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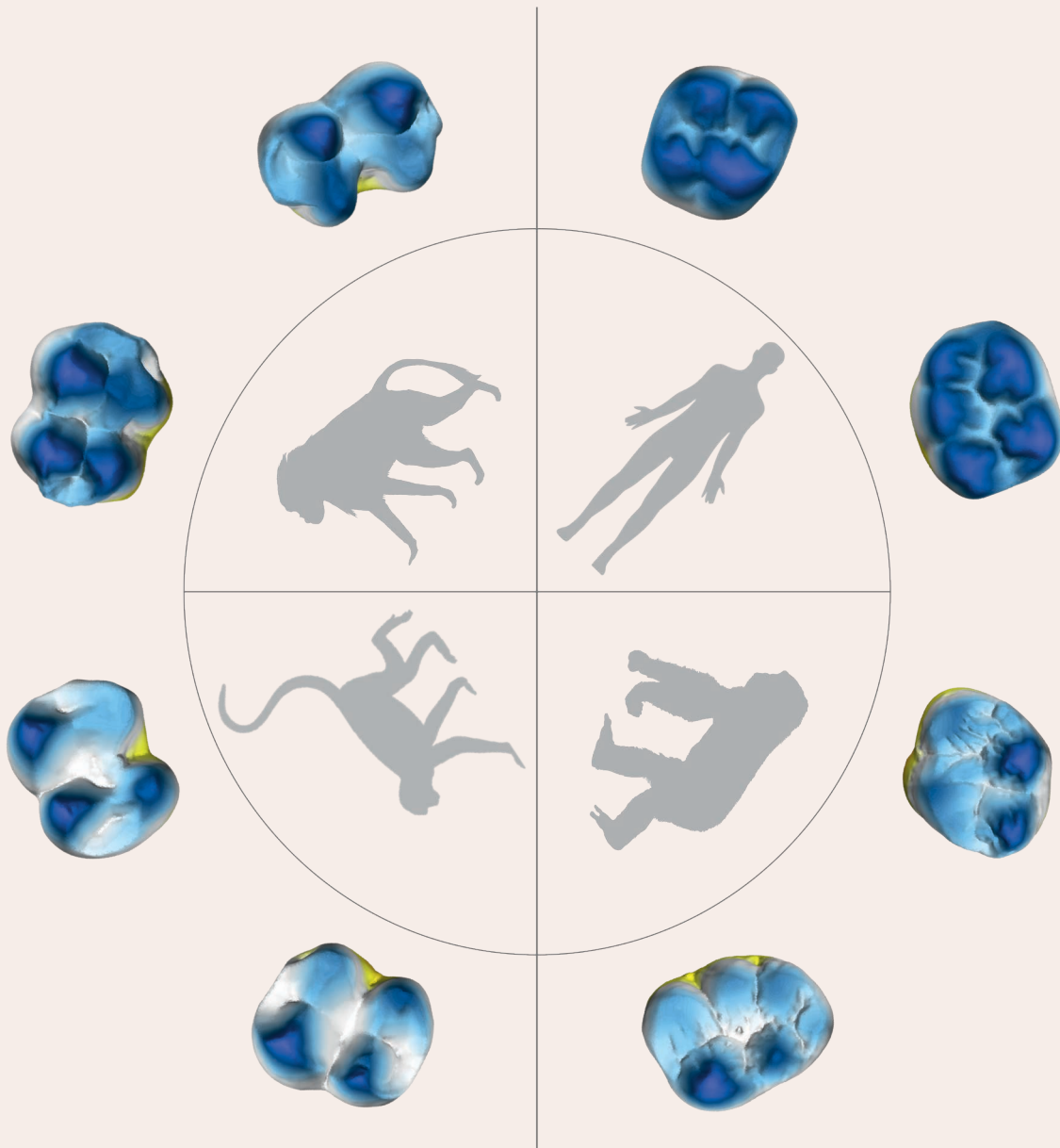
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Revue des Analyses Dynamiques Multicorps versus Éléments Finis appliquées en paléanthropologie : que pouvons-nous en attendre pour l'étude des restes postcrâniens d'hominines ?

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Cette note fait suite à une communication présentée lors des 1846^{es} journées de la Société d'Anthropologie de Paris dans le cadre de la session "Humanité(s) : définition(s), diversités et limites"

Abstract – “Multibody Dynamic Analysis” (MDA) and “Finite Element” Analysis (FEA) are commonly used to investigate biomechanical solicitations relative to a movement. These approaches have been also used in palaeontology to bring extinct animals, such as hominins, “back to life”. The purpose of this study is to report on the available literature on the use of MDA and FEA in postcranial palaeo-anthropology. We briefly introduce the theoretical aspects of modelling and simulation applied to biomechanics. The theoretical basis and fields of application of MDA and FEA are then presented. A synthesis of the literature highlights palaeoanthropological issues, variables derived, findings obtained and methodological limitations to keep in mind. More generally, this study synthesizes a conceptual framework and recommendations for the use of such approaches in form-function relationships in an evolutionary context.

Keywords – Multibody Dynamic Analysis, Finite Element Analysis, form-function relationships, palaeoanthropology, biomechanics

Résumé – Les méthodes d'Analyse “Dynamique Multicorps” (MDA) et en “Éléments Finis” (FEA) sont utilisées pour étudier les sollicitations biomécaniques associées à un mouvement. En paléontologie, ces approches de simulation numérique “redonnent vie” aux espèces éteintes, et notamment les hominines. Ce travail propose une analyse de la littérature sur l'utilisation des méthodes MDA et FEA en paléanthropologie postcrânienne. Les concepts de modélisation et de simulation appliqués au champ de la biomécanique sont tout d'abord introduits. Les bases théoriques et champs applicatifs des méthodes MDA et FEA sont

présentés. Une synthèse de la littérature met ensuite en lumière les questionnements paléanthropologiques, les variables manipulées, les conclusions tirées ainsi que les limites méthodologiques à retenir. De manière plus générale, ce travail vise à synthétiser un cadre conceptuel et quelques recommandations pour l'utilisation de telles approches numériques dans l'étude des relations forme-fonction dans un contexte évolutif.

Mots clés – Analyse Dynamique Multicorps, Analyse en Éléments Finis, relations forme-fonction, paléanthropologie, biomécanique

Introduction

In palaeontology, the bulk of inferences bearing on behaviour, ecology and phylogeny are based on relationships between form and function (Witmer, 1995; Ward, 2002; Rayfield, 2019). Generally, these relationships are investigated by applying three distinct approaches: comparative anatomy, experiments and numerical simulations (Hutchinson and Gatesy, 2006; Benton, 2010). The comparative anatomy approach aims to describe and quantify morphological characters from a selection of extant and extinct taxa in order to assess their potential functions. Knowledge of the behavioural repertoire of extant species provides a baseline for making behavioural inferences from fossil specimens. However, no mechanical evidence is given on putative relationships, which sometimes leads to confusion between phylogenetic and functional signals (Lauder, 1995; Witmer, 1995; Ward, 2002). Conversely, experiments (in-vivo, ex-vivo) with extant analogues give insights into the mechanical

processes that link morphologies to functions, but may require challenging protocols (e.g. ethics, difficulty of access to biological variables, numerous variables that make it hard to control the experimental framework) (Lauder, 1995; Shi et al., 2012). In addition, given that fossils generally display unique character combinations with no extant equivalent, the choice of analogues is potentially open to criticism (Susman, 1998; Hutchinson and Gatesy, 2006). Here, we focus on numerical simulations that complement both approaches by giving access to biological variables that are not experimentally accessible and by taking the particular morphology of fossils into account. In addition, “what-if” scenarios, meaning assessments of different hypothetical scenarios predicting an outcome, can put fossil bones in their anatomical context, including soft tissues and range of joint motion, which are critical to understanding form-function relationships (Preuschoft and Witzel, 2004; Hutchinson and Gatesy, 2006; Brassey et al., 2017; Bishop et al., 2021).

The simulation approaches most frequently used in palaeontology, Multibody Dynamics Analysis (MDA) and Finite Element Analysis (FEA), arose from the field of engineering (Richmond et al., 2005; Ross, 2005; Bright, 2014; Brassey et al., 2017; Rayfield, 2019; Lautenschlager, 2020). MDA was initially used to address questions of hominin bipedalism (Crompton et al., 1998; Wang et al., 2004) and dinosaur locomotion (Hutchinson, 2004; Hutchinson et al., 2005; Bates et al., 2010). FEA has brought insights into hominin craniodental debates (Spears and Crompton, 1994; Strait et al., 2009) and the morphology of the face in extant *H. sapiens* (Ichim et al., 2006a ; 2006b; Gröning et al., 2011; Wroe et al., 2018).

Previous reviews of FEA/MDA applied to palaeontological questions have addressed simulation principles (Benton, 2010; Hutchinson, 2012) and the theory behind the method (FEA: Richmond et al., 2005; Ross, 2005; Rayfield, 2019 / MDA: Lautenschlager, 2020; Bishop et al., 2021) with sometimes an emphasis on sensitivity and validation (Rayfield, 2007; Panagiotopoulou, 2009; Bright, 2014; Brassey et al., 2017). This article sheds light on the use of MDA and FEA in postcranial palaeoanthropology through (1) a theoretical summary of MDA and FEA methods and (2) a review of studies using MDA and FEA in postcranial palaeoanthropology. More specifically, we aim to provide a mean to help determine whether, and which, numerical simulation may be relevant to address a given question, and what are the main steps of the process.

Biomechanical modelling and simulation

The essence of modelling is the simplification of a complex question through a defined framework, which ensures that the model setup is valid in a given limited and controlled environment. Simulation then consists of executing the ensuing workflow. The modelling process may be divided into (1) understanding the initial question, i.e. defining research hypotheses and objectives, (2) identifying outputs, i.e. results of the simulation, (3) identifying

inputs, i.e. variables of the experimental framework, (4) determining relationships between model components and assumptions and simplification compatible with the initial question, (5) creating the model and testing its validity (Robinson, 2008). Each of these steps is detailed below:

- Outputs are the mechanical performance indicators that enable testing of the initial hypotheses at best. In biomechanics, mechanical performance is assessed via minimizing biological functions (e.g. metabolic energy, muscle forces, stress, strain) or maximizing other parameters, such as torque generation capacities or mechanical strength (figure 1). In other words, the mechanical performance of two structures can be compared in terms of which one is the most efficient or, for example, better distributes stress to avoid failure. The choice of the output determines whether the simulation process is appropriate, and which type of simulation should be used;
- Inputs are the variables of the experimental framework. In biomechanics, inputs represent all variables that constitute the model (geometrical data, mass data, material properties), boundary conditions and the loading scenario or the motion data (figure 1). Inputs can be changeable (independent variables) or fixed (fixed coefficients that will remain the same in all the simulations);
- Assumptions and simplifications define the model's complexity. The greater the complexity, the better the representation of reality. However, beyond a certain level, increasing complexity will no longer increase either precision (repeatability) or accuracy (exactness relative to real value) and results in time wasted on model design and calculation (Robinson, 2008; Sargent, 2010; Hutchinson, 2012). In biomechanics, model complexity may be dictated by the need for accurate representation of morphology. As an example, Brassey et al. (2013) raised the question of the utility of considering the morphology of long bones instead of modelling them as beams;
- Testing of model validity (distance between experimental values and model outputs) investigates the validity of the model outputs relative to reality while also testing its sensitivity (how much the analysis outputs depend on the fixed input value) and identifies the critical inputs that deserve to be quantified accurately (Hutchinson, 2012). These two approaches are complementary, but the validation step is not always achievable in palaeontology because of the lack of data (Sellers and Crompton, 2004). These missing fixed inputs therefore have to be estimated (e.g. with the extant phylogenetic bracket concept, which is based on biological homologies between the two closest extant outgroups to provide a bounded estimation of the missing data; Witmer, 1995); the sensitivity of the model outputs to these fixed inputs therefore needs to be tested (see Hicks et al., 2015; Rayfield, 2019 for extensive recommendations on how to conduct sensitivity and validation studies). Testing the model may lead to readjusting the model parameters and inputs (figure 1).

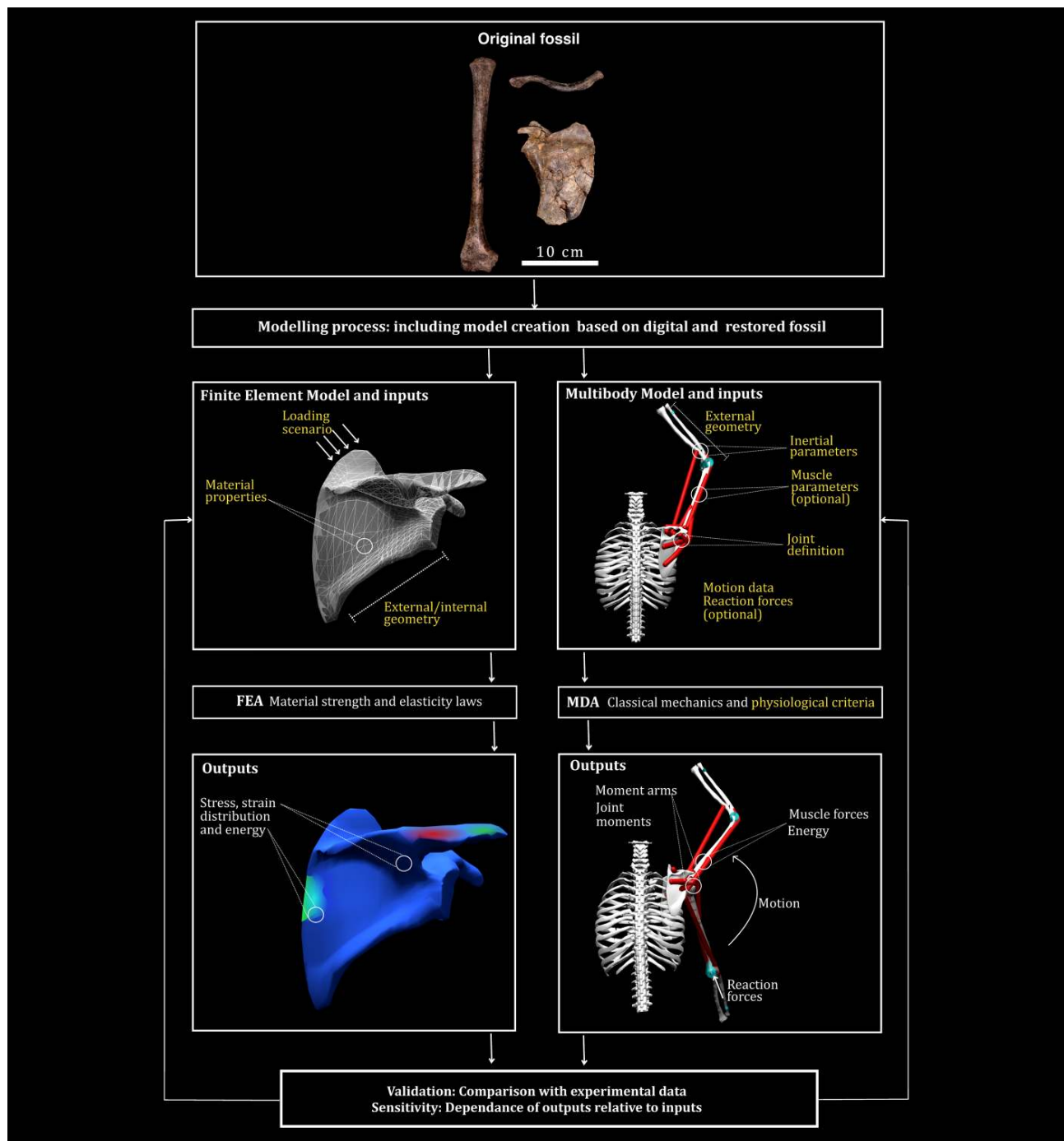


Figure 1. Schematic view of the FEA and MDA simulation process. The modelling process consists of defining research hypotheses and objectives, identifying outputs/inputs, determining relationships between elements and the assumptions/simplifications compatible with research hypotheses, and creating a model from the original fossil (Robinson, 2008). The digitization and numerical restoration of a fossil process are detailed by Sutton et al. (2016) and are beyond the scope of this article. Once the model is created, inputs must be applied and the analysis can be run (FEA or MDA). The simulation process then computes the outputs and the validation and sensitivity analysis must be done to validate the model. If the model shows poor congruence with the experimental data or is highly sensitive to the input data, then it needs to be adjusted / *Schéma des méthodes de simulation FEA et MDA. La modélisation consiste en la définition des hypothèses de recherche et des objectifs, en l'identification des paramètres de sortie et d'entrée, en la détermination des relations entre les éléments et des simplifications compatibles avec les hypothèses de recherche et la création du modèle à partir du fossile d'origine (Robinson, 2008). Les procédés de digitalisation et de restauration numérique des fossiles sont détaillés par Sutton et al. (2016) et dépassent le cadre de cet article. Une fois le modèle créé, les paramètres d'entrée doivent être appliqués et l'analyse peut être lancée (FEA ou MDA). Les paramètres de sortie sont alors calculés et les analyses de validation et de sensibilité doivent être faites pour valider le modèle. Si le modèle montre une congruence faible avec les données expérimentales ou s'il est trop sensible aux paramètres d'entrée, alors le modèle doit être ajusté*

Multibody Dynamics Analysis (MDA)

MDA is an engineering method used for the mechanical analysis of structures, including vertebrate skeletons. This method addresses animal motion and its biomechanical performance. Biological structures are modelled as kinematic chains, composed of non-deformable solids (bones) connected by joints (articulations). The external geometry (bone length, enthesis location), inertial parameters (mass, inertia, centre of gravity), joints (centre of rotation, range of motion) and muscle parameters (length, isometric maximal force, physiological cross-sectional area, *etc.*) contribute to the model. Motion data (from an *in-vivo* or simulated kinematics record or from muscle activation profiles) or a static scenario (substrate reaction force) may load the model to simulate a behaviour. Thus, bony elements experience loadings (gravity, substrate reaction forces, joint reaction forces, muscle forces, *etc.*) and musculotendon units that span articulations generate forces and move the structure (Brassey et al., 2017; Lautenschlager, 2020; Bishop et al., 2021; Sylvester et al., 2021) (figure 1). Outputs may be geometrical variables, such as muscle moment arm in relation to a joint, or dynamic variables such as joint moments, muscle moments, and muscle forces. Outputs are calculated based on Newtonian mechanics, with bones considered as non-deformable and musculotendon units modelled as viscoelastic and contractile components. Some analyses include an optimization process based on a physiological criterion in order to solve the indeterminate problem due to muscle redundancy, i.e. when a system of equations is unsolvable due to several possible combinations of muscle forces produced by muscles around a single joint resulting in the same joint moment (Prilutsky and Zatsiorsky, 2010). Despite these assumptions, the approach showed its relevance for the study of human biomechanics (Thelen et al., 2003; Prilutsky and Zatsiorsky, 2010; Rajagopal et al., 2016; Seth et al., 2019).

Finite Element Analysis (FEA)

FEA is also a generalist engineering method used to simulate the behaviour of mechanical structures and fluids. FEA does not assume rigid bodies but includes the deformable aspect of structures, including bones and teeth, to determine stress or strain distribution within a structure with known internal material properties under a certain load. Material constitutive laws and elasticity equations are known for simple geometries (e.g. beam theory) but biological structures are often complex and FEA is better suited than beam theory to account for their external and internal morphologies (Brassey et al., 2013). FEA discretizes the structure into a finite number of simple volume elements for which equations are known. Strains and stresses are computed at each node and displacement and deformation are discretized in the overall structure (Ross, 2005; Rayfield, 2007; Brassey et al., 2013; Bright, 2014). The finite element model

considers external geometry (external surface), internal geometry (cancellous, cortical bone), and material properties (Young's modulus, Poisson's ratio, homo- or heterogeneity, iso- or orthotropy). As inputs, a loading scenario is applied that represents all the forces exerted on the bone during a typical motion (reaction force applied to the structure, forces estimated with the help of physiological cross-sectional area of each muscle, electromyography or MDA, ligament force) (figure 1). FEA approximates the geometry by discretizing it into a finite number of elements, and the precision of results can be verified with a convergence test (Bright, 2014). The main limitations of this approach mentioned in the palaeontological literature are (1) the loading scenario representing a particular motion is often oversimplified (Shefelbine et al., 2002; Macho et al., 2010; Gröning et al., 2011; Burchi et al., 2020; Stamos and Berthaume, 2021); and (2) material properties are assumed to be the same for all species studied (for interspecies comparisons) (Püschel et al., 2020; Stamos and Berthaume, 2021).

Comparison between MDA and FEA

Because MDA and FEA require different inputs and compute different outputs, their aims and application are different. With regard to the fossil record, MDA is particularly relevant for considering variations in proportions, including relative bone length, enthesis location and range of joint motion, in order to compare gross external morphology and kinematic chain variations. In other words, the bone shape is not as important as their general dimensions that affect joints and kinematic chains (Wang et al., 2004). FEA studies microvariations in morphology because the stress and strain results depend on the external and internal morphologies of the fossil. In other words, the exact shape of the bone is critical here.

Both MDA and FEA can generate a chimeric model derived from an existing one to test the significance of morphological characters in fossil species. For example, Richmond (2007) used FEA to study the role of phalangeal curvature in arboreal locomotion: they compared a naturally curved gibbon's phalanx with an artificially straight gibbon phalanx morphology in stress distribution and resistance to failure.

The two methods are complementary. MDA uses rigid solids to represent the appendicular skeleton, while adding a criterion based on FEA of hyperelastic structures (such as ligaments) that estimates their deformation, internal stress and strength to failure, helping to resolve the effect of this deformation on the overall motion of the rigid skeleton (Halloran et al., 2010). A difficulty in FEA is the estimation of the loading scenario i.e. stresses generated by muscles, ligaments, joints and external forces such as body weight. MDA can provide a detailed estimation of muscle and joint reaction forces given the external loading (Marcé-Nogué et al., 2015; Dutel et al., 2021; Watson et al., 2021).

Application to hominin postcranial remains

In palaeoanthropology, most simulations have addressed craniodental functions such as feeding (Spears and Macho, 1998; Preuschoft and Witzel, 2004; Strait et al., 2009; 2010; Berthaume et al., 2010; Macho et al., 2010; DeSantis et al., 2020; Marcé-Nogué et al., 2020; Cook et al., 2021;) or language (Ichim et al., 2006a; 2007; D'Anastasio et al., 2013). Appendix 1 focuses on postcranial studies that address the origin of bipedalism, the degree of arboreality of early hominins and their ancestors, the obstetrical dilemma and stone tool use and making. Bipedalism has drawn the most attention. In particular, while morphological comparisons of the *Australopithecus afarensis* postcranial skeleton could not agree on the type of bipedalism performed by this species, “bent-hip, bent-knee” or “erect” human-like gait, simulation studies have given support to the “erect” gait hypothesis: *A. afarensis* did not display anatomical incapacities (Kramer, 1999; Kramer and Eck, 2000), did not have a high energy cost of locomotion (Wang et al., 2004) and could perform the “erect” gait more efficiently than the “bent-hip, bent-knee” gait (Crompton et al., 1998).

Appendix 1 shows that despite increasing model complexity with the evolution of computing power, MDA outputs have tended to become simpler. The earliest studies using MDA, in bipedalism especially, computed energy cost (Kramer, 1999; Sellers et al., 2003; Nagano et al., 2005), whereas some recent studies have relied on simpler and more controllable outputs such as muscle moment arm, muscle forces or muscle moment capacities (Domalain et al., 2017; Bardo et al., 2018; Karakostis et al., 2021). Extensive research on dinosaur locomotion has shown that although the muscle moment arm provides the first interpretation of muscle effectiveness (Hutchinson et al., 2005; Molnar et al., 2021), it is not necessarily optimized by the musculoskeletal system: a muscle may be at its optimal length for force production with a non-optimal muscle moment arm (Hutchinson et al., 2015). Therefore, dynamic factors such as muscle forces are deemed to be more appropriate for locomotor optimization (Hutchinson et al., 2015).

The main limitation of these studies is that both MDA and FEA need information on soft tissues as input data, and this is unavailable in the fossil record. Some general concepts such as the extant phylogenetic bracket (Witmer, 1995) may be applied to overcome this limitation. Rayfield (2019) provides advice for performing sensitivity analyses. One possibility is to limit inputs by using a range of variables taken from extant species (phylogenetically close to the fossil specimen) that represent plausible scenarios, so that outputs are within the range of plausible results. As an example, Domalain et al. (2017) ran simulations of an australopithecine's hand alternatively with human and chimpanzee muscle parameters and demonstrated that their model outputs were not sensitive to muscle parameters, so that either chimpanzee or human muscle values could be used to draw the same conclusions.

The FEA studies listed in Appendix 1 were all performed with a static loading scenario. Although dynamic loading helps to make a better assessment of strain and stress magnitude distribution in the structure considered (Kayabaşı et al., 2006; Geramizadeh et al., 2016), FEA studies rarely perform dynamic analysis except for crash testing and modal analysis in bone fracture prediction (Gupta and Tse, 2013), mainly because of the considerable increase in complexity of the resulting equations. When applied to palaeoanthropology, it could be useful to take a dynamic loading scenario into consideration to better represent a behaviour. However, the absolute magnitude of stress and strain are often mis-estimated due to material properties or internal geometry issues, so that adding dynamic loading may not improve the accuracy.

Palaeoanthropology would benefit from methodological advances in other fields such as human sport and medicine. In MDA, for example, some advances have been made in muscle force estimation by coupling in-vivo electromyographic data with the resolution of muscle redundancy equations (Vigouroux et al., 2007; Assila et al., 2020; Sarshari et al., 2020) or in joint stability compliance (Dickerson et al., 2007; Blache et al., 2017a; 2017b Akhavanfar et al., 2019). Both aspects are crucial for an accurate solution of muscle redundancy issues and to compute muscle forces in humans, and, therefore, by extension, to apply it to the hominin fossil record (Blasi-Toccaceli et al., 2020). As another example, FEA may complement bone functional remodelling laws, since bone morphological adaptation occurs in response to mechanical loading (Ruff et al., 2006). FEA can predict the strain experienced by the bone before computing bone morphological modifications (Hambli, 2014). The overall approach is quite similar to the theory behind studies of the diaphyseal cross-section as bones change under the influence of locomotor constraints (Carlson et al., 2006; Sládek et al., 2016; Ruff et al., 2020). Here, FEA and functional bone remodelling laws simulate how the bone changes under constraint, with a possible application to the hominin fossil record (Shefelbine et al., 2002).

Conclusion

To sum up, although MDA and FEA are used to investigate different types of questions, i.e. MDA to explore the influence of variations in proportions among fossils and FEA to test the mechanical strength of their morphology under loads, both encompass the use of “what-if” scenarios and are complementary to some extent. We have summarised some of the general advice and good practices highlighted in the literature. The “simpler is better” principle should be kept in mind, but the challenge is to find the right balance between the model's complexity/precision/accuracy and its simplicity. Sensitivity tests are also widely recommended, as well as validation whenever possible. Finally, this review highlights a lack of FEA application in hominin postcranial morphology. Although they are time-consuming, these

approaches allow evolutionary issues to be investigated directly and in a different way to the usual practice in morpho-functional analyses. With MDA and FEA, the role of morphological features of primary evolutionary interest can be tested, validated and then prioritized in their functional context. These perspectives are promising because the MDA and FEA approaches could lead to the identification of suites of morphological characters that are possibly functionally related, which represents a major issue in palaeoanthropology (and more generally in palaeontology) in our understanding of form-function relationships.

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Appendix 1. Summary of MDA and FEA studies on hominin postcranial morphology. Studies are sorted by theme, then by species studied and finally by date of publication. An input parameter in bold represents the independent variable examined. Other input parameters are not examined and are fixed in the study. N.I.D. = no input data. / *Synthèse des études de MDA et FEA sur la morphologie postcrânienne des hominines. Les études sont triées par thème, puis par espèce étudiée et enfin par date de publication. Les paramètres d'entrée en gras représentent la variable indépendante examinée. Les autres paramètres d'entrée ne sont pas examinés et sont fixés dans l'étude. N.I.D. = pas de données d'entrée*

Scope/Studied taxa	Context	Outputs - Biomechanical performance indicator	Numerical model(s)	Inputs	Outcomes	Reference
BIPEDALISM						
<i>H. neanderthalensis</i>	To assess the significance of morphological differences of <i>H. sapiens</i> and <i>H. neanderthalensis</i> on their locomotor mechanical performance	Joint moments, muscle moment arms (Static MDA)	<i>H. sapiens</i> , <i>H. neanderthalensis</i> (Shanidar 1,2,5,6, Tabun C1, La Chapelle-aux-Saints 1, La Ferrassie 1,2, Kiik-Koba 1, Spy 2), <i>H. sapiens</i> , with a Neandertal patella and a Neandertal tibial tuberosity ; joint range of motion (human in-vivo observations); musculotendon parameters (human or Neandertal-adjusted parameters)	N.I.D.	Supports advantage in Neandertals for locomotor performance	Miller and Gross, 1998
<i>H. neanderthalensis</i>	<i>H. neanderthalensis</i> was expected to have greater mechanical advantage relative to <i>H. sapiens</i>	Muscle moment arms (Static MDA)	<i>H. neanderthalensis</i> (Spy 2, Neandertal 1, Kebara 2), <i>H. sapiens</i>	Squatting motion (human in-vivo kinematics)	Supports that Neandertals were more robust than <i>H. sapiens</i> with mechanical advantages during locomotion	Chapman et al., 2010; 2013
<i>A. afarensis</i>	To assess mechanical effectiveness of <i>A. afarensis</i> bipedal gait for erect or «bent-hip, bent-knee» posture	Mechanical joint power (Inverse dynamics MDA - no muscle)	<i>A. afarensis</i> (A.L. 288-1)	“Bent-knee, bent-hip” vs. “erect” gait motion (human in-vivo kinematics); ground reaction forces (human in-vivo experimentation)	Supports “erect gait” hypothesis for <i>A. afarensis</i>	Crompton et al., 1998
<i>A. afarensis</i>	To assess mechanical power expenditure and significance of leg length of <i>A. afarensis</i> bipedal gait compared to <i>H. sapiens</i>	Mechanical power expenditure, energy, walking/running transition speed (Inverse dynamics MDA 2D)	<i>A. afarensis</i> (A.L. 288-1), <i>H. sapiens</i> (female)	Bipedal walking (human in-vivo kinematics); model equations (human-like vs. chimpanzee-like)	Supports that short australopithecine legs did not compromise human-like bipedal walking	Kramer, 1999; Kramer and Eck, 2000
<i>A. afarensis</i>	To estimate the metabolic energy expenditure of <i>A. afarensis</i> from its skeletal proportions	Metabolic energy (Forward dynamics MDA 2D + genetic algorithm)	<i>A. afarensis</i> (A.L. 288-1), <i>H. sapiens</i> (female); mass distribution and muscle parameters (fixed, in-vitro data)	Bipedal walking (genetic algorithm)	Supports that hominins adopted “erect” gait instead of “bent-hip, bent-knee”, unless bipedal behaviour was not often performed	Sellers et al., 2003; 2004
<i>A. afarensis</i>	<i>A. afarensis</i> shows adaptations or exaptations towards bipedalism and was expected to be able to perform <i>H. sapiens</i> -like bipedal walking	Body energy expenditure (Forward dynamics MDA)	<i>A. afarensis</i> (A.L. 288-1), <i>H. sapiens</i> ; muscle parameters (scaled human in-vitro data), geometry (morphological data)	Muscle activation during bipedal walking (simulated data)	Supports “erect gait” hypothesis for <i>A. afarensis</i>	Nagano et al., 2005
<i>A. afarensis</i>	To assess metabolic cost for different speeds and stride lengths for <i>A. afarensis</i> performing upright walk (based on Laetoli footprints)	Body energy expenditure, speed gait (Forward dynamics MDA 2D + genetic algorithm)	<i>A. afarensis</i> (A.L. 288-1), <i>H. sapiens</i> ; segment proportions (observation data), muscles parameters (in-vitro experiments, estimation from human data for fossil)	Speed gait (estimation), stride length (estimation)	Supports that <i>A. afarensis</i> may have adopted habitual bipedalism to reduce its metabolic cost of locomotion	Sellers et al., 2005
<i>A. afarensis</i>	The Laetoli footprints resemble either human or non-human great ape footprints.	Foot pressure on substrate (Forward dynamics MDA + genetic algorithm + pedobarographic statistical parametric mapping)	<i>A. afarensis</i> (A.L. 288-1 and other specimens)	“Erect” vs. “bent-hip, bent-knee” muscle activation (computed data)	Supports that Laetoli footprints were likely made by a habitual biped and suggests more likely “erect” bipedalism	Crompton et al., 2012
Hominins	Bicondylar angle develops with stress and strain induced by bipedalism	Growth or strain rate (Static FEA)	<i>H. sapiens</i> (juvenile)	Single-leg stance phase loading (1/1.2/3 times loading on the medial condyle compared to the lateral)	Supports that bicondylar angle is a good indicator for bipedalism	Shefelbine et al., 2002
Hominins	The evolution of bipedalism was expected to explain the gracilisation and size increase of hominins	Power expenditure (Inverse dynamics MDA 2D)	<i>A. afarensis</i> (A.L. 288-1, A.L. 333), <i>A. africanus</i> (Sts 14), <i>P. robustus</i> (Sk 82), <i>P. boisei</i> (KNM-ER 738, KNM-ER 993, KNM-ER 1503, KNM-ER 3728), <i>H. habilis</i> (OH 62), <i>H. erectus</i> (KNM-WT 15000), <i>H. sapiens</i> (male, female, juvenile); material density (estimation), mass (estimation), stature (estimation)	Bipedal walking	Supports that hominin stature increased to minimize power expenditure for locomotion. However, mobility and stability criteria do not follow this trend and could show that stature would not increase in the future	Wang and Crompton, 2003
Hominins	Do differences in proportion between hominins lead to multiple forms of bipedalism?	Muscle force, length, velocity, work and power (Inverse dynamics MDA 2D)	<i>A. afarensis</i> (A.L. 288-1), <i>H. ergaster</i> (KNM-WT 15000), <i>H. sapiens</i> ; muscle parameters (in-vitro observations), segment length (in-vitro observation)	“Erect” vs. “bent-hip, bent-knee” motion (human in-vivo kinematics)	Supports that <i>Australopithecus</i> body proportions may not have been beneficial for long-distance walking	Wang et al., 2004
Hominins	To recover the plausible motion of fossil hominins based solely on skeletal remains	Joint angle, mechanical work (Inverse kinematics MDA)	<i>H. sapiens</i> , <i>Pan paniscus</i>	Trajectory of the ankle joint (computed and iteratively optimized)	Validation studies; results are not sensitive to the initial ankle joint trajectory, which suggests application to the fossil record	Nicolas et al., 2007; 2009
Hominins	To explore the role of elastic storage from soft tissues on biped running performance	Maximum running speed, cost of locomotion (Forward dynamics MDA + genetic algorithm)	<i>H. sapiens</i> ; tendon stiffness	Minimum running speed, metabolic energy expenditure	Supports the significant value of tendon elasticity and particularly the Achilles tendon in human running. Identification of the presence of such a structure in fossil hominins is advised	Sellers et al., 2010
Hominins	Japanese macaques were expected to perform inverted-pendulum in a similar way to humans during bipedalism	Joint angles (kinematics), muscle fibre length, potential and kinetic energies (Inverse dynamics MDA) + Metabolic energy cost (Forward dynamics MDA 2D)	<i>Macaca fuscata</i>	Muscle activation patterns during bipedal walking (macaque in-vivo experiments), motion data (human in-vivo kinematics acquisitions + adjustment to simulate different hip joint trajectories: flat/human-like/non-human primate-like walking)	Supports that Japanese macaques use inverted-pendulum mechanism in a less effective manner than <i>H. sapiens</i> probably because of musculoskeletal restrictions. The use of the inverted-pendulum in Homo was probably acquired with long legs	Ogihara et al., 2009; 2010; 2011

Scope/Studied taxa	Context	Outputs - Biomechanical performance indicator	Numerical model(s)	Inputs	Outcomes	Reference
BIPEDALISM						
Hominins	To compare pelvis and hindlimb kinematics during chimpanzee and human bipedal gait	Muscle moment arms, joint moments over joint angles (Static MDA) + Joint angles (Inverse kinematics MDA)	<i>Pan troglodytes</i> ; muscle parameters (in-vitro observation data)	Bipedal motion (chimpanzee in-vivo kinematics), range of joint motion	Supports that the extreme morphology of the human soleus is an adaptation for bipedal walking and that the large variations observed in chimpanzee kinematics were maybe the basis allowing natural selection to choose the most efficient bipedal gait in early hominids	O'Neill et al., 2013; 2015
Hominins	To assess the mechanical effectiveness of different hominin species during bipedal gait	Dimensionless muscle moment arm (static MDA 2D + morphometric geometry)	<i>Ardipithecus ramidus</i> (ARA-VP-6/500), <i>A. afarensis</i> (A.L. 288-1), <i>A. africanus</i> (Sts 14), <i>Ekembo nyanzae</i> (KNM-MW 13124), <i>H. sapiens</i> , <i>cercopithecids</i> , <i>platyrrhines</i>	N.I.D.	The critical parameters are the length of ischium and hamstring muscles, which would have made bipedal walking more efficient in early hominins without reducing the capacity of these muscles for climbing	Kozma et al., 2018
Hominins	The plantigrade human-like foot was expected to be energetically more efficient than digitigrade foot during bipedal walking	Joint angles, ground reaction force, joint moments, muscle forces, energy (Forward dynamics MDA 2D + genetic algorithm)	Digitigrade vs. Plantigrade <i>Macaca fuscata</i> foot	Muscle activity pattern during bipedal walking (simulated data with genetic algorithm)	Supports that the digitigrade to plantigrade foot transition is a possible evolutionary scenario for human-like bipedalism	Oku et al., 2021
Hominins	To understand the relationship between foot anatomy, kinematic patterns and hominin fossil tracks with an application to fossil hominin tracks	Tracks depth repartition (Static FEA + biplanar X-ray experiments)	<i>H. sapiens</i> + substrate	Bipedal foot motion data (rigid/deforming foot, in-vivo experiment)	There was no direct relationship between foot motion and track morphology. Tracks do not resemble the foot and more in-depth investigations are needed to understand track ontogeny and foot motion	Hatala et al., 2021
Hominoids	Femoral distal epiphyseal surface depends on the mode of locomotion such as straight gait leading to flat morphology and "bent-knee" leading to complex morphology, and would give mechanical advantages for the locomotor behaviour	Maximum and mean von Mises stress (static FEA - at the highest joint reaction force time) + metaphyseal surface topography complexity (Dirichlet energy of the normal)	<i>Pan troglodytes verus</i> , <i>Pan troglodytes schweinfurthii</i> , <i>Pan paniscus</i> , <i>H. sapiens</i> (Juveniles)	Straight-leg extended vs. flexed gait joint reaction force (human in-vivo experimental trials)	Complex-chimpanzee metaphysis displayed mechanical advantages during knee-flexion, whereas flat-human morphology was neutral during erect bipedal walking. These results can be extended to fossil and other extant animals	Stamos and Berthaume, 2021
ARBOREAL LOCOMOTION						
<i>A. anamensis</i> , <i>A. afarensis</i>	Hominin lineage displays wrist morphological changes and it is unknown whether the primitive capitate of <i>A. anamensis</i> may be functional retention, phylogenetic retention or selectively neutral	Stress distribution (Static FEA)	<i>A. anamensis</i> (KNM-KP 31724), <i>A. afarensis</i> (KNM-WT 22944), <i>Theropithecus</i> (KNM-OG 977), <i>Homo</i> , <i>Pan</i> , <i>Gorilla</i> , <i>Pongo</i> ; internal geometry (in-vitro observational data)	Arboreal locomotion loading (simulated data)	Supports that <i>A. afarensis</i> abandoned arborealism conversely to <i>A. anamensis</i> and that a behavioural locomotor shift occurred between the two species	Macho et al., 2010
Hominoids	Phalangeal curvature is likely to develop with arboreal behaviour and to improve mechanical performance.	Strain distribution (Static FEA 2D + Static FEA 3D)	Curved vs. Uncurved <i>Hylobates syndactylus</i> phalanx (with internal geometry or not)	Suspension grasping - muscle recruitment (in-vivo experiments data, EMG), substrate reaction force (calculated data), joint reaction forces (calculated data)	Supports that a curved phalanx is an ontogenetic process which gives mechanical advantages during suspension	Richmond, 2007; Huynh Nguyen et al., 2014
Hominoids	Scapula shape is thought to reflect locomotor function in primates	Von Mises stress distribution (Static FEA + Geometric morphometry)	<i>H. sapiens</i> , <i>Hylobates lar</i> , <i>Pongo abelii</i> , <i>Pongo pygmaeus</i> , <i>Pan paniscus</i> , <i>Pan troglodytes</i> , <i>Gorilla gorilla</i>	Quadrupedal standing vs. Bimanual suspension - muscle recruitment (simulated data), substrate reaction force (calculated data)	Scapula shape has a significant phylogenetic signal but part of the scapula shape variation is due to functional demands	Püschel and Sellers, 2016
Hominoids	Invest <i>Gorilla</i> hindlimb function relative to locomotion (bipedalism, quadrupedalism, vertical climbing)	Muscle torques, muscle moment arms (Static MDA)	<i>Gorilla gorilla</i> ; Muscle parameters (in-vitro observations)	N.I.D.	Supports that <i>Gorilla</i> displays grasping abilities for vertical supports and small objects and that its ability to walk bipedally is not restricted by musculoskeletal adaptations for quadrupedalism	Goh et al., 2017; 2019
Hominins	The human shoulder is not adapted for climbing as reflected by the numerous injuries caused by this activity, but the underlying adaptive process in hominins remains unknown	Muscle forces, subacromial space (Static MDA)	<i>Pan troglodytes</i> , <i>H. sapiens</i>	Bimanual suspension motion (human in-vivo kinematics), substrate reaction force (estimated data)	Supports that humans are less adapted for suspension than chimpanzees and that there was a slow adaptation away from arborealism in the human evolutionary tree	MacLean and Dickerson, 2020
Hominoids	Powerful arm abduction is crucial for climbing and suspension and several ape-like features have been inferred to provide such an improvement	Moment arms, maximum moment capacity (Static MDA)	<i>Gorilla gorilla</i> vs. <i>H. sapiens</i>	N.I.D.	Features associated with arborealism in hominins do not always display a mechanical advantage for this function	van Beesel et al., 2021
<i>Proconsul heseloni</i> , <i>Proconsul nyanzae</i>	<i>Proconsul</i> is thought to be arboreal climber and quadruped but how he performed quadrupedalism is under investigation	Substrate reaction force and torques (Inverse kinematics MDA 2D)	<i>Proconsul heseloni</i> ; Mass parameters from <i>Proconsul nyanzae</i> estimations	Quadrupedal motion (coati, dog, ruffed lemur, white-fronted capuchin, Sulawesi macaque, and chimpanzee in-vivo kinematics)	Macaque kinematics best fit the <i>Proconsul</i> model	Li et al., 2002
Hominoids	The knuckle-walker hypothesis suggests that the last common ancestor of great apes and hominins was a knuckle-walker. The central-scaphoid fusion in the hominoid wrist is a synapomorphy between apes and hominins and may had a functional role	Von Mises stress (Static FEA)	<i>Hylobates lar</i> , <i>Pongo abelii</i> , <i>Gorilla gorilla</i> , <i>Pan troglodytes</i> , <i>H. sapiens</i>	Knuckle-walking body weight (in-vivo data), ligament reaction force (in-vivo data)	Supports the knuckle-walker hypothesis as fused morphologies offer mechanical advantages	Püschel et al., 2020

Scope/Studied taxa	Context	Outputs - Biomechanical performance indicator	Numerical model(s)	Inputs	Outcomes	Reference
“OBSTETRICAL DILEMMA”						
Hominins	The «obstetrical dilemma» suggests that a large pelvis is expected to be detrimental to locomotion.	Von Mises stress (Static FEA)	<i>H. sapiens</i> ; material properties, cortical bone thickness, femoral neck length, femoral neck-shaft angle , body weight constraint during considered motion	Running and jumping, single-leg stance phase	Supports that the “obstetrical dilemma” has consequences on femoral mechanics. In addition, when applied to fossils such as Australopithecines, morphological changes may lead to kinematic gait changes and additional disadvantages.	Voo et al., 2004 ; Ruff, 2017
Hominins	The pelvic floor hypothesis suggests that the increase in size of the birth canal leads to less support for internal organs and for foetuses.	Von Mises stress, displacement and stretch (Static FEA)	<i>H. sapiens</i> ; material properties (in-vivo experimental data), obstetrical canal ray, pelvis floor width, stress-stretch relationship	N.I.D.	Supports the pelvic floor hypothesis and that pelvic floor shape observed today in women is a trade-off between constraint for birth (large canal) and constraint to avoid prolapse	Stansfield et al., 2021
MANIPULATION - TOOL USE AND MAKING						
Hominins	To explore the arm swing in Oldowan stone flaking	Joint moments (MDA)	<i>H. sapiens</i>	Oldowan knapping motion (in-vivo human data)	Supports that stone flaking is not biomechanically demanding and that this activity was accessible to a large number of individuals	Dapena et al., 2006
Hominins	To assess manual dexterity in fossil hominins from hand morphology	Area over which an object held by the finger-thumb pinch can be manipulated (MDA 2D)	<i>A. afarensis</i> (A.L. 333w-39, A.L. 333-69, A.L. 333-159, A.L. 333-48, A.L. 333-93, A.L. 333-32, A.L. 333w-11, A.L. 333w-50), <i>A. sediba</i> (MH2), <i>H. neanderthalensis</i> (Kebara 2), <i>early H. sapiens</i> (Qafzeh 9, Ohalo II H2), <i>H. sapiens</i> , <i>Pongo Pygmaeus</i> , <i>Macaca fascicularis</i> , <i>Loris tardigradus</i> , <i>Tarsius syrichta</i> , <i>Microcebus murinus</i> , <i>Nycticebus coucang</i>	N.I.D.	Supports that all the hominin hands tested had great dexterity capabilities	Feix et al., 2015
<i>A. afarensis</i>	<i>A. afarensis</i> may give insights into the question of whether human-like traits, particularly the fifth ray morphology, arose in the fossil record because of intensive manipulation behaviour or because of a locomotor behaviour shift	Muscle forces (Static MDA)	<i>A. afarensis</i> (A.L. 333-50, A.L. 333w-89), <i>H. sapiens</i> , <i>Pan troglodytes</i> ; muscle parameters (chimpanzee vs. Humans) ; fifth carpometacarpal joint mobility ; joint posture and fifth ray orientation	External force magnitude simulating the holding of a large object (simulated data)	Supports that <i>A. afarensis</i> displays limited capacities to produce sufficient forces to adequately face the surface of a large object, hence for lithic tools manufacture	Domalain et al., 2017
<i>H. naledi</i> , <i>A. sediba</i>	The intrinsic hand proportions are generally used to investigate the manipulative abilities of fossil hominins, assuming that modern human-like proportions are requirements for a precision grip. However, several grip techniques similar to humans are observed in extant primates	Joint angle, net joint muscle moments, muscle forces, muscle coordination (Static MDA)	<i>H. sapiens</i> , <i>A. sediba</i> (MH2), <i>H. naledi</i> (Hand 1)	6 grip joint posture (in-vivo data)	Supports that species display variations in their intrinsic manual proportions and in their mechanical advantages for each grip. Such a variation may be extended to fossils	Bardo et al., 2018
Hominins	The hominin hand would be the result of selective pressures caused by manipulation whereas other primate hands would reflect locomotion	Von Mises stress (Static FEA)	<i>H. sapiens</i> , <i>H. neanderthalensis</i> (Krapina), <i>Pan troglodytes</i> , <i>Gorilla gorilla</i> , <i>Pongo pygmaeus</i> , <i>Hylobates lar</i>	Tool use loading - size/mass of the hammerstone ; tool orientation ; muscle forces (2 activity pattern - EMG in-vivo data scaled with PCSA in-vitro data)	Supports that stronger evolutionary factors than stone tool use may have acted on human thumb morphology	Bucchi et al., 2020
Hominins	Although the origin of hominin manufacture is unclear, numerous hypotheses are based on the statement that fossil human-like traits reflect a propensity for stone tool use or making	Joint torque capacity for trapezio-metacarpal joint flexion (Static MDA + geometric morphometry enthesal analysis)	<i>A. afarensis</i> (A.L. 333-80, A.L. 333w-39), <i>A. africanus</i> (StW 418), <i>A. sediba</i> (MH2), <i>early Homo or P. robustus</i> (SK 84, SKX 5020), <i>H. naledi</i> (Hand 1), <i>H. neanderthalensis</i> (Shanidar 4, Kebara 2, La Ferrassie 1,2), <i>H. sapiens</i> (early and modern), <i>Pan troglodytes</i> ; muscle opponens pollicis enthesal location and shape (geometric morphometry), muscle parameters (human-like or chimpanzee-like PCSA)	N.I.D.	Supports that some hominins developed greatly increased thumb opposition efficiency about 2 Mya	Karakostis et al., 2021
Early hominins	Stone tool knapping could have emerged with <i>Australopithecus</i> or <i>Keyanthropus</i> rather than <i>Homo</i>	(Inverse kinematics MDA)	<i>H. sapiens</i>	3 stone tool making techniques (human in-vivo kinematics)	Supports that some techniques may have demanded more joint excursion to be performed, particularly pronation capabilities.	Macchi et al., 2021