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- Does the Introduction adequately introduce the subject and make it clear who the audience is/what the motivation is?

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- Article content is within the [Aims and Scope](#) of the journal.
- Rigorous investigation performed to a high technical & ethical standard.
- Methods described with sufficient detail & information to replicate.
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- Are sources adequately cited? Quoted or paraphrased as appropriate?
- Is the review organized logically into coherent paragraphs/subsections?

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- Impact and novelty not assessed. Meaningful replication encouraged where rationale & benefit to literature is clearly stated.
- Conclusions are well stated, linked to original research question & limited to

- Is there a well developed and supported argument that meets the goals set out in the Introduction?
- Does the Conclusion identify unresolved questions / gaps / future directions?

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3



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I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC

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One step further in palaeontology: A nonlinear finite element analysis review

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Finite Element Analysis (FEA) is no longer a novel technique that has emerged in the last years in the field of palaeontology, anthropology, and evolutionary biology. Instead, nowadays is a well-established technique of the functional virtual morphology toolkit. However, practically the totality of the works published in the field are using the most basic part of FEA possibilities: linear materials in static structural problems. But nonlinearities are natural in biomechanical models: modelling soft tissues, ~~establish~~ contacts between separated bones or the inclusion of buckling results. In some of the cases, these assumptions are a simplification of the reality because a nonlinear system requires a more time-consuming mathematical solution. In fact, we use linear and static approximations because they are computationally easier and faster, and the error related with these assumptions can be accepted. The aim of this review is, firstly, put value on non-linearities when they can be of utility and secondly, a tool for researchers that work in functional morphology and biomechanics for improving their FEA models showing a set of possibilities and ideas that currently are not used in palaeontology and anthropology.

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1 Introduction

Computational biomechanics represents the application of computational tools in mechanical problems to study biological systems. During the last years, computational methods such as finite element analysis (FEA) have been widely used in the field of palaeontology to study the biomechanics of fossils (Rayfield, 2007). However, practically the totality of the works published in the field are using the most basic part of FEA possibilities: liner materials in static structural problems, where we can easily define the relationship between physical parameters by means of linear equations. This kind of equations are easy to solve using direct solvers implying a low computational cost only affected by the size of the finite element mesh. Large number of nodes in the finite element mesh implies more unknowns in the equation and, consequently, more dedicated time in solving the mathematical system of equations. Nevertheless, mathematical nonlinearities are natural in physical models and the assumption of linearity and staticity is a simplification of reality to make the problem easy to solve. This is because a nonlinear system is characterized with an output that is not proportional to the change of the input. The inclusion of this complexity implies an increase in the computational cost of solving the equations and the necessity of using iterative solvers. Consequently, palaeontologists have primarily used linear approximations and static problems because are easier to compute, computationally faster and solutions can be superposed on each other to avoid an iterative process.

Considering that, nowadays, most of the FEA commercial and non-commercial packages can solve non-linearities and that some of these cases are already published in living species or in humans for medical purposes, it would make sense to explore if all the possibilities of FEA can improve our palaeontological and anthropological models to explore a broader range of scientific questions that are currently unsolved or not modelled accurately enough. The aim of this review is, firstly, put value on non-linearities when they can be of utility and secondly, a tool for other researchers that work in functional morphology and biomechanics for improving their FEA models showing a set of possibilities that currently are not used in this field. Therefore, this review can be of interest for palaeontologists that seek for ideas in their research, functional morphologists that want to be one step beyond in their research and other researchers who work in life sciences or in computational mechanics that want to know the state-of-the-art in biomechanical non-linear FEA models. But, above all, this review wants to be the road map for the next generation of palaeontologists, anthropologists and functional morphologists exposing which are the unexplored ways that will require attention in Finite element Analysis.

40 2 Search Methodology

41 The literature cited in this text is based on a personal selection by the author to reliably exemplify
42 the methods described along with the text. A previous search in the Google Scholar database was
43 done to select the appropriate references to cover the examples. Different keywords were used in
44 each analysed case to fit the expected search. The final selection of the references was based on
45 covering -if possible- diverse animal families, different morphologies, or different fields.

46 3 Discovering all the FEA elements: Solids, shells, plates, beams, springs, and 47 trusses.

48 Finite element analysis (FEA) is the mathematical way to solve problems of elasticity in complex
49 geometries by dividing the geometry in tiny elements where the equations are easy to solve
50 (Zienkiewicz & Taylor, 1981). The equations of the elasticity relate the external forces applied in
51 a body to understand how it deforms and how the inner forces are distributed inside them
52 (Timoshenko & Goodier, 1986). The underlying premise of the method is that a complex geometry
53 can be subdivided into a mesh consisting of a finite number of elements in which the respective
54 equations are approximately solved (Marcé-Nogué et al., 2015). This method has been widely used
55 in palaeontology, anthropology and functional morphology in general because we can easily
56 digitize bony structures (Lautenschlager, 2016) to apply FEA to realistic geometries. It cannot be
57 omitted that created models are not literal representations of reality, but they still may be useful
58 for answering scientific questions (Anderson et al., 2012). Following the idea of simplification
59 there are different kind of elements that we can use when we are creating a FEA model (Figure 1).
60 The use of some of these elements will result in a greater degree of simplification from reality than
61 others because we are assuming simplifications in the geometry and the behaviour, but also implies
62 a reduction of the complexity of the mathematical equations and the computational time.

63 The elements **beam** and **spring** or **truss** are used when the original geometry is a line or can be
64 assumed as a line and the model is defined either in the 3D space or in 2D. The primary difference
65 between these elements is that beam elements are following beam theory (Timoshenko, 1955),
66 which allows calculation of the loads and deflection of beams subjected to outer forces (including
67 bending, shear, torsion and axial forces). Springs and truss elements, in contrast, are designed only
68 to handle tensile and compressive forces in the axial direction of the element. Examples can be
69 found simplifying the skull of reptiles and mammals to a beam model (Preuschoft & Witzel, 2002)
70 or simplifying the skull of a fish in a linkage of four trusses (Anderson & Westneat, 2007) although
71 they are not widely used because the model in most of the times can be solved by hand without a
72 computer. However, the use of springs or truss are widely extended as a complement of the model
73 when it is necessary to include tendons, ligaments, or other complementary biological structures
74 of the main model. For example, FEA models of the carpal bones include spring elements to model
75 the presence of ligaments between bones (Gíslason et al., 2017).

76 **Shell** and **plate** elements are used when the geometry is a surface or can be assumed as a surface
77 and the model is defined in the 3D space. Both shells and plates are defined by creating the mesh
78 of the elements in the surface and defining a constant thickness. The difference between shells and
79 plates are that shells are used in curved surfaces and plates only in plane surfaces. Mechanically
80 speaking, both shells and plates can handle bending, but shells develop membrane forces whereas

81 plates do not. This means that shell elements include the membrane effects of resistance to
82 compressive and tensile forces, whereas plates do not. In most of the biological models coming
83 from bone structures, shell is the preferred option. An example of shell elements can be found in
84 works of carpal bones (Püschel et al., 2020a) or talar morphologies (Püschel et al., 2020b) because
85 they have a tiny layer of cortical bone with cancellous bone inside where the cortical bone can be
86 assumed as a surface or when modelling something thin as dragonfly wings (Rajabi et al., 2016a).

87 Another assumption that may further reduce the dimensions of the problem may be simplifying to
88 a surface that lie in a 2D plane using **plane** elements. These kinds of elements cannot be confused
89 with shells and plates, which work in a 3D space, and cannot be called as 2D elements because
90 they use the equations of plane elasticity. When solving the equations of the elasticity, plane
91 elasticity refers to the study of specific solutions of the elastic problem in bodies that are surfaces
92 with a constant thickness that are lying in a plane and the forces you apply should lie in this plane.
93 Examples of plane models can be widely found in studies of mammal mandibles (Lautenschlager
94 et al., 2020; Marcé-Nogué et al., 2020) or in dinosaurs and other fossils (Neenan et al., 2014; Ma
95 et al., 2021). Plane models also can be useful in modelling other morphologies such as trilobites
96 (Esteve et al., 2021), claws (Patiño, Pérez Zerpa & Fariña, 2019), beaks (Miller et al., 2020) or
97 teeth (Ballell & Iñón, 2021).

98 It is important to point out the differences between shell and plate elements and plane elements.
99 First, shell elements are not lying in a plane whereas plane and plate elements are. Secondly, plate
100 element allows forces that are not in the plane, like perpendicular forces, supporting bending
101 whereas plane elements do not. This difference can be seen in previous FEA modelling studies of
102 several temnospondyl amphibians (Fortuny et al., 2012) or crocodylomorphs (Pierce, Angielczyk
103 & Rayfield, 2009) where the forces applied are perpendicular to the flat surface of the skull during
104 bilateral cases where plate elements where used.

105 Finally, **solid** elements are used when the geometry is a volume, and the model is built in the 3D
106 space. They have been the most widespread use in palaeontology and anthropology because they
107 can be easily created from a digitalization of the real geometry using CT scanning,
108 photogrammetry, or laser. Examples can be found in FEA models of mandibles which have been
109 modelled in 3D (e.g. (Zhou et al., 2019)), unlike the simpler plane models described above. Solid
110 elements can also be found in models of skulls (Zhou et al., 2017), teeth (Benazzi et al., 2012) and
111 a broad range of postcranial (Püschel & Sellers, 2016; McCabe et al., 2017; Bucci et al., 2020)
112 and other biological structures (Nagel-Myers et al., 2019; Bicknell et al., 2021; Klunk et al., 2021;
113 Krings, Marcé-Nogué & Gorb, 2021).

114 4 Non-linearities in FEA models

115 In general, a nonlinear system is a mathematical system in which the change of the output variable
116 is not proportional to the change of the input variable and, consequently, the equations cannot be
117 written as a linear combination of the unknown variables (Kim, 2015). Therefore, the equations of
118 nonlinear systems are more difficult to solve. Hence, a common strategy to deal with them is to
119 approximate the system by linear equations performing multiple iterations to converge to the
120 correct solution (Figure 2). In elastic problems being solved using the finite element method, the
121 non-linearity can be originated by different phenomenon.

122 1) **Material non-linearity:** The relationship between stress and strain is not following the linear
123 Hooke's law. It appears in plasticity or hyperelastic materials where the relationship between
124 stress and strain is not following a lineal proportion.

125 2) **Large deformation non-linearity:** The so-called finite strain theory, large strain theory, or
126 large deformation theory is used when strains are large enough to invalidate the assumptions
127 of the small strain theory, which is the theory commonly used in linear elastic problems. In
128 this case, the deformed and undeformed configurations of the body under analysis are notably
129 different, requiring a clear distinction between them in the formulation that, consequently, also
130 affects the relation between stress and strain in the constitutive equation. This theory is
131 common in elastomers and soft tissues and needs to be used in hyperelastic materials.

132 3) **Large displacement non-linearity:** Also called as geometrical non-linearity, assumes small
133 strains but large rotations and displacements. In the geometrically linear case, the forces are
134 applied in the undeformed geometry when solving the model whereas in the geometrically
135 nonlinear cases, the applied forces depend on the deformed upcoming geometry. It implies an
136 iterative solution accounting ^{for} the displacements and needs to be considered when analysing
137 buckling.

138 4) **Non-linear contacts:** Separate surfaces of two bodies are in contact without overlapping in
139 such a way that they become mutually tangential. Depending on the relationship between these
140 two surfaces, contacts that allow separation in the perpendicular direction imply a nonlinear
141 solution because there are unknowns at the start of the solving process: where and which force
142 is applied.

143 The mathematical methods applied to solve general nonlinear functions are all iterative starting
144 from an initial estimation. The solution is obtained by solving iteratively a linearization of the non-
145 linear system in different steps towards the convergence of the solution. Different methods are
146 available depending on the procedure of calculating the increment of the steps: the Newton-
147 Raphson method, the incremental secant method or the incremental force method among others
148 (Kim, 2015). Therefore, the computational cost of the solving procedure of a nonlinear FEA model
149 is now not only affected by the size of the mesh, but also affected by the number of iterative
150 resolutions before convergence.

151 4.1 Non-linear materials: Hyperelasticity and Plasticity

152 Non-linear materials are materials in which the constitutive equation that defines their behaviours
153 establishes a relationship between stress and strain that is not proportional ^{to} a constant. Typical
154 material non-linearities can be found in phenomena such as plasticity and hyperelasticity. Plasticity
155 describes the deformation of a material undergoing non-reversible changes of shape in response to
156 applied forces. In a typical stress-strain curve for a plastic material there is a linear elastic region
157 which satisfies Hooke's law and a plastic region before fracture that can also follow a linear law
158 or can be defined using different linear sections (Figure 3). The transition from elastic behaviour
159 to plastic behaviour is called yield and a non-linear solution is required because the solver needs
160 to discover if the body is in the plastic region or ^{not}. The total strain is defined by $\varepsilon_{total} = \varepsilon_{elastic} +$
161 $\varepsilon_{plastic}$ and the value of stress will depend ^{on} it. In a biological context, plasticity can be found in
162 trabecular bone formulations to capture tension-compression asymmetry in the yield strength

163 (Gupta et al., 2007) or, in general, in works where a permanent deformation or plasticity is assumed
164 in cortical bone or other biological materials such as dentin, enamel or nacre (An, 2016).

165 Hyperelastic materials are ideal elastic materials in which the stress-strain relationship is non-
166 linear because derives from a strain energy function instead of Hooke's law (Figure 3) and,
167 moreover, it uses the large deformation theory described above. However, the response of the
168 material is not plastic because deformations are fully recoverable. Typical formulations of
169 hyperelastic materials are, among others, phenomenological descriptions of observed behaviour in
170 Mooney–Rivlin and Ogden formulations or equations describing the underlying structure of the
171 material in the Neo–Hookean model (Ogden, 1984). Hyperelastic formulations are common in soft
172 tissues such as ligaments or tendons (Shearer, 2015). Specifically, they can be found in the PDL
173 (Bucchi et al., 2019), muscles such as the pelvic floor (Stansfield et al., 2021), the abdominal
174 muscle (Tuset et al., 2019) or a generic muscle tissue (Hedenstierna, Halldin & Brolin, 2008), skin
175 (Ito et al., 2022), corneas (Shan et al., 2010), cartilage (Pataky, Koseki & Cox, 2016), the
176 temporomandibular joint (Sagl et al., 2019) or in the modelling of the blood vessels (Vorp, 2007).

177 Sometimes the equations that are defined to govern soft tissue behaviour include a viscous term
178 (Huang et al., 2017). Viscoelasticity describes the variation of material response within time
179 containing an elastic and a viscous part. The viscous part can describe creep, when stress remains
180 constant and the deformation increases with time, or relaxation, when the deformation remains
181 constant and stress decreases over time. On the other hand, the elastic response is instantaneous
182 and can be defined using a linear material (Booker & Small, 1977) or a nonlinear hyperelastic
183 material (Kulkarni et al., 2016).

184 More complex models, including fibres in their formulation, exist for the arterial vessels (Gasser,
185 Ogden & Holzapfel, 2006) or the intervertebral discs (Noailly, Planell & Lacroix, 2011) among
186 others. Despite the complexity of these formulae, which combines the overlay of the stiffness in
187 the preferred directions of the fibres with the hyperelastic formulation of the matrix, the
188 constitutive equation is also nonlinear, and it must be solved following an iterative procedure.

189 **4.2 Non-linearities in Geometry: Buckling**

190 In a linear problem, the equations of equilibrium are formulated in the original undeformed state
191 and are not updated with the deformation. This is common in most engineering problems because
192 the deformations are small enough to not differentiate the original geometry and the deformed one.
193 However, there are cases where the deformation cannot be ignored, and we need to include large
194 displacement non-linearities due to the geometrical update during the application of forces: This
195 is the case of **buckling**.

196 Buckling implies a sudden change in shape of a body under load because the loss of stability when
197 this load reaches certain critical value (Figure 4). If a body -such as a column under compression
198 or a plate under shear, for example- is subjected to a gradually increasing load, when the load
199 reaches the critical value, the body may suddenly change shape. Although buckling appears before
200 failure, it can be decisive in the ergonomics of certain biological bodies, limiting the range of
201 forces under which they are able to remain functional. Buckling is caused by nonlinearities in the
202 geometry and can be approached by a linearisation that drives to a bifurcation problem of
203 eigenvalues. Therefore, the linear buckling analysis is done in parallel to a linear elastic analysis.

204 Otherwise, the full nonlinear solution of the point of collapse can be obtained by increasing the
205 load in smaller steps with an iterative method while the geometry is updated to its deformed state.
206 This latter is significantly more computationally expensive but might be more accurate than the
207 linear buckling. In a biomechanical context, buckling can be found when study slender bodies such
208 as the swordfish rostrum (Habegger et al., 2020), the weevil rostrum (Matsumura et al., 2021) or
209 even in bones under compression such as the vertebrae (Williams et al., 2021).

210 4.3 Non-linearities in contacts

211 Contacts between two bodies are divided between **linear contacts** and **non-linear contacts**. Linear
212 contacts can be included in a linear elastic model without modifying the solving mode and keeping
213 the direct solution. It continues implying a low computational cost only affected by the size of the
214 finite element mesh (namely, the number of elements and nodes). However, the inclusion of non-
215 linear contacts changes the solving mode to a non-linear solution with an iterative solver,
216 increasing the computational cost of the analysis. Contacts can be described according to the
217 relationship between the two separate surfaces of each body that become mutually tangential in
218 five general different types according to how they can move perpendicularly to each other and how
219 they can move in the tangential plane. In other words, if they are allowed to separate and slide
220 (Figure 5).

- 221 1) **Bonded contacts:** when separation and sliding is not allowed. It is a linear contact.
- 222 2) **No-separation contact:** when separation is not allowed but sliding in the tangential plane is
223 allowed. It is a linear contact.
- 224 3) **Frictionless contact:** when separation and sliding is allowed. It is a non-linear contact.
- 225 4) **Rough contact:** when separation is allowed but sliding in the tangential plane is not allowed.
226 It is a non-linear contact.
- 227 5) **Frictional contact:** when separation is allowed but sliding in the tangential plane is controlled
228 by a friction coefficient. It is a non-linear contact.

229 Frictional contact can be understood as an intermediate status, where sliding in the tangential plane
230 is not free but is allowed and bonded contact is used when we have two bodies that are perfectly
231 joined but they are created or defined as separate bodies during the FEA modelling. For example
232 can be used for defining all the pieces involving a teeth such as the cortical bone, dentine, enamel,
233 pulp and the PDL (Benazzi et al., 2013; Bucchi et al., 2019)

234 In general, contacts are found in FEA models involving more than one body and the definition of
235 each contact depends on the nature of its behaviour. When studying the carpal bones of the wrist
236 (Gislason et al., 2017; Püschel et al., 2020a) or the feet (Ito et al., 2022), the ossicles of the auditory
237 system (Marcé-Nogué & Liu, 2020), the intervertebral discs and the vertebrae of the spine (Guan
238 et al., 2019), all the tissues in the hip (Fleps et al., 2018) or the patella (Fitzpatrick & Rullkoetter,
239 2012), the mandible, the temporomandibular joint and the skull (Sagl et al., 2019) or the interaction
240 between the bodies in the wings of dragonflies (Rajabi et al., 2016b) and bees and wasps (Eraghi
241 et al., 2021) among others. Therefore, contacts can be used to establish relationship between bones
242 or soft tissues. Contacts are also useful when studying occlusal forces during mastication to model
243 the interaction between teeth and food (Skamniotis, Elliott & Charalambides, 2019) or even the
244 impact of eggshells with the floor (Sellés et al., 2019).



245 **5 Summary: Ideas for palaeontologists**

246 FEA is no longer a novel technique that has emerged in the last years in the field of palaeontology,
247 anthropology, and evolutionary biology. Instead, nowadays is a well-established technique of the
248 functional virtual morphology toolkit used in more than 750 biological and evolutionary
249 publications between 2005 and 2020 (Tseng, 2021). Most of this works present FEA models
250 without non-linearities. This, *a priori*, is not a problem if the linear approach itself is sufficient to
251 answer the scientific question of interest. Indeed, a lot of engineering problems can be solved
252 without trespassing the threshold of the linear models. Therefore, this text does not want to spread
253 an incorrect idea regarding the use of supposedly more accurate non-linear models. In fact, the use
254 of linear low computational approaches without nonlinearities can also be of utility to understand
255 the behaviour of the biological bodies under analysis. Certainly, the majority of the FEA works
256 that are including fossils are based in studying bones as a reconstruction of the fossil remains,
257 which can be modelled successfully using linear elastic material properties and solved using a
258 static analysis under small strains and displacements, therefore, without non-linearities. At this
259 point, the reader is starting to ask why we need to include non-linearities in FEA when studying
260 fossil remains. The aim of this text is to highlight the value of non-linearities when they can be of
261 utility, or they are needed to improve the knowledge we have in fields such as palaeontology and
262 anthropology.

263 **5.1 Non-linear soft tissues**

264 Little is known about soft tissue properties in fossils. The direct examination of fossil soft tissues
265 and preserved blood cells is of little utility for studying palaeontological remains due to the
266 degradation or the contamination from modern remains (van Dongen et al., 2017). The
267 reconstruction of soft tissues from fossils is an issue that it is unresolved but can be approached
268 through investigating extant relatives to infer the palaeo-physiology of extinct taxa (Witmer,
269 1995). Therefore, all the FEA models can potentially include an inference of the soft tissues. In
270 fact, cranial sutures are deformable joints between adjacent bones bridged by collagen fibres and
271 there are several works on fossil taxa that have include soft tissues, for example modelling sutures
272 in *Tyrannosaurus rex* skull (Cost et al., 2020), australopithecines (Dzialo et al., 2014) or in
273 *Dicynodonts* (Jasinoski, Rayfield & Chinsamy, 2009) as well as FEA models of current lizard
274 species (Dutel et al., 2021), *sphenodon* (Curtis et al., 2013) or some mammals (Bright & Gröning,
275 2011). All of these examples used linear material properties to characterize the elastic behaviour
276 of soft tissues which can be an appropriate simplification if this is validated experimentally (Bright
277 & Gröning, 2011). However a recent diagnosis suggested that the lack of sutures or and
278 inappropriate modelling can result in inaccurate results of stress, strain or deformation (Rayfield,
279 2019) although it is not clear how the soft tissue can be accurately predicted in fossils (Broyde et
280 al., 2021). Is at this point that the researcher needs, at least, to be aware that a more accurate
281 modelling of these soft tissues should be done using nonlinear material properties implying an
282 increase in the computational cost of the model.

283 **5.2 Plasticity in retrodeformations**

284 Retrodeformation is very common in fossil taxa as the process that produces the original form of
285 the taxon prior to **fossildiagenesi** when this has been recovered in any deformed way. Deformation

286 in fossils is produced due taphonomic and tectonic processes. Overburden stress due to the weight
287 of the overlying sediments linearly compacts the fossil from above causing the fossil to break
288 and/or warp. Other causes of fossil deformation include tectonic stresses and sediment cracking.
289 Under the action of these loads, the fossil can break in a brittle manner or can be distorted
290 plastically, preserving the structure of the fossil due to the lack of breakage. Fossils under plastic
291 deformation, where forces applied during time modify the original shape of the bone structure may
292 be restored. Although there are several techniques to virtually restore deformed specimens
293 available without using mechanical equations (Lautenschlager, 2016), it has sense to use methods
294 from mechanics such as FEA that involve forces if one want to guess which was the process that
295 drove the fossil to be deformed (Arbour & Currie, 2012; Di Vincenzo et al., 2017). At this point
296 is where the nonlinear definition of plastic behaviour of bone could be useful because
297 retrodeformation is a permanent deformation in cortical bone. In this case FEA should be applied
298 inversely defining the plastic behaviour of the material of the fossil specimen in the material
299 properties and setting the forces as the unknowns of the problem to answer this question: Which
300 forces do I need to apply in this deformed body to recover its original form?

301 **5.3 Buckling in slender bones**

302 In palaeontology there are a lot of slender structures that are susceptible to be analysed using
303 buckling. Probably the most common and useful case would be in bones under compression such
304 as the leg bones of large, heavy dinosaurs and mammals. This is because mass is considered as
305 one of the main factors affecting the morphology and osteological adaptation of these bones
306 (Etienne et al., 2020). To understand how these bones are adapted to the heavy weight that they
307 needed to support, evaluation of the maximal stress as a measure of bone strength is not the only
308 informative metric (Hutchinson, 2021). In this case, buckling needs to be considered, because it
309 can cause the collapse of the legs before the fracture of the bone. Usually, buckling reduces the
310 capacity of the strength of the structure because it appears in a lower value than the yield stress
311 and the fracture stress that defines the strength of the material.

312 If we assume leg bones in heavy dinosaurs as slender columns in a building, Euler's critical load
313 is defined as the compressive load at which the column will suddenly buckle (Timoshenko, 1955).
314 This equation can give clues about the relationship between geometrical factors such as the length
315 of the bones or how they are joined to the articulations. Given that the length, material, or boundary
316 conditions cannot be modified from the original model, Euler's critical force will depend on the
317 second moment of area or moment of inertia. Increasing the value of the critical force implies a
318 modification of the cross-section of the bone through more inertial geometries. Therefore, if we
319 assume the cross-section of leg bones as an annulus, thicker annulus will increase the inertia. But
320 also, if the thickness is kept constant, a broader annulus will increase the inertia of the cross section.
321 This simple consequence can be obtained assuming leg bones with a straight morphology not close
322 enough to the reality, but very useful for the purpose of study. However, in case of analysis of the
323 real and irregular geometry of the bones, the simple formula of Euler cannot be used but the
324 problem of buckling can be solved via computational methods by means of FEA solving an
325 eigenvalue problem. Few works are paying attention to it, discarding the effect of buckling in the
326 morphology of the long bones in living mammals (Brassey et al., 2013). Considering that an
327 eigenvalue problem in a FEA model is not increasing the computational cost of the analysis too

328 much, it would be worth to test more in deep if leg bones of heavy dinosaurs or **mastodontic extant**
329 mammals are affected by buckling.

330 **5.4 Bone grouping using contacts**

331 Functional implications of fossil bones have been widely studied in fossil taxa using FEA models
332 (Richmond et al., 2005). Depending on the purpose, bones can be studied alone or as a group and
333 the main difference between these two cases is the absence or presence of contacts. When
334 separation between bones is not desired, for example in the analysis of teeth, considering the
335 bonding of the cortical bone, dentine, enamel, pulp and the PDL (Benazzi et al., 2013), the contacts
336 used are linear and it does not imply an increase in the computational cost of the solving process.
337 This is something that can be considered when creating FEA models because allows the inclusion
338 of several bones in the model without nonlinearities.

339 On the other side, nonlinear contacts allow separation between the bones. Although the inclusion
340 of this contacts implies an iterative solution through convergence, it may be necessary to
341 implement when a group of bones need to be studied together such as the carpal bones of the wrist
342 (Gíslason et al., 2017) or the bones of the foot (Ito et al., 2022). This has been done extensively in
343 biomechanical models of living primates; therefore, it should be considered in other FEA works
344 in the field of the palaeontology and anthropology. In fact, literature is full of biomechanical
345 analysis of kinematics and dynamics of solid bodies where bones of fossils are grouped to study
346 its performance (Sellers et al., 2017; Bishop et al., 2021). Therefore, it makes sense when creating
347 FEA models, to include more than one bone in the model if it can be useful for the desired analysis
348 despite increasing the computational cost of the solution. Also when the contact between bones is
349 through articular cartilage, the contact can be defined between cartilages that are also in contact
350 with the bone (Püschel et al., 2020a).

351 **5.5 Models with shells, plates, beams, springs, and trusses.**

352 Finally, although this is not related with the use of a nonlinear iterative solving, the use of other
353 kind of elements other than solid elements can be of great utility when dealing with nonlinear
354 models. This is because they provide a useful way to reduce the number of elements and nodes of
355 the FEA mesh and, consequently, a reduction of the time spent solving the equation in each
356 iteration. Hence, a nonlinear model will particularly benefit from the use these elements.

357 The use of shell elements to model cortical bone in morphologies that can be assumed as thin and
358 with a constant thickness, such as carpal bones or talar morphologies, implies a lower number of
359 elements and nodes because there is only one layer of mesh. Using solid elements in the same
360 morphology, at least four or five layers of elements would be needed along the thickness to
361 properly build an adequate mesh to accurately capture the results. This was used in an analysis of
362 carpal bones (Gíslason et al., 2017) to model both the cortical bone and the articular cartilage,
363 reducing significantly the number of elements to allow a smooth non-linear solution, due to the
364 presence of non-linear contacts. The same example uses non-linear spring elements to model the
365 behaviour of the ligaments. This decision is also in favour of not increasing the number of nodes
366 and elements of the model, because spring or truss elements can be defined using only one element
367 with the origin and final nodes. In this manner, the model avoids the inclusion of a three-
368 dimensional geometry modelled with solid elements for each ligament, which would increase

369 exponentially the number of nodes an element of the mesh and consequently, increase the
370 computational cost of the solution.

371 When creating FEA models of fossils and considering the inclusion of some of the non-linearities
372 previously described it is a good option to evaluate if the use of this simpler elements can reduce
373 the computational cost. Although researchers should be aware of the potential ramifications of
374 simplifying their models, it is also true that any model will necessarily not represent a literal
375 representation of reality. Instead, the requirements necessary to answer the research question of
376 interest should always be kept in mind when making decisions about model complexity.

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382 **7 References**

383 An B. 2016. Constitutive modeling the plastic deformation of bone-like materials. *International Journal of Solids and*
384 *Structures* 92–93:1–8. DOI: 10.1016/j.ijsolstr.2016.05.003.

385 Anderson PSL, Bright J a., Gill PG, Palmer C, Rayfield EJ. 2012. Models in palaeontological functional analysis.
386 *Biology Letters* 8:119–122. DOI: 10.1098/rsbl.2011.0674.

387 Anderson PSL, Westneat MW. 2007. Feeding mechanics and bite force modelling of the skull of Dunkleosteus terrelli,
388 an ancient apex predator. *Biology Letters* 3:77–80. DOI: 10.1098/rsbl.2006.0569.

389 Arbour VM, Currie PJ. 2012. Analyzing taphonomic deformation of ankylosaur skulls using retrodeformation and
390 finite element analysis. *PLoS ONE* 7:1–13. DOI: 10.1371/journal.pone.0039323.

391 Ballell A, Ferrón HG. 2021. Biomechanical insights into the dentition of megatooth sharks (Lamniformes:
392 Otodontidae). *Scientific Reports* 11:1232. DOI: 10.1038/s41598-020-80323-z.

393 Benazzi S, Kullmer O, Grosse IR, Weber GW. 2012. Brief communication: Comparing loading scenarios in lower
394 first molar supporting bone structure using 3D finite element analysis. *American Journal of Physical*
395 *Anthropology* 147:128–134. DOI: 10.1002/ajpa.21607.

396 Benazzi S, Nguyen HN, Kullmer O, Hublin J-J. 2013. Unravelling the Functional Biomechanics of Dental Features
397 and Tooth Wear. *PLoS ONE* 8:e69990. DOI: 10.1371/journal.pone.0069990.

398 Bicknell RDC, Holmes JD, Edgecombe GD, Losso SR, Ortega-Hernández J, Wroe S, Paterson JR. 2021.
399 Biomechanical analyses of Cambrian euarthropod limbs reveal their effectiveness in mastication and durophagy.
400 *Proceedings of the Royal Society B: Biological Sciences* 288:20202075. DOI: 10.1098/rspb.2020.2075.

401 Bishop PJ, Falisse A, De Groote F, Hutchinson JR. 2021. Predictive simulations of running gait reveal a critical
402 dynamic role for the tail in bipedal dinosaur locomotion. *Science Advances* 7:1–14. DOI:
403 10.1126/sciadv.abi7348.

404 Booker JR, Small JC. 1977. Methods for the numerical solution of the equations of viscoelasticity. *International*
405 *Journal for Numerical and Analytical Methods in Geomechanics* 1:139–150. DOI: 10.1002/nag.1610010203.

406 Brassey C a., Margetts L, Kitchener AC, Withers PJ, Manning PL, Sellers WI. 2013. Finite element modelling versus
407 classic beam theory: comparing methods for stress estimation in a morphologically diverse sample of vertebrate
408 long bones. *Journal of the Royal Society, Interface / the Royal Society* 10:20120823. DOI:
409 10.1098/rsif.2012.0823.

410 Bright JA, Gröning F. 2011. Strain accommodation in the zygomatic arch of the pig: A validation study using digital
411 speckle pattern interferometry and finite element analysis. *Journal of Morphology* 272:1388–1398. DOI:

412 10.1002/jmor.10991.

413 Broyde S, Dempsey M, Wang L, Cox PG, Fagan M, Bates KT. 2021. Evolutionary biomechanics: hard tissues and
414 soft evidence? *Proceedings of the Royal Society B: Biological Sciences* 288:20202809. DOI:
415 10.1098/rspb.2020.2809.

416 Bucchi C, Marcé-Nogué J, Galler KM, Widbiller M. 2019. Biomechanical performance of an immature maxillary
417 central incisor after revitalization: a finite element analysis. *International Endodontic Journal*:iej.13159. DOI:
418 10.1111/iej.13159.

419 Bucchi A, Püschel TA, Lorenzo C, Marcé-Nogué J. 2020. Finite element analysis of the proximal phalanx of the
420 thumb in Hominoidea during simulated stone tool use. *Comptes Rendus Palevol*. DOI:
421 10.5852/palevol2020v19a2.

422 Cost IN, Middleton KM, Sellers KC, Echols MS, Witmer LM, Davis JL, Holliday CM. 2020. Palatal Biomechanics
423 and Its Significance for Cranial Kinesis in *Tyrannosaurus rex*. *The Anatomical Record* 303:999–1017. DOI:
424 10.1002/ar.24219.

425 Curtis N, Jones MEH, Evans SE, O'Higgins P, Fagan MJ. 2013. Cranial sutures work collectively to distribute strain
426 throughout the reptile skull. *Journal of the Royal Society Interface* 10:1–9. DOI: 10.1098/rsif.2013.0442.

427 van Dongen B, Manning PL, Warwood S, Buckley M, Kitchener AC. 2017. A fossil protein chimera; difficulties in
428 discriminating dinosaur peptide sequences from modern cross-contamination. *Proceedings of the Royal Society
429 B: Biological Sciences* 284:20170544. DOI: 10.1098/rspb.2017.0544.

430 Dutel H, Gröning F, Sharp AC, Watson PJ, Herrel A, Ross CF, Jones MEH, Evans SE, Fagan MJ. 2021. Comparative
431 cranial biomechanics in two lizard species: impact of variation in cranial design. *Journal of Experimental
432 Biology* 224. DOI: 10.1242/jeb.234831.

433 Dzialo C, Wood SA, Berthaume MA, Smith AL, Dumont ER, Benazzi S, Weber GW, Strait DS, Grosse IR. 2014.
434 Functional implications of squamosal suture size in *paranthropus boisei*. *American Journal of Physical
435 Anthropology* 153:260–268. DOI: 10.1002/ajpa.22427.

436 Eraghi SH, Toofani A, Khaheshi A, Khorsandi M, Darvizeh A, Gorb S, Rajabi H. 2021. Wing Coupling in Bees and
437 Wasps: From the Underlying Science to Bioinspired Engineering. *Advanced Science* 2004383:2004383. DOI:
438 10.1002/advs.202004383.

439 Esteve J, Marcé-Nogué J, Pérez-Peris F, Rayfield EJ. 2021. Cephalic biomechanics underpins the evolutionary success
440 of trilobites. *Palaeontology*:pala.12541. DOI: 10.1111/pala.12541.

441 Etienne C, Mallet C, Cornette R, Houssaye A. 2020. Influence of mass on tarsus shape variation: A morphometrical
442 investigation among Rhinocerotidae (Mammalia: Perissodactyla). *Biological Journal of the Linnean Society*
443 129:950–974. DOI: 10.1093/biolinnean/blaa005.

444 Fitzpatrick CK, Rullkoetter PJ. 2012. Influence of patellofemoral articular geometry and material on mechanics of the
445 unresurfaced patella. *Journal of Biomechanics* 45:1909–1915. DOI: 10.1016/j.jbiomech.2012.05.028.

446 Fleps I, Enns-Bray WS, Guy P, Ferguson SJ, Cripton PA, Helgason B. 2018. Correction: On the internal reaction
447 forces, energy absorption, and fracture in the hip during simulated sideways fall impact (PLoS ONE (2018) 13:8
448 (e0200952) DOI: 10.1371/journal.pone.0200952). *PLoS ONE* 13:1–18. DOI: 10.1371/journal.pone.0208286.

449 Fortuny J, Marcé-Nogué J, Gil L, Galobart À. 2012. Skull Mechanics and the Evolutionary Patterns of the Otic Notch
450 Closure in Capitosaurs (Amphibia: Temnospondyli). *The Anatomical Record: Advances in Integrative Anatomy
451 and Evolutionary Biology* 295:1134–1146. DOI: 10.1002/ar.22486.

452 Gasser TC, Ogden RW, Holzapfel GA. 2006. Hyperelastic modelling of arterial layers with distributed collagen fibre
453 orientations. *Journal of The Royal Society Interface* 3:15–35. DOI: 10.1098/rsif.2005.0073.

454 Gislason MK, Foster E, Bransby-Zachary M, Nash DH. 2017. Biomechanical analysis of the Universal 2 implant in
455 total wrist arthroplasty: a finite element study. *Computer Methods in Biomechanics and Biomedical Engineering*
456 20:1113–1121. DOI: 10.1080/10255842.2017.1336548.

457 Guan W, Sun Y, Qi X, Hu Y, Duan C, Tao H, Yang X. 2019. Spinal biomechanics modeling and finite element
458 analysis of surgical instrument interaction. *Computer Assisted Surgery* 24:151–159. DOI:

459 10.1080/24699322.2018.1560086.

460 Gupta A, Bayraktar HH, Fox JC, Keaveny TM, Papadopoulos P. 2007. Constitutive modeling and algorithmic
461 implementation of a plasticity-like model for trabecular bone structures. *Computational Mechanics* 40:61–72.
462 DOI: 10.1007/s00466-006-0082-5.

463 Habegger L, Motta P, Huber D, Pulaski D, Grosse I, Dumont ER. 2020. Feeding Biomechanics in Billfishes:
464 Investigating the Role of the Rostrum through Finite Element Analysis. *The Anatomical Record* 303:44–52.
465 DOI: 10.1002/ar.24059.

466 Hedenstierna S, Halldin P, Brolin K. 2008. Evaluation of a combination of continuum and truss finite elements in a
467 model of passive and active muscle tissue. *Computer Methods in Biomechanics and Biomedical Engineering*
468 11:627–639. DOI: 10.1080/17474230802312516.

469 Huang H, Tang W, Tan Q, Yan B. 2017. Development and parameter identification of a visco-hyperelastic model for
470 the periodontal ligament. *Journal of the Mechanical Behavior of Biomedical Materials* 68:210–215. DOI:
471 10.1016/j.jmbbm.2017.01.035.

472 Hutchinson JR. 2021. The evolutionary biomechanics of locomotor function in giant land animals. *Journal of
473 Experimental Biology* 224. DOI: 10.1242/jeb.217463.

474 Ito K, Nakamura T, Suzuki R, Negishi T, Oishi M, Nagura T, Jinzaki M, Ogihara N. 2022. Comparative Functional
475 Morphology of Human and Chimpanzee Feet Based on Three-Dimensional Finite Element Analysis. *Frontiers
476 in Bioengineering and Biotechnology* 9:1–13. DOI: 10.3389/fbioe.2021.760486.

477 Jasinoski SC, Rayfield EJ, Chinsamy A. 2009. Comparative feeding biomechanics of *Lyrosaurus* and the generalized
478 dicynodont *Oudenodon*. *Anatomical Record* 292:862–874. DOI: 10.1002/ar.20906.

479 Kim N. 2015. *Introduction to Nonlinear Finite Element Analysis*. New York, NY: Springer US. DOI: 10.1007/978-1-
480 4419-1746-1.

481 Klunk CL, Argenta MA, Casadei-Ferreira A, Economo EP, Pie MR. 2021. Mandibular morphology, task
482 specialization and bite mechanics in *Pheidole* ants (Hymenoptera: Formicidae). *Journal of The Royal Society
483 Interface* 18:20210318. DOI: 10.1098/rsif.2021.0318.

484 Krings W, Marcé-Nogué J, Gorb SN. 2021. Finite element analysis relating shape, material properties, and dimensions
485 of taenioglossan radular teeth with trophic specialisations in *Paludomidae* (Gastropoda). *Scientific Reports*
486 11:22775. DOI: 10.1038/s41598-021-02102-8.

487 Kulkarni SG, Gao XL, Horner SE, Mortlock RF, Zheng JQ. 2016. A transversely isotropic visco-hyperelastic
488 constitutive model for soft tissues. *Mathematics and Mechanics of Solids* 21:747–770. DOI:
489 10.1177/1081286514536921.

490 Lautenschlager S. 2016. Reconstructing the past: methods and techniques for the digital restoration of fossils. *Royal
491 Society Open Science* 3:160342. DOI: 10.1098/rsos.160342.

492 Lautenschlager S, Figueirido B, Cashmore DD, Bendel E-M, Stubbs TL. 2020. Morphological convergence obscures
493 functional diversity in sabre-toothed carnivores. *Proceedings of the Royal Society B: Biological Sciences*
494 287:20201818. DOI: 10.1098/rspb.2020.1818.

495 Ma W, Pittman M, Butler RJ, Lautenschlager S. 2021. Macroevolutionary trends in theropod dinosaur feeding
496 mechanics. *Current Biology*:1–10. DOI: 10.1016/j.cub.2021.11.060.

497 Marcé-Nogué J, Liu J. 2020. Evaluating fidelity of CT based 3D models for Zebrafish conductive hearing system.
498 *Micron* 135:102874. DOI: 10.1016/j.micron.2020.102874.

499 Marcé-Nogué J, Fortuny J, Gil L, Sánchez M. 2015. Improving mesh generation in Finite Element Analysis for
500 functional morphology approaches. *Spanish Journal of Palaeontology* 31:117–132.

501 Marcé-Nogué J, Püschel TA, Daasch A, Kaiser TM. 2020. Broad-scale morpho-functional traits of the mandible
502 suggest no hard food adaptation in the hominin lineage. *Scientific Reports* 10:6793. DOI: 10.1038/s41598-020-
503 63739-5.

504 Matsumura Y, Jafarpour M, Reut M, Shams Moattar B, Darvizeh A, Gorb SN, Rajabi H. 2021. Excavation mechanics

505 of the elongated female rostrum of the acorn weevil Curculio glandium (Coleoptera; Curculionidae). *Applied*
506 *Physics A: Materials Science and Processing* 127:1–11. DOI: 10.1007/s00339-021-04353-8.

507 McCabe K, Henderson K, Pantinople J, Richards HL, Milne N. 2017. Curvature reduces bending strains in the quokka
508 femur. *PeerJ* 5:e3100. DOI: 10.7717/peerj.3100.

509 Miller CV, Pittman M, Kaye TG, Wang X, Bright JA, Zheng X. 2020. Disassociated rhamphotheca of fossil bird
510 *Confuciusornis* informs early beak reconstruction, stress regime, and developmental patterns. *Communications*
511 *Biology* 3:519. DOI: 10.1038/s42003-020-01252-1.

512 Nagel-Myers J, Mastorakos I, Yuya P, Reeder G. 2019. Modelling crushing crab predation on bivalve prey using finite
513 element analysis. *Historical Biology* 00:1–10. DOI: 10.1080/08912963.2019.1699555.

514 Neenan JM, Ruta M, Clack JA, Rayfield EJ. 2014. Feeding biomechanics in *Acanthostega* and across the fish-tetrapod
515 transition. *Proceedings of the Royal Society B: Biological Sciences* 281:20132689–20132689. DOI:
516 10.1098/rspb.2013.2689.

517 Noailly J, Planell JA, Lacroix D. 2011. On the collagen criss-cross angles in the annuli fibrosi of lumbar spine finite
518 element models. *Biomechanics and Modeling in Mechanobiology* 10:203–219. DOI: 10.1007/s10237-010-
519 0227-5.

520 Ogden RW. 1984. *Non-Linear Elastic Deformations*. Dover.

521 Pataky TC, Koseki M, Cox PG. 2016. Probabilistic biomechanical finite element simulations: whole-model classical
522 hypothesis testing based on upcrossing geometry. *PeerJ Computer Science* 2:e96. DOI: 10.7717/peerj-cs.96.

523 Patiño S, Pérez Zerpa J, Fariña RA. 2019. Finite element and morphological analysis in extant mammals' claws and
524 quaternary sloths' ungual phalanges. *Historical Biology* 2963:1–11. DOI: 10.1080/08912963.2019.1664504.

525 Pierce SE, Angielczyk KD, Rayfield EJ. 2009. Shape and mechanics in thalattosuchian (Crocodylomorpha) skulls:
526 implications for feeding behaviour and niche partitioning. *Journal of anatomy* 215:555–76. DOI:
527 10.1111/j.1469-7580.2009.01137.x.

528 Preuschoft H, Witzel U. 2002. Biomechanical investigations on the skulls of reptiles and mammals. *Senckenbergiana*
529 *Lethaea* 82:207–222. DOI: 10.1007/BF03043785.

530 Püschel TA, Marcé-Nogué J, Chamberlain AT, Yoxall A, Sellers WI. 2020a. The biomechanical importance of the
531 scaphoid-centrale fusion during simulated knuckle-walking and its implications for human locomotor evolution.
532 *Scientific Reports* 10:3526. DOI: 10.1038/s41598-020-60590-6.

533 Püschel TA, Marcé-Nogué J, Gladman J, Patel BA, Almécija S, Sellers WI. 2020b. Getting Its Feet on the Ground:
534 Elucidating Paralouatta's Semi-Terrestriality Using the Virtual Morpho-Functional Toolbox. *Frontiers in Earth*
535 *Science* 8:1–15. DOI: 10.3389/feart.2020.00079.

536 Püschel TA, Sellers WI. 2016. Standing on the shoulders of apes: Analyzing the form and function of the hominoid
537 scapula using geometric morphometrics and finite element analysis. *American Journal of Physical Anthropology*
538 159:325–341. DOI: 10.1002/ajpa.22882.

539 Rajabi H, Rezasefat M, Darvizeh A, Dirks J-H, Eshghi S, Shafiei A, Mostofi TM, Gorb SN. 2016a. A comparative
540 study of the effects of constructional elements on the mechanical behaviour of dragonfly wings. *Applied Physics*
541 *A* 122:19. DOI: 10.1007/s00339-015-9557-6.

542 Rajabi H, Shafiei A, Darvizeh A, Dirks J-H, Appel E, Gorb SN. 2016b. Effect of microstructure on the mechanical
543 and damping behaviour of dragonfly wing veins. *Royal Society Open Science* 3:160006. DOI:
544 10.1098/rsos.160006.

545 Rayfield EJ. 2007. Finite Element Analysis and Understanding the Biomechanics and Evolution of Living and Fossil
546 Organisms. *Annual Review of Earth and Planetary Sciences* 35:541–576. DOI:
547 10.1146/annurev.earth.35.031306.140104.

548 Rayfield EJ. 2019. What Does Musculoskeletal Mechanics Tell Us About Evolution of Form and Function in
549 Vertebrates? In: Springer International Publishing, 45–70. DOI: 10.1007/978-3-030-13739-7_3.

550 Richmond BG, Wright BW, Grosse I, Dechow PC, Ross CF, Spencer MA, Strait DS. 2005. Finite element analysis in

551 functional morphology. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary*
552 *Biology* 283A:259–274. DOI: 10.1002/ar.a.20169.

553 Sagl B, Schmid-Schwap M, Piehslinger E, Kundi M, Stavness I. 2019. A Dynamic Jaw Model With a Finite-Element
554 Temporomandibular Joint. *Frontiers in Physiology* 10:1–12. DOI: 10.3389/fphys.2019.01156.

555 Sellers WI, Pond SB, Brassey CA, Manning PL, Bates KT. 2017. Investigating the running abilities of Tyrannosaurus
556 rex using stress-constrained multibody dynamic analysis. *PeerJ* 5:e3420. DOI: 10.7717/peerj.3420.

557 Sellés AG, Marcé-Nogué J, Vila B, Pérez MA, Gil L, Galobart À, Fortuny J. 2019. Computational approach to
558 evaluating the strength of eggs: Implications for laying in organic egg production. *Biosystems Engineering*
559 186:146–155. DOI: 10.1016/j.biosystemseng.2019.06.017.

560 Shan G, Visentin P, Elsheikh A, Ballo A, Moritz N, Zhao J, Liao D. 2010. *Biomechanics. Principles, Trend and*
561 *Applications*.

562 Shearer T. 2015. A new strain energy function for the hyperelastic modelling of ligaments and tendons based on
563 fascicle microstructure. *Journal of Biomechanics* 48:290–297. DOI: 10.1016/j.jbiomech.2014.11.031.

564 Skamniotis CG, Elliott M, Charalambides MN. 2019. Computer simulations of food oral processing to engineer teeth
565 cleaning. *Nature Communications* 10:3571. DOI: 10.1038/s41467-019-11288-5.

566 Stansfield E, Kumar K, Mitteroecker P, Grunstra NDS. 2021. Biomechanical trade-offs in the pelvic floor constrain
567 the evolution of the human birth canal. *Proceedings of the National Academy of Sciences* 118:e2022159118.
568 DOI: 10.1073/pnas.2022159118.

569 Timoshenko S. 1955. *Strength of Materials*. Van Nostrand.

570 Timoshenko S, Goodier JN. 1986. Theory of Elasticity. *Journal of Elasticity*. DOI: 10.1007/BF00046464.

571 Tseng ZJ. 2021. Rethinking the use of finite element simulations in comparative biomechanics research. *PeerJ*
572 9:e11178. DOI: 10.7717/peerj.11178.

573 Tuset L, Fortuny G, Herrero J, Puigjaner D, López JM. 2019. Implementation of a new constitutive model for
574 abdominal muscles. *Computer Methods and Programs in Biomedicine* 179:104988. DOI:
575 10.1016/j.cmpb.2019.104988.

576 Di Vincenzo F, Profico A, Bernardini F, Cerroni V, Dreossi D, Schlager S, Zaio P, Benazzi S, Biddittu I, Rubini M,
577 Tuniz C, Manzi G. 2017. Digital reconstruction of the Ceprano calvarium (Italy), and implications for its
578 interpretation. *Scientific Reports* 7:13974. DOI: 10.1038/s41598-017-14437-2.

579 Vorp DA. 2007. Biomechanics of abdominal aortic aneurysm. *Journal of Biomechanics* 40:1887–1902. DOI:
580 10.1016/j.jbiomech.2006.09.003.

581 Williams CJ, Pani M, Bucchi A, Smith RE, Kao A, Keeble W, Ibrahim N, Martill DM. 2021. Helically arranged cross
582 struts in azhdarchid pterosaur cervical vertebrae and their biomechanical implications. *iScience* 24:102338. DOI:
583 10.1016/j.isci.2021.102338.

584 Witmer LM. 1995. The Extant Phylogenetic Bracket and the importance of reconstructing soft tissues in fossils. In:
585 Thomason J ed. *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press.,

586 Zhou Z, Fortuny J, Marcé-Nogué J, Skutschas PP. 2017. Cranial biomechanics in basal urodeles: the Siberian
587 salamander (*Salamandrella keyserlingii*) and its evolutionary and developmental implications. *Scientific Reports*
588 7:10174. DOI: 10.1038/s41598-017-10553-1.

589 Zhou Z, Winkler DE, Fortuny J, Kaiser TM, Marcé-Nogué J. 2019. Why ruminating ungulates chew sloppily:
590 Biomechanics discern a phylogenetic pattern. *PLOS ONE* 14:e0214510. DOI: 10.1371/journal.pone.0214510.

591 Zienkiewicz, Taylor. 1981. Finite Element Method - The Basis (Volume 1). *Academy of Engineering Polish Academy*
592 *of Science Chinese Academy of Sciences National Academy of Science Italy (Academia dei Lincei)*.

593

594 **Figure Captions**

595 Figure 1 - Examples of bar elements (Anderson & Westneat, 2007), shell elements (Püschel et al.,
596 2020a), plane elements (Marcé-Nogué et al., 2020) and solid finite elements (Zhou et al., 2017)

597 Figure 2 - Relationship between external forces applied in a body and displacements in a) linear
598 problem b) non-linear problem

599 Figure 3 - Constitutive equations between stress and strain for a) plastic materials using a bilinear
600 model and b) hyperelastic materials

601 Figure 4 - Deformed shape and displacement of a column under compression loads solved by a)
602 an elastic linear solution b) a linear buckling and c) deformed shape and displacement of a squared
603 plate under compression loads solved by a linear buckling.

604 Figure 5 - Different types of contact. The labelling of "bonded", "no-separation", "rough",
605 "frictionless" and "frictional" is according ANSYS 2021. Other FEA packages could use other
606 labelling

607

Figure 1

Examples

Examples of bar elements (Anderson & Westneat, 2007), shell elements (Püschel et al., 2020a), plane elements (Marcé-Nogué et al., 2020) and solid finite elements (Zhou et al., 2017)

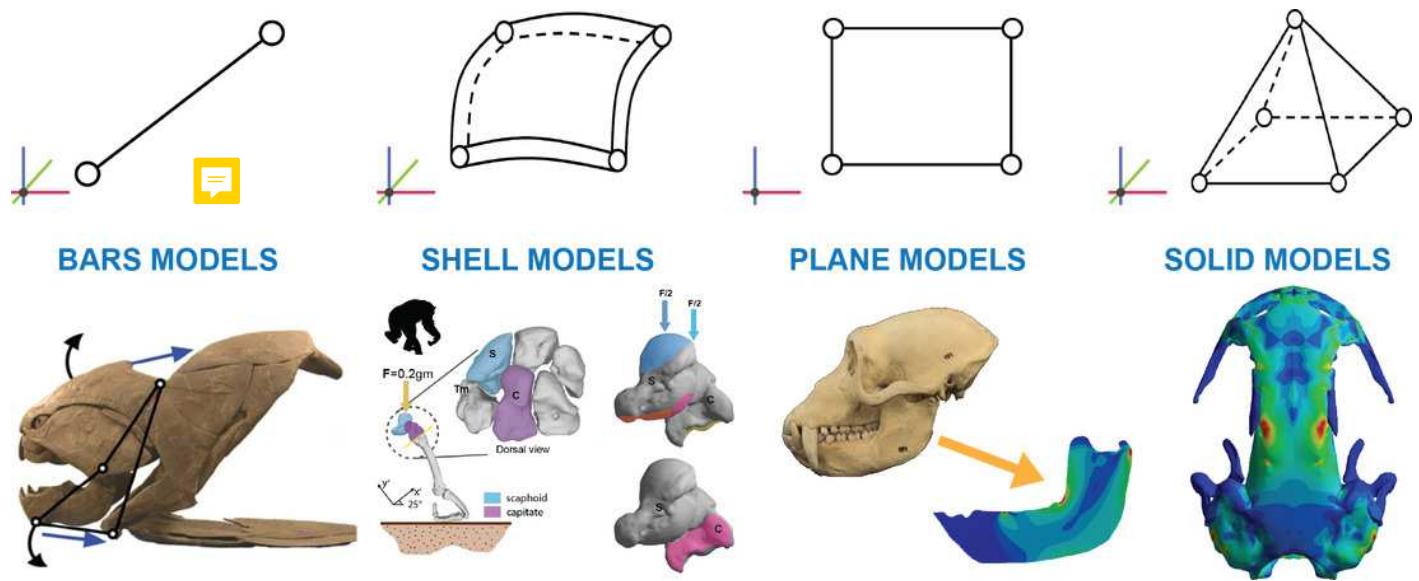


Figure 2

Convergence

Relationship between external forces applied in a body and displacements in a) linear problem b) non-linear problem



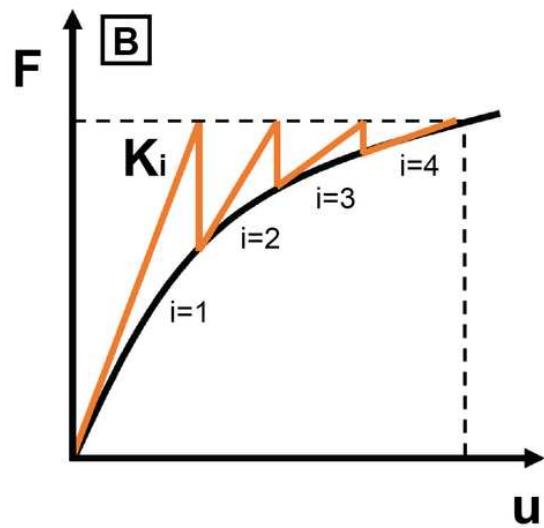
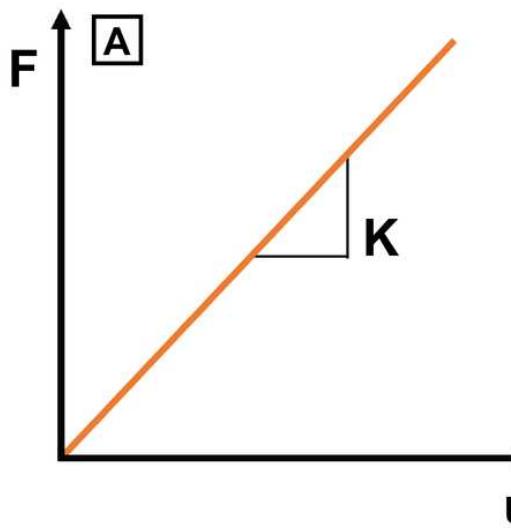


Figure 3

Materials

Constitutive equations between stress and strain for a) plastic materials using a bilinear model and b) hyperelastic materials



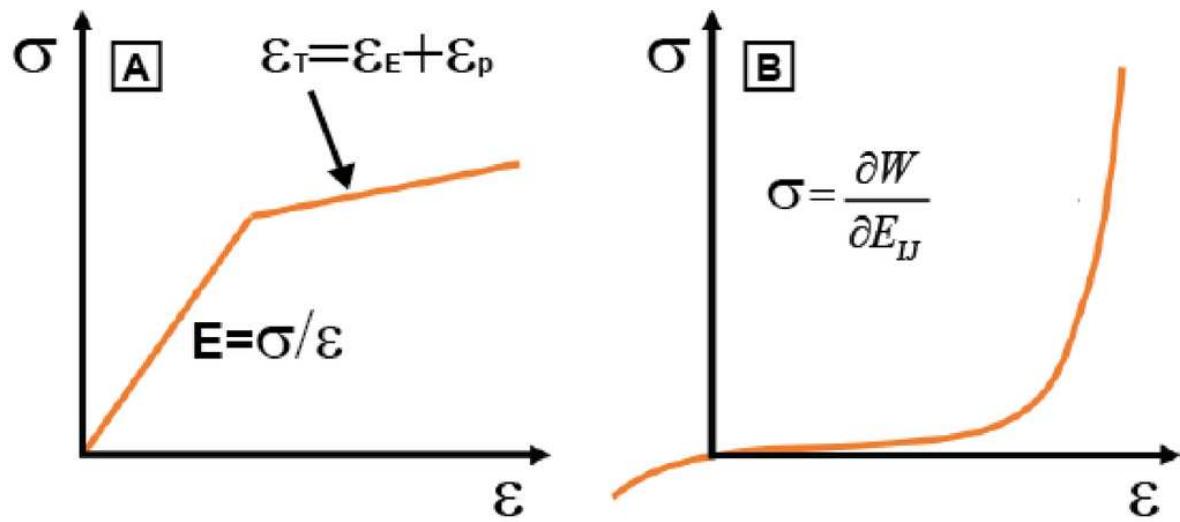


Figure 4

Buckling

Deformed shape and displacement of a column under compression loads solved by a) an elastic linear solution b) a linear buckling and c) deformed shape and displacement of a squared plate under compression loads solved by a linear buckling.



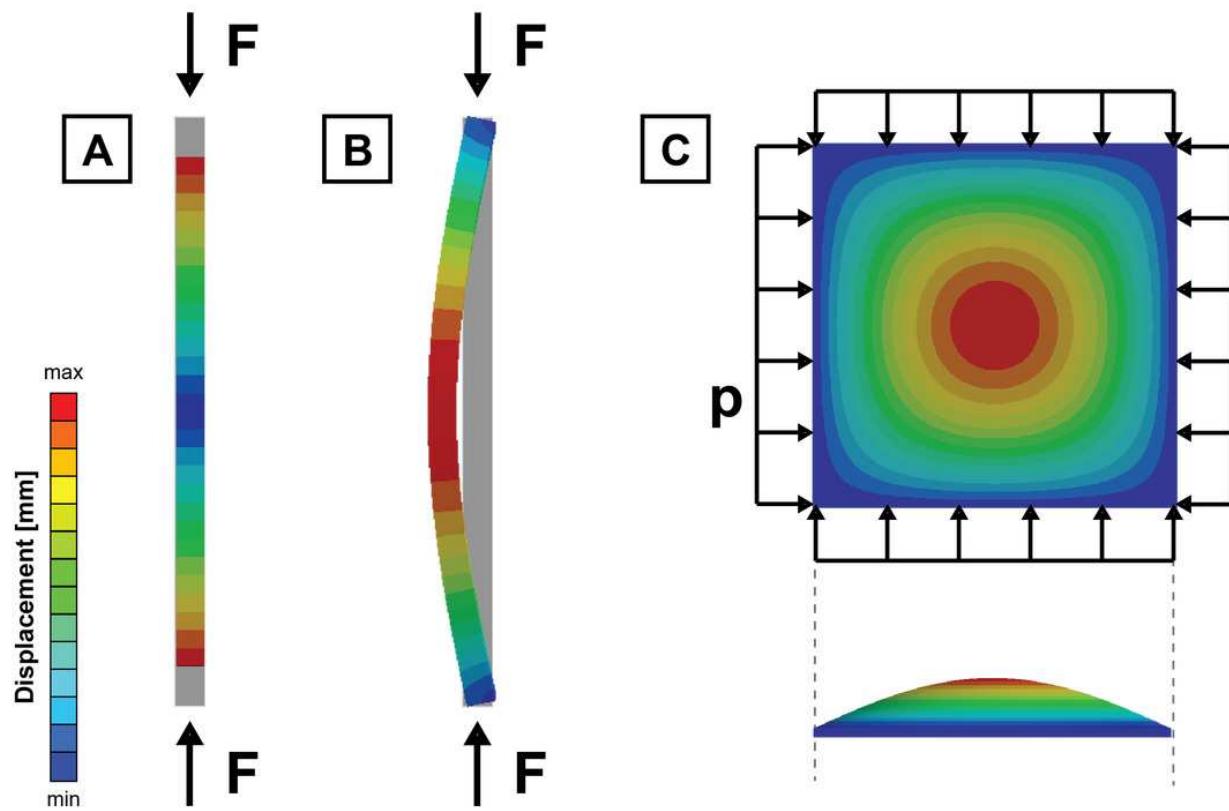
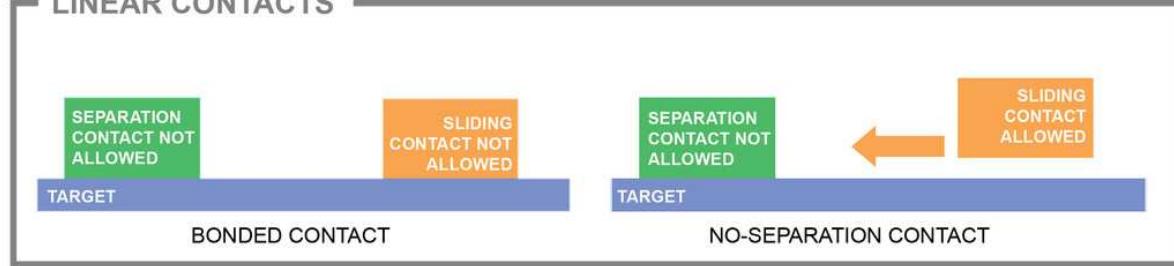


Figure 5

Contacts

Different types of contact. The labelling of "bonded", "no-separation", "rough", "frictionless" and "frictional" is according ANSYS 2021. Other FEA packages could use other labelling



LINEAR CONTACTS**NON-LINEAR CONTACTS**