas a ball-and-socket-type joint is suitable to model the movement of the femur against the pelvis in the hip joint, and a pivot-type joint would be used to simulate the interaction between cervical vertebrae. Often, and in addition to the joint type, the specific degrees of freedom and the direction and range of motion can be defined to control the relative motion between components further.

In a final step, force elements are set up to link the rigid bodies and to provide possible input parameters for the analysis. In most software, flexible spring elements or muscle actuators are used to represent the relevant muscles involved in the analysis, linking corresponding attachment sites (insertion and origin) on the rigid bodies. Muscle-specific properties, including maximum force, contraction velocity, stiffness, activation and dampening, can be defined for each spring element, although properties can vary with software. While spring elements represent straight point-to-point connections, curved muscle anatomy (such as cranial muscles wrapping around the braincase, e.g. *m. temporalis*, or the lower jaw, e.g. *m. pterygoideus ventralis*) can be replicated by successively linking spring elements together to achieve the same effect.

Obtaining accurate muscle properties can be challenging for extant as well as extinct animals. While these properties are often known for well-studied species (e.g. humans) and can be taken from the primary literature, it will be difficult to find appropriate muscle properties for fossil vertebrates. Some properties (e.g. muscle volume, cross-section area, fibre length) can be obtained using dissections or contrast-enhanced CT scanning of modern species (Gignac *et al.* 2016), while several methods exist to estimate these properties in fossils (Lautenschlager 2013, 2016b; see also Requirements, above). However, it is unlikely that all muscles can be reconstructed or obtained. In these cases, a simplified muscle model can be simulated which assumes a constant strength of the muscle and requires only the definition of the initial or

maximum muscle force (Zajac 1989; David *et al.* 2016). Sensitivity studies have shown that, in particular for slow movements, a simplified muscle model can be a viable alternative to models for which all muscle properties are known (Damsgaard *et al.* 2006; Duprey *et al.* 2015).

Where necessary, additional components that are not part of the actual model can be created. For example, artificial food items (in the form of simple cylinders or boxes) that are used to obtain reaction forces (= bite forces) whenever contact with the teeth or the jaw occurs. As mentioned above, this approach requires the definition of contacts between the individual components to detect collisions/intersections. Furthermore, when setting up additional components (e.g. food item) that are not connected to the main model (e.g. skull) and that undergo movement, it is necessary to define the relative motion of such components in reference to the main model.

Analysis

Following the completion of the analysis setup outlined above, the MDA can be performed (Fig. 2). Different types of MDA exist that test specific questions: forward and inverse dynamic analysis (Curtis 2011).

Forward dynamic analysis simulates the absolute and relative motion of the rigid bodies under the influence of forces. Forces driving the acceleration of bodies and their activation times for the duration of the simulation are defined before the analysis and have been assigned to the spring elements. This approach requires information on muscle forces, activation patterns and other properties, which have either been obtained experimentally (for extant species) or need to be estimated (for fossil and extant species) on the basis of measurements or reconstructions (see above). The forward dynamic simulation results in the motion of the rigid bodies based on the defined muscle properties and is best suited to replicate experimental settings, to perform validation studies, and to estimate (palaeo)biological properties, such as bite force measurements.

In contrast, the inverse dynamic analysis approach attempts to predict which input forces (and combinations thereof) are necessary to achieve a specific pre-defined motion. More automated MDA can be used to determine complex muscle activation patterns in a full walking cycle or feeding simulations. However, the large number of unknown properties and possible combinations to achieve the desired motion or force criterion can make it difficult to find a single possible solution. Additional optimization criteria must be defined to minimize the possibilities. For example, a linear criterion would be appropriate if the optimization aims to recruit the smallest number of the available muscles to achieve motion and force output.

Alternatively, a minimum/maximum criterion will aim to maximize force output while keeping the activation levels of all muscles as low as possible (Rasmussen *et al.* 2001; Damsgaard *et al.* 2006). Other studies have used a quadratic muscle criterion which takes muscle position into account and preferentially activates muscles with an optimal angle of attack (force transfer is highest if the muscle is perpendicular to the rigid body but lowest if the muscle is parallel to the rigid body). Which of these (or other) criteria are used will depend on the specific question to be tested but they usually relate to meaningful biological functions, such as the maximization of bite force, minimization of joint reaction forces or energy expenditure (Koolstra & van Eijden, 2001; Rasmussen *et al.* 2001, Curtis 2011).

Results and post-processing

The results of an MDA can be visualized and presented in different forms. For FEA and CFD, results are often displayed in the form of multi-colour contour plots (Bright 2014; Rahman 2017). This option does not exist for MDA results. Depending on the tested question or hypothesis, results can be visualized using the kinematic simulations directly in the form of three-dimensional animations showing the motion of the rigid bodies, their range of motion, acceleration or other properties. However, displaying the results in that format is difficult to transfer into traditional forms of publication, and although methods exist to present animations in academic publications (Lautenschlager & Rücklin 2014), showing MDA results as animations are primarily useful for conference presentations and supplementary online content. Nevertheless, a wide variety of visually static results can be extracted from MDA (Fig. 2). These include motion paths, velocity and acceleration of the rigid bodies, reaction forces, muscle activation patterns and insertion angles and other properties, which can be plotted against the running time of the analysis (Figs 2, 3B). Depending on the software used, different properties can also be exported for further downstream analysis.

EXAMPLES IN PALAEOLOGY

Similar to other computational techniques, such as FEA and CFD, which have transformed the way the functional morphology and biomechanical behaviour of fossil organisms can be tested rigorously, MDA has a large potential for deciphering and reconstructing palaeobiology. However, traditionally, studies using MDA have predominantly focused on extant animals and modelling the human musculoskeletal system (for an overview see e.g.

Vasavada *et al.* 1998; Curtis *et al.* 2008; Moazen *et al.* 2008). It is only recently that MDA has also found its way into palaeontological research. With a few exceptions, studies using MDA have focused on dinosaur palaeontology and primarily on the reconstruction of feeding behaviour and locomotion.

In one of the first studies to test different palaeobiological hypotheses of a fossil vertebrate, Hutchinson *et al.* (2005) built a musculoskeletal model of *Tyrannosaurus rex* to evaluate its locomotory capabilities. In this study, the authors only modelled the animal's hindlimb and used the software SIMM (Software for interactive musculoskeletal modeling; Musculographics Inc., Chicago IL, USA) to calculate muscle moment arms for over 30 different hindlimb muscles. By manipulating the model into various poses representing different stances and gaits from crouching to up-right running, the study found that *T. rex* was probably not a fast runner. The reduced complexity of the model allowed the authors to obtain meaningful results while keeping computational requirements to a minimum as only parts of the skeleton were manually simulated.

In a similar but computationally more complex study, Sellers *et al.* (2009) used a full multibody dynamics approach to reconstruct the gait of another dinosaur. The authors created a digital musculoskeletal model of the duck-billed ornithomorph *Edmontosaurus annectens* derived from laser-scanning and the software GaitSym (<https://animalsimulation.org>) to simulate different gaits (bipedal vs quadrupedal) and styles (e.g. trotting, running, galloping) of the animal. The results showed that bipedal running at higher speeds and with facultative quadrupedal walking at lower speeds were the most likely scenarios for *E. annectens*. To achieve consistency in the modelling results, the simulations were run multiple (several thousand) times requiring a multicore computer for simultaneous processing.

Since then similar studies have focused on reconstructing the locomotion of different dinosaurs, such as the sauropod dinosaur *Argentinosaurus huinculensis* (Sellers *et al.* 2013) and again *T. rex* (Sellers *et al.* 2017) (Fig. 3C) using increasingly complex models and refined simulations, combining multibody dynamics analysis with additional biomechanical techniques, such as stress analysis to evaluate the impact of compression and tension in skeletal elements. In addition, the simplified MDA approach of calculating muscle moment arms has been used to elucidate locomotory behaviours of different dinosaur species (Bates *et al.* 2012a, b; Maidment *et al.* 2014; Klinkhamer *et al.* 2018).

Using a combination of manual manipulation of digital models and MDA, Mallison (2010a, b) assessed the mass distribution, posture, and range of motion of the sauropodomorph dinosaur *Plateosaurus engelhardti*. For the

studies, the individual bones of a nearly complete skeleton were CT scanned and virtually reassembled. The mass distribution and centre of mass of *P. engelhardti* were obtained using MSC Nastran (originally designed as FEA solver but capable of performing kinematic analyses of rigid bodies). The analyses recovered a bipedal posture for *P. engelhardti* as more plausible, whereas a quadrupedal posture was found to restrict locomotion and feeding range. Applying the same methodological approach, Mallison (2011) estimated the defensive capabilities of the spiked tail of the stegosaurian dinosaur *Kentrosaurus aethiopicus*. Simulations based on digital models of the complete skeleton and the reconstructed tail musculature showed that *K. aethiopicus* was capable of continuous or whiplash tail motion with sufficient energy to penetrate soft-tissue and fracture bone.

Bates & Falkingham (2012) and Snively *et al.* (2013) were among the first to apply MDA to investigate the cranial and cervicocephalic biomechanics of a fossil vertebrate. Both studies focused on the feeding behaviour of theropod dinosaurs. While Bates & Falkingham (2012) used digital skull models of *Allosaurus fragilis* and *Tyrannosaurus rex* in GaitSym to estimate the maximum bite force, Snively *et al.* (2013) modelled the skull, vertebral column and selected soft tissues (e.g. trachea, air spaces) of *A. fragilis* in MSc Adams (MSC Software, Santa Ana CA, USA) to investigate inertial properties and acceleration during head movement. The first study found distinct bite force differences between both theropod species, with *T. rex* generating a force of up to 57 000 N, whereas *A. fragilis* only reached about 10% of this value. These results complement Snively *et al.*'s (2013) findings that *A. fragilis* had a distinctive feeding style, using avian raptor-like head ventroflexion and retraction.

More recently, MDA has been applied in conjunction with other biomechanical analysis techniques, such as FEA. Lautenschlager *et al.* (2016) used MDA to estimate bite forces and investigate the similarities in feeding behaviour of different herbivorous dinosaurs. The predicted biomechanical loading regimes of the skull obtained from the MDA were then subsequently used to inform boundary conditions of the corresponding FEA models. This combined analytical approach demonstrated distinct functional differences between the analysed dinosaur species (*Plateosaurus*, *Stegosaurus* and *Erlikosaurus*) despite the convergently evolved similarities in skull morphology. In a similar approach, Lautenschlager *et al.* (2018) used MDA to predict bite and joint reaction forces in the mandibles of non-mammalian cynodonts and mammaliaformes. Those loading conditions were then incorporated into FEA models to show that miniaturization played a key role in reducing joint loads across during the evolution of early mammals and of the mammalian middle ear.

OUTSTANDING CHALLENGES AND FUTURE DIRECTIONS

Multibody dynamics analysis has routinely been used in engineering and biomedical applications for several decades now and while it has been adopted by the biological sciences to simulate and predict the biomechanical behaviour of modern animals, it has yet to witness broadscale use by the palaeontological community.

There are several probable reasons contributing to this slow uptake in palaeontology. Firstly, and as with other computational techniques, MDA and the required software have a steep learning curve, while the complexity of models can often exceed that of models used for other techniques. The publication and documentation of detailed analytical protocols as well as overview articles, including this one and others (Curtis 2011), outlining the key steps of the process may help to reduce this perceived barrier. Secondly, access to hardware and software necessary to perform MDA is limited due to the often large cost of commercial products. However, a range of freely available programs (e.g. GaitSym, OpenSim, ArtiSynt; Table 1) now exists, although functionality and ease-of-use vary considerably. A key problem lies in the restriction of proprietary file formats capable of collision detection (see Software and file formats, above). This problem could potentially be overcome by using 3D modelling software such as Blender (Waldon *et al.* 2014), which contains some collision detection algorithms for video game development. However, harnessing this functionality requires further customization of the software. For example, Lautenschlager (2015) used Blender to estimate muscle strain and jaw gape angles in theropod dinosaurs and their extant relatives (crocodiles, birds) in an MDA-like approach (Fig. 3D, E). The animation capabilities and customization via Python scripting of Blender allowed the simulation of musculoskeletal interactions. While the study replicated some of the multibody dynamics functionality, the lack of collision detection, setting of mass, inertial and other properties, and force-driven spring elements distinguishes this approach from a conventional MDA. However, some of these functions could potentially be implemented in future studies. A further challenge relates to how analytical results, underlying data and model files can best be disseminated and made available alongside publications to other researchers. It is suggested that the 3D models of species used for the analysis and the analysis setup files are provided along with a documentation of model properties and settings (Davies *et al.* 2017). However, for complex analyses, these can quickly lead to file sizes of several gigabytes, whereas the analysis files derived from commercial software packages are likely to be in a proprietary format and thus not easily accessible.

Considering that MDA is a computational simulation technique the question of how accurately MDA models and results reflect reality might be raised. As with related techniques (FEA, CFD), using modern organisms to ground-truth the methodology can help to answer this question. Many of the case studies in palaeontology mentioned above have to some extent used comparative models of extant, related taxa for which results can be compared more easily with published data (e.g. Bates & Falkingham 2012; Sellers *et al.* 2013; Lautenschlager *et al.* 2018). In addition, validation studies have compared experimentally derived results with those predicted by MDA models (e.g. Sellers & Crompton 2004; Curtis *et al.* 2008, 2010; Moazen *et al.* 2008; Watson *et al.* 2014; Hicks *et al.* 2015), which can help to identify limitations when simulating extant or extinct taxa. Generally, the comparison between in-vivo results and those obtained from MDA shows that bite forces and muscle activation patterns can be predicted reasonably well (within approximately 80–90% range of experimental values) for biomechanical models of vertebrate skulls (Curtis 2011; Gröning *et al.* 2013; Watson *et al.* 2014). However, MDA results were also found to be sensitive to changes of the input parameters, in particular muscle properties (e.g. fibre length, orientation of muscle vectors) (Gröning *et al.* 2013).

For MDA models of fossil species, it may not be possible to perform validation tests due to a lack of published comparative data and ethical considerations to avoid experiments involving living animals. In these cases, sensitivity tests can provide an estimate of how input properties can influence the results and can help avoid problems of using MDA as a black box system without scrutinizing the role of the input parameters.

As is apparent from the presented examples above, MDA has so far been exclusively applied to study the locomotion or feeding behaviour of fossil vertebrates, with a strong focus on reconstructing dinosaur palaeobiology. However, the application of MDA is not restricted taxonomically and can also be used to test and address a variety of questions in other vertebrate groups. Similarly, MDA can be applied to fossil invertebrate organisms, and particularly those with complex body plans, locomotory behaviours and feeding mechanisms, such as arthropods and insects (Garwood & Dunlop 2014; David *et al.* 2016; Blanke *et al.* 2017). Given the steady advances in computer technology and the increasing affordability of necessary equipment, it is likely that MDA will find its place in the palaeontological community alongside other computational methods, such as CFD and FEA. The possibility of combining these analytical techniques in an integrated approach further highlights the potential and versatility for reconstructing the palaeobiology of extinct organisms (Kumbhar 2013; Marcé-Nogué *et al.* 2015). Their non-invasive and exploratory utility

makes them ideally suited for testing biomechanical hypotheses and studying form and function in animals for which no modern analogues exist.

Acknowledgements. Andrew Smith and Barry Lomax are thanked for the invitation to contribute this article as part of the Palaeontological Association Annual meeting symposium 2019. Eric Snively, Sally Thomas and two anonymous reviewers are acknowledged for their helpful comments and suggestions that improved the manuscript.

Editor. Barry Lomax

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